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Growth of the skull of the bottlenose dolphin, *Tursiops truncatus*, in the Southwest Atlantic Ocean

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Abstract. Defining the age of attainment of physical maturity is important for many studies, including identification of stocks, populations or species. In order to identify the age when the skull of the bottlenose dolphin, *Tursiops truncatus,* reaches maturity, skulls of fifty-three specimens found stranded along the coasts of southern Brazil, Uruguay and northern Argentina (27°35'S, 48°34'W-36°49'S, 55°19'W) were analyzed. Sixty skull measurements were taken to compare the growth rate of the different functional apparatuses. Age was estimated by counts of growth layer groups in the dentine of decalcified, stained longitudinal sections of teeth. Von Bertalanffy's equation was applied to assess the growth and determine the age at maturity of each apparatus. Generally the maturation of skull starts at age two and stabilizes at age five, and the age of reaching the mature size varies amongst different characters. The braincase is the most precocious apparatus, while the feeding is the one that last stabilizes. The development patterns observed for the hearing, vision and breathing apparatuses were similar. Statistic analysis revealed significant differences among the ages at maturity, but not for von Bertalanffy's growth equation parameters for each functional apparatus. For the studied population it is suggested that skulls can be considered mature in animals with more than five years.

Resumo. A definição da idade de maturidade física é importante para diversos estudos, incluindo a identificação de estoques, populações e espécies. Para se identificar a idade de maturidade craniana do boto, *Tursiops truncatus*, foram utilizados 53 crânios de espécimes encontrados encalhados ao longo das costas do sul do Brasil, Uruguai e Argentina (27°35'S, 48°34'W-36°49'S, 55°19'W). Sessenta medidas cranianas foram analisadas para comparar o crescimento dos diferentes aparatos funcionais do crânio. Idades foram estimadas através da contagem de camadas de crescimento de dentes descalcificados, corados e cortados longitudinalmente. A equação de crescimento de Von Bertalanffy foi utilizada para estimar o crescimento e determinar a idade de maturidade de cada aparato. De um modo geral, a maturidade do crânio se inicia na idade dois e estabiliza na idade cinco, mas a idade de atingimento do tamanho maduro varia entre os diferentes caracteres. A caixa craniana é o aparato mais precoce, enquanto que o alimentar é o último a se estabilizar. Os padrões de desenvolvimento dos aparatos auditivo, visual e respiratório foram similares. Análises estatísticas indicaram diferenças significativas entre as idades de maturação, mas não para os parâmetros da equação de Von Bertalanffy de cada aparato funcional. Para a população estudada, se sugere que o crânio pode ser considerado maduro em animais com mais de cinco anos de idade.

Introduction

Many studies of morphological variation that aim to identify stocks or populations deal with skull characters (*e.g.* Ross, 1977; Gao *et al.*, 1995; Mead and Potter, 1995; Wang *et al.*, 2000; Turner and Worthy, 2003; Charlton-Robb *et al.*, 2011). Although some of these characters are expected to be age-independent (*e.g.* number of teeth), most usually change with age due to growth. Therefore studies of geographic variation of morphological characters should be performed only on physically mature specimens.

Different criteria to separate physically mature and immature specimens of delphinids have been used in the past, for example: distal fusion of premaxilla and maxilla (Dailey and Perrin, 1973), fusion of vertebral epiphyses and the distal epiphyseal fusion of radius and ulna in flipper radiographs (Mead and Potter, 1990) and fusion of cranial sutures (*e.g.* Perrin and Heyning, 1993; van Waerebeek, 1993; Chen *et al.*, 2011). Each of these methods has its advantages and may be more appropriate for specific data sets or research needs. However, defining the age of maturity can also be done by studying the growth patterns of a species, and identifying the age when growth ends. The method of using mathematical models to study growth has been extensively used in many research fields, in part due to its usefulness in generating growth metrics that can be compared between species, populations and stocks.

On the Southwest Atlantic Ocean, the bottlenose dolphin *Tursiops* spp. occurs regularly, both in coastal and offshore waters (see Lodi *et al.*, 2016 Workshop Report on Distribution, this volume). A marked geographical variation has been observed in studies dealing with bottlenose dolphins' skulls from this area, both in linear measurements and meristic characters, with two morphotypes distributed latitudinally in the area (Barreto, 2000). Even though the differences observed by that author are not restricted to the skulls' overall size, the general pattern is to find larger animals, both in total length and overall skull size, occurring in Argentina, Uruguay and southern Brazil up to approximately 27°30'S, while animals further north are markedly smaller. It has been suggested that these two forms are separate species[1,2], but there is still debate on their taxonomic status (see Ott *et al.*, 2016 Workshop Report on Taxonomy and Stock Identity, this volume). In order to use skull characters to answer these questions, it is fundamental to know the age when the animals reach maturity. Therefore, the scope of this paper is to analyze the growth of the different components of the skull of the southern morphotype bottlenose dolphins that inhabit the Southwest Atlantic Ocean, using von Bertalanffy's growth equation, and to define the age of attainment of cranial maturity for these specimens.

Material and Methods

Skulls and teeth from 53 animals from the states of Santa Catarina and Rio Grande do Sul in Brazil, Uruguay and northern Argentina were analyzed for 60 measurements. Due to some skulls being partially damaged or missing parts (*e.g.* mandibles, tympanic bulla), sample sizes for each measurement varied. Specimens were either found stranded or were incidentally caught in fisheries between 1905 and 1998, and all correspond to the southern morphotype identified by Barreto (2000). The allocation of skulls to this morphotype was done using either the discriminant equations provided by that author or the shape of the pterygoids, since the northern form exhibits both pterygoids in close contact, while in the southern form they are usually more separated (Barreto, 2000; see also the Ott *et al.*, 2016 Workshop Report on Taxonomy and Stock Identity, this volume). A list of all specimens can be found in the supplementary material (Appendix 1).

Measurements used in this study (Table 1 and Figure 1) were based on Perrin (1975) and Pinedo (1991). However, after an initial examination of the skulls it was decided to include three other measurements that could also exhibit variation during growth: distance between ethmoid and nuchal crest, distance between maxilla and supraoccipital crest and vertex height (numbers 50, 51 and 52, Table 1). All measurements were taken with calipers and read to the nearest millimeter. The measurements were grouped in five functional apparatuses, or units (*sensu* Perrin, 1975) to analyze the development of the skull. These apparatuses were: (1) braincase, (2) breathing and sounds, (3) vision, (4) hearing and (5) feeding (Table 2).

Age was estimated by counts of growth layer groups (GLGs) (Perrin and Myrick, 1980) in the dentine of decalcified and stained longitudinal sections of teeth, following the methodology described by Hohn *et al.* (1989). From the teeth available for each animal, the straightest ones were chosen, regardless of their position in the mandibles. The central part of each tooth was first cut in 3-5mm sections, using an IsoMet® low speed saw. These sections were then decalcified in RDO® from three to 24 hours, depending on teeth size and animal's age. Thin sections of decalcified teeth were cut using a freezing microtome, and stained with Mayer's hematoxylin. Age reading followed the protocol in Hohn *et al.* (1989), with two researchers reading the GLGs of each tooth independently, with an interval of at least one week between readings. When there was a difference between readings, a third reading was performed by both researchers simultaneously. The result of this reading was considered the age of the animal.

As in most mammals, growth in cetaceans is fast in the fetal and post-natal phases, and decelerates asymptotically when approaching physical maturity (Gaskin, 1982). Even though

[1]Barreto, A.S. (2004) *Tursiops* in Atlantic South America: is *Tursiops gephyreus* a valid species? Page 12 *in* Abstracts, *Cetacean Systematics: Approaches in Genetics, Morphology and Behavior*, Symposium April 30 – May 2, 2004, La Jolla, California.

[2]Wickert, J.C., Moreno, I.B., Oliveira, L.R., Ott, P.H., Danilewicz, D. and Machado, R. (2008) *Tursiops gephyreus* Lahille 1908, no Rio Grande do Sul, evidência da existência de duas espécies no Brasil. Page 211 *in* Abstracts, *12ª Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur*, 13-17 October 2008, Montevideo, Uruguay.

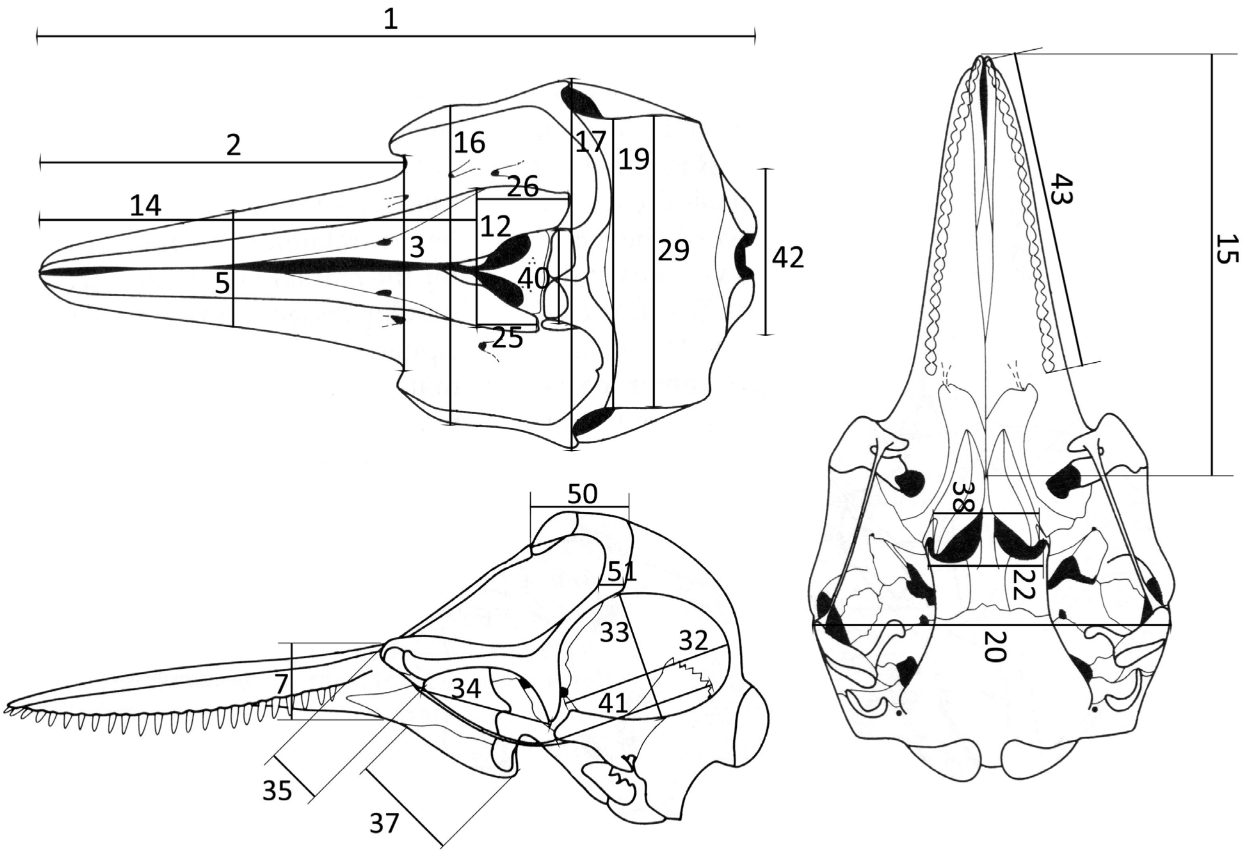

Figure 1. Diagram of an adult bottlenose dolphin *Tursiops truncatus* skull. The numbers indicate the measuring sites of each character used in the analyses, referred in Table 1. Drawings adapted from Rommel (1990).

bottlenose dolphin total body length has been mathematically described using many different models (*e.g.* Fernandez and Hohn, 1998; Mattson *et al.*, 2006; Siciliano *et al.*, 2007; McFee *et al.*, 2010), no study has used mathematical equations to model skull growth. From an initial screening of the data it was clear that different measurements exhibited different patterns of growth. However, in order to compare the growth patterns it would be necessary to select a single model to apply to all measurements. Even though there are mathematical ways to select the most appropriate growth model, such as using Schnute's generalized growth model (Schnute, 1981; Barreto and Rosas, 2006), it was decided to apply the specialized von Bertalanffy's model to describe the skull's growth. This was done because a visual inspection of the age/length plots suggested that the model could adequately represent most characters' growth patterns, due to its widespread use and also to the biological meaning of its parameters. The model can be described by

$$L_t = L_\infty(1 - e^{-k(t - t_0)})$$

where the length L at a given age, L_t, is a function of the maximum (asymptotic) measurement L_∞, the growth coefficient k, and age; e is the base of the natural logarithm. The time unit, t, is measured in years, and t_0 is a theoretical point where the measurement would have length 0.

The growth curves of each measurement were estimated using the raw values against age, in the non-linear estimation module of the *Statistica for Windows* package, version 5.1 (StatSoft Inc. 1998), using the *quasi-Newton* iterative estimation method.

As the von Bertalanffy's growth equation is asymptotic, the age where the apparatuses reached the L_∞ was not an appropriate indicator of the onset of maturation. One of the objectives of this study was to find a starting point from which growth would not interfere with other analyses, so the age of maturation (in 0.5 year intervals) of each measurement was defined as the point where after one year its variation would be less than 1% of the L_∞. The age of cranial maturity was defined considering the age where all measurements had attained maturity, as defined above. The age of maturity for a given functional apparatus was calculated as the average of the age of maturation of each character in the apparatus. The significance of the differences in the ages of maturity

Table 1. Characters used in the analyses of bottlenose dolphin *Tursiops truncatus* skull. Measurements with an '*' are not shown on Figure 2. Sexually dimorphic characters (according to Barreto, 2000) are in bold.

1. Condylo-basal length (CONBASLT);	31. Internal length of braincase (**BRCSLT**)*;
2. Rostrum length (ROSTLT);	32. Greatest length of left temporal fossa (**FOSSLT**);
3. Rostrum width at base (ROSTWDB);	33. Greatest height of left temporal fossae (FOSSHT);
4. Rostrum width at ¼ of ROSTLT (ROSTWD14)*;	34. Length of orbital (ORBITLT);
5. Rostrum width at ½ of ROSTLT (ROSTWD12);	35. Length of lacrimal (LACRILT);
6. Rostrum width at ¾ of ROSTLT (**ROSTWD34**)*;	36. Separation of pterygoid (SEPPTER)*;
7. Rostrum height at base (ROSTHTB);	37. Length of pterygoid (PTERLT);
8. Rostrum height at ¼ of ROSTLT (**ROSTHT14**)*;	38. Greatest width of pterygoid (PTERWD);
9. Rostrum height at ½ of ROSTLT (ROSTHT12)*;	39. Point to point width of pterygoid (PPPTERWD)*;
10. Rostrum height at ¾ of ROSTLT (ROSTHT34)*;	40. Greatest width of naso-frontal (NASFRWD);
11. Premaxillary width at ½ of ROSTLT (PMAXWD12)*;	41. Length of squamosal (SQULT);
12. Premaxillary width at base of nares (PMAXWDN);	42. Greatest intercondylar length (INTCONLT)*;
13. Distance between the posteriormost 2 maxillary foramina (2FORMXDT)*;	43. Length of upper left tooth row (UPTRLT);
14. Length from tip of rostrum to external nares (ROSEXNLT);	44. Length of lower left tooth row (LWTRLT)*;
15. Length from tip of rostrum to pterygoid hamulus (ROSPTRLT);	45. Length of mandibular ramus (RAMUSLT)*;
16. Greatest pre-orbital width (PREORBWD);	46. Greatest height of left mandibular ramus (RAMUSHT)*;
17. Greatest post-orbital width (**POSORBWD**);	47. Width of articular process of left mandible (ARTPROWD)*;
18. Width of maxillary at the last foramen (MAXFORWD)*;	48. Height of articular process of left mandible (ARTPROHT)*;
19. Width of parietal at the supra occipital (PARSOCWD);	49. Length of left mandibular fossa (MANFOSLT)*;
20. Width of zygomatic (**ZIGOWD**);	50. Distance between ethmoid and nuchal crest (ETMNUCDT);
21. Greatest width of dorsal nares (DORNARWD)*;	51. Distance between the posterior margin of the ascending process of the maxilla and supraoccipital crest (MAXOCCDT);
22. Greatest width of ventral nares (VENNARWD);	52. Vertex height (VRTXHT);
23. Anterior width of the left ascending process of the premaxillary, measured at the same level of PMAXNWD (**LPMXANWD**)*;	53. Greatest length of bulla of left tympanoperiotic (BULLALT)*;
24. Anterior width of the right ascending process of the premaxillary, measured at the same level of PMAXNWD (RPMXANWD)*;	54. Greatest length of periotic of left tympanoperiotic (PERIOTLT)*;
25. Left nare length (LNARLT);	55. Skull average (AVGSKULL=(BRCSHT+BRCSLT+PARWD)/3)*;
26. Right nare length (RNARLT);	56. Anterior skull asymmetry (**ANASS**= LPMXANWD / LPMXANWE); *
27. Posterior width of the left premaxillary, measured at ½ of LNARLT (LPMXPSWD)*;	57. Posterior skull asymmetry (PSASS= LPMXPSWD / LPMXPSWE); *
28. Posterior width of the right premaxillary, measured at ½ of RNARLT (RPMXPSWD)*;	58. Pre-nasal length (**PRENASLT**= ROSEXNLT - ROSTLT); *
29. Greatest width of parietal (PARWD);	59. Position of nares (POSNAR= (PRENASLT /(CONBASLT - ROSTLT)); *
30. Braincase height (BRCSHT);	60. Rostral ratio (ROSRT= ROSTLT /ROSTWDB)*.

and the von Bertalanffy's parameters among apparatuses was determined by an analysis of variance (ANOVA).

Published studies on bottlenose dolphin skulls have shown different degrees of sexual dimorphism. Hersh *et al.* (1990) observed no significant differences in skulls from the east coast of Florida. On the other hand, Turner and Worthy (2003) observed sexual dimorphism in the skull morphometry of dolphins that stranded on Gulf of Mexico's Texas coast but not in those stranding on the Florida Gulf coast. For the studied area, a previous work with the southern morphotype of *T. truncatus* observed that 10 out of 60 metric skull variables were sexually dimorphic (Barreto, 2000; Table 1). In the present study, only 29 specimens could be sexed (17 males, 12 females) and calculating separate growth curves for each sex was unfeasible. Therefore, considering the results mentioned above and the scarcity of sexed specimens, the effect of sex on the age of maturity was excluded in the analyses, although it might be an important factor influencing the growth process of bottlenose dolphins.

Table 2. Characters used for each functional apparatus. Acronyms refer to Table 1.

Braincase	Feeding	Vision	Hearing	Breathing and Sounds
PARSOCWD	ROSTLT	ORBITLT	RAMUSHT	PMAXWDN
BRCSHT	ROSTWDB	LACRILT	MANFOSLT	ROSEXNLT
BRCSLT	ROSTWD14		PTERLT	DORNARWD
PARWD	ROSTWD12		PTERWD	VENNARWD
AVGSKULL	ROSTWD34		PPPTERWD	LPMXANWD
	ROSTHTB		BULLALT	RPMXANWD
	ROSTHT14		PERIOTLT	LNARLT
	ROSTHT12			RNARLT
	ROSTHT34			LPMXPSWD
	PMAXWD12			RPMXPSWD
	PREORBWD			ANASS
	POSORBWD			PSASS
	FOSSLT			PRENASLT
	FOSSHT			POSNAR
	UPTRLT			
	LWTRLT			
	RAMUSLT			
	ARTPROWD			
	ARTPROHT			
	ZIGOWD			
	ROSRT			

Results

The sample was composed of animals with less than one year (age '0') up to 26 years (Figure 2). Growth of most measurements had a good fit with the von Bertalanffy growth equation (43 characters with $r > 0.80$, Table 3, Figure 3). Characters that were sexually dimorphic also exhibited a good fit, with an average r of 0.88. This suggests that pooling both sexes did not increase the variability in the data.

Von Bertalanffy's equation could not adequately describe growth in 10 characters, with the equation being able to explain less than 50% of variation in those measurements. Eight of those were either too variable or did not exhibit enough variation with age to allow a reliable estimation of the equation parameters (2FORMXDT, VRTXHT, NASFRWD, PERIOTLT, SEPPTER, ANASS, PSASS and ROSRT). Two others (MAXOCCDT and ETMNUCDT) decreased with age, and thus could not be described by von Bertalanffy's equation. Since the criteria described above for defining the skull maturity were based on von Bertalanffy's equation, these 10 variables were not considered when defining the age of maturity for each apparatus.

The ages at which maturity was attained varied among different characters (Table 3). Most characters reached their asymptotical size before age 5, with only one character of the feeding apparatus (ARTPROWD) still growing at age 5 and stabilizing at age 6. Maturity of the functional apparatuses was also attained at different ages, the braincase being the most precocious at three years old, and the feeding apparatus the most delayed, maturing at age 5 (Table 3). Considering the ages of maturity for each individual character and the apparatuses, the onset age of cranial maturity was therefore considered to occur at age 5.

The ages of maturity for each apparatus were significantly different (ANOVA, $F_{(4,40)}=3.566$; $p=0.014$). A pairwise comparison using Tukey's HSD test showed that this was due to the difference between the braincase and feeding apparatuses (Table 4). However, when comparing the k coefficient, the ANOVA did not reveal significant differences among apparatuses ($F_{(4,40)}=1.848$; $p=0.139$).

Table 3. Parameters of von Bertalanffy's growth equation for each character, and age of attainment of maturation (see text for details) of bottlenose dolphin *Tursiops truncatus*. Sexually dimorphic characters (according to Barreto, 2000) are in bold. '--' indicate characters that did not have an adequate fit for von Bertalanffy's growth equation and could not have these parameters calculated.

	Measurement	N	L_∞ (mm)	t0	k	r	Age of Maturation
1	CONBASLT	53	578.07	-0.64	1.14	0.96	3.5
2	ROSTLT	53	337.80	-0.50	1.15	0.96	3.5
3	ROSTWDB	52	146.73	-0.59	1.01	0.94	4.0
4	**ROSTWD14**	52	113.98	-0.61	1.03	0.94	3.5
5	ROSTWD12	47	99.49	-0.54	1.16	0.92	3.5
6	**ROSTWD34**	42	77.85	-2.24	0.55	0.80	5.0
7	ROSTHTB	52	75.43	-1.06	0.79	0.84	4.5
8	ROSTHT14	53	45.54	-1.40	0.77	0.79	4.0
9	ROSTHT12	53	38.87	-1.24	0.79	0.86	4.0
10	ROSTHT34	52	32.77	-1.30	0.69	0.88	4.5
11	PMAXWD12	52	58.17	-0.55	0.96	0.91	4.0
12	PMAXWDN	52	107.89	-0.60	1.11	0.95	3.5
13	2FORMXDT	53	22.15	-0.18	1.53	0.61	3.0
14	ROSEXNLT	53	394.70	-0.50	1.14	0.96	3.5
15	ROSPTRLT	53	372.40	-0.48	1.18	0.95	3.5
16	PREORBWD	52	253.70	-0.66	1.02	0.94	3.5
17	**POSORBWD**	52	287.29	-0.67	1.02	0.94	3.5
18	MAXFORWD	45	86.23	-0.54	1.05	0.90	3.5
19	PARSOCWD	53	216.32	-0.18	1.73	0.93	2.5
20	**ZIGOWD**	52	291.89	-0.79	0.89	0.93	4.0
21	DORNARWD	50	67.42	-1.09	1.07	0.88	3.0
22	VENNARWD	48	77.60	-0.92	0.97	0.89	3.5
23	**LPMXANWD**	52	42.97	-0.49	1.03	0.91	4.0
24	RPMXANWD	52	53.68	-0.45	1.25	0.85	3.0
25	LNARLT	50	55.33	-0.60	1.27	0.73	3.0
26	RNARLT	51	66.52	-0.35	1.92	0.74	2.0
27	LPMXPSWD	50	17.65	-0.43	1.23	0.71	3.5
28	RPMXPSWD	50	30.58	-0.74	0.95	0.82	4.0
29	PARWD	53	201.33	-0.91	1.52	0.88	2.0
30	BRCSHT	52	171.20	-0.67	1.32	0.93	3.0
31	**BRCSLT**	48	154.86	-2.89	0.56	0.76	4.0
32	**FOSSLT**	52	125.10	-0.30	1.33	0.92	3.0
33	FOSSHT	51	84.83	-0.65	0.99	0.91	4.0
34	ORBITLT	52	76.42	-0.66	1.28	0.91	3.0
35	LACRILT	50	54.23	-0.68	1.02	0.81	3.5
36	SEPPTER	48	8.30	-0.82	2.53	0.10	1.0
37	PTERLT	48	65.57	-0.52	1.37	0.77	3.0
38	PTERWD	44	64.51	-0.71	1.33	0.81	3.0
39	PPPTERWD	41	59.99	-0.54	1.55	0.82	2.5
40	NASFRWD	43	61.64	0.06	3.51	0.69	1.5
41	SQULT	51	101.89	-0.45	1.02	0.84	4.0
42	INTCONLT	50	116.88	-1.12	0.97	0.81	3.5
43	UPTRLT	46	281.63	-0.51	1.15	0.96	3.5
44	LWTRLT	42	269.08	-0.62	1.25	0.95	3.0
45	RAMUSLT	42	487.93	-0.60	1.17	0.96	2.5
46	RAMUSHT	42	106.95	-0.66	0.99	0.94	4.0
47	ARTPROWD	42	43.31	-0.78	0.58	0.93	6.0
48	ARTPROHT	42	44.67	-0.77	0.73	0.92	5.0
49	MANFOSLT	41	167.13	-0.73	0.93	0.94	4.0
50	ETMNUCDT	48	40.00	-6.55	4.47	--	--
51	MAXOCCDT	46	14.22	-4.97	9.04	--	--
52	VRTXHT	37	32.14	0.44	33.79	0.19	1.0
53	BULLALT	28	42.90	-3.24	0.64	0.80	3.0
54	PERIOTLT	27	55.80	-133.02	0.01	0.68	--
55	AVGSKULL	48	175.70	-1.49	0.98	0.82	3.0
56	**ANASS**	52	1.29	-6.52	4.69	--	--
57	PSASS	49	1.76	-6.77	4.48	--	--
58	**PRENASLT**	53	56.87	-0.46	1.06	0.88	3.5
59	POSNAR	53	0.24	-0.90	1.13	0.77	3.0
60	ROSRT	52	2.34	-6.93	4.18	--	--

Table 4. Tukey HSD test for pairwise comparison between the apparatuses age of maturity and *k*. Above the diagonal are *p* values for comparisons between von Bertalanffy's *k*, below diagonal are *p* values for comparisons between ages of maturity. Significant values are in bold. First line: mean values of von Bertalanffy's *k* for each apparatus; first column: mean age of maturity for each apparatus.

	Mean k	0.95	1.23	1.18	1.13	1.15
Mean Age of Maturity		**Feeding**	**Braincase**	**Breathing and Sounds**	**Hearing**	**Vision**
3.94	**Feeding**	-----	0.3020	0.1957	0.6232	0.8748
2.90	**Braincase**	**0.0318**	-----	0.9975	0.9832	0.9974
3.29	**Breathing and Sounds**	0.0895	0.8181	-----	0.9982	0.9999
3.25	**Hearing**	0.2117	0.9149	0.9999	-----	0.9999
3.25	**Vision**	0.6545	0.9725	0.9999	1.0000	-----

Discussion

The growth pattern of the bottlenose dolphin skull is similar to the growth of its body length. Studies of the age-length relationship on this species in different areas of the western North Atlantic and Gulf of Mexico (Hohn, 1980; Cockcroft and Ross, 1990*a*; Mead and Potter, 1990; Fernandez and Hohn, 1998; Mattson *et al.*, 2006, McFee *et al.*, 2010) found a remarkable reduction in the growth rates after the fourth year of life. In the present work almost all measurements were still growing in the first two years of life; 91% have stopped at age 4 and only one (ARTPROWD) continued growing after age 5. Only two characters (MAXOCCDT and ETMNUCDT) exhibited an inverse behavior, decreasing with age. MAXXOCCDT is a measurement of the frontal bone taken between the posterior margin of the ascending process of the maxilla and the supraoccipital crest, and therefore reduces with age, with the growth of the maxilla. ETMNUCDT roughly measures the length of the cranial vertex (*sensu* Mead and Fordyce, 2009), but since its reference point is the nuchal crest, with growth of the latter, the measurement tends to reduce with age.

The apparatus related to the central nervous system (braincase) developed earlier than other apparatuses, which should be expected since it is essential to the maintenance of physiological conditions and survival (Oelschläger and Oelschläger, 2008). Along with primates, bottlenose dolphin exhibits one of the highest encephalization quotients of all mammals (Worthy and Hickie, 1986; Changizi, 2003; Marino, 2004). It is born with a brain in an advanced stage of development, weighting an average of 42.5% of the mean adult brain weight (Ridgway, 1990). At 18 months old, bottlenose dolphin brain is over 80% of mean adult weight; however, full brain development is only attained in nine or 10 years (Ridgway, 1990). Even so, the bones composing the braincase mature quickly, before the complete development of the brain.

The hearing apparatus is expected to develop earlier than other apparatuses, since odontocetes probably are highly dependent on sounds for communication and acquiring information of their surroundings ('echolocation'; Au, 2008). Indeed, it is one of the most precocious apparatuses to develop and reach maturity in pantropical spotted dolphin *Stenella attenuata*, spinner dolphin *S. longirostris* (Perrin, 1975) and franciscana dolphin *Pontoporia blainvillei* (Pinedo, 1991); however, that was not the case here. The distinct development pattern of the hearing apparatus observed here and in previous works might be a result of different measurements being included in it. Since this work followed Perrin (1975) who considered 'the portion of the underside of the skull posterior to the base of the rostrum and lateral to the bony nares and basicranial trough, excluding the zygomatic arch, the glenoid fossa of the squamosal, and the orbital processes, to be functional in hearing' (Perrin, 1975, p. 52) these areas, together with the mandibular fossa, were considered part of the hearing apparatus. Therefore, many measurements used to represent the hearing apparatus were also related either to the mandibular ramus (RAMUSHT and MANFOSLT) or

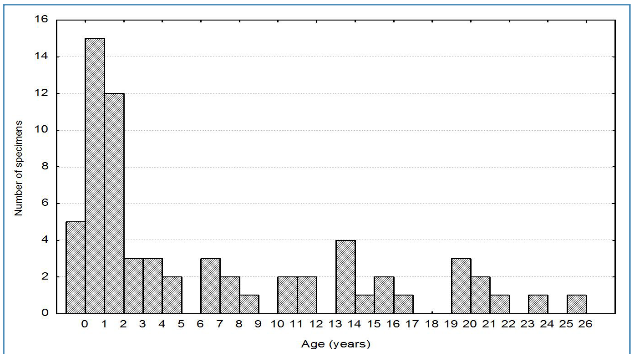

Figure 2. Age distribution of the bottlenose dolphin *Tursiops truncatus* specimens used for the determination of growth curves.

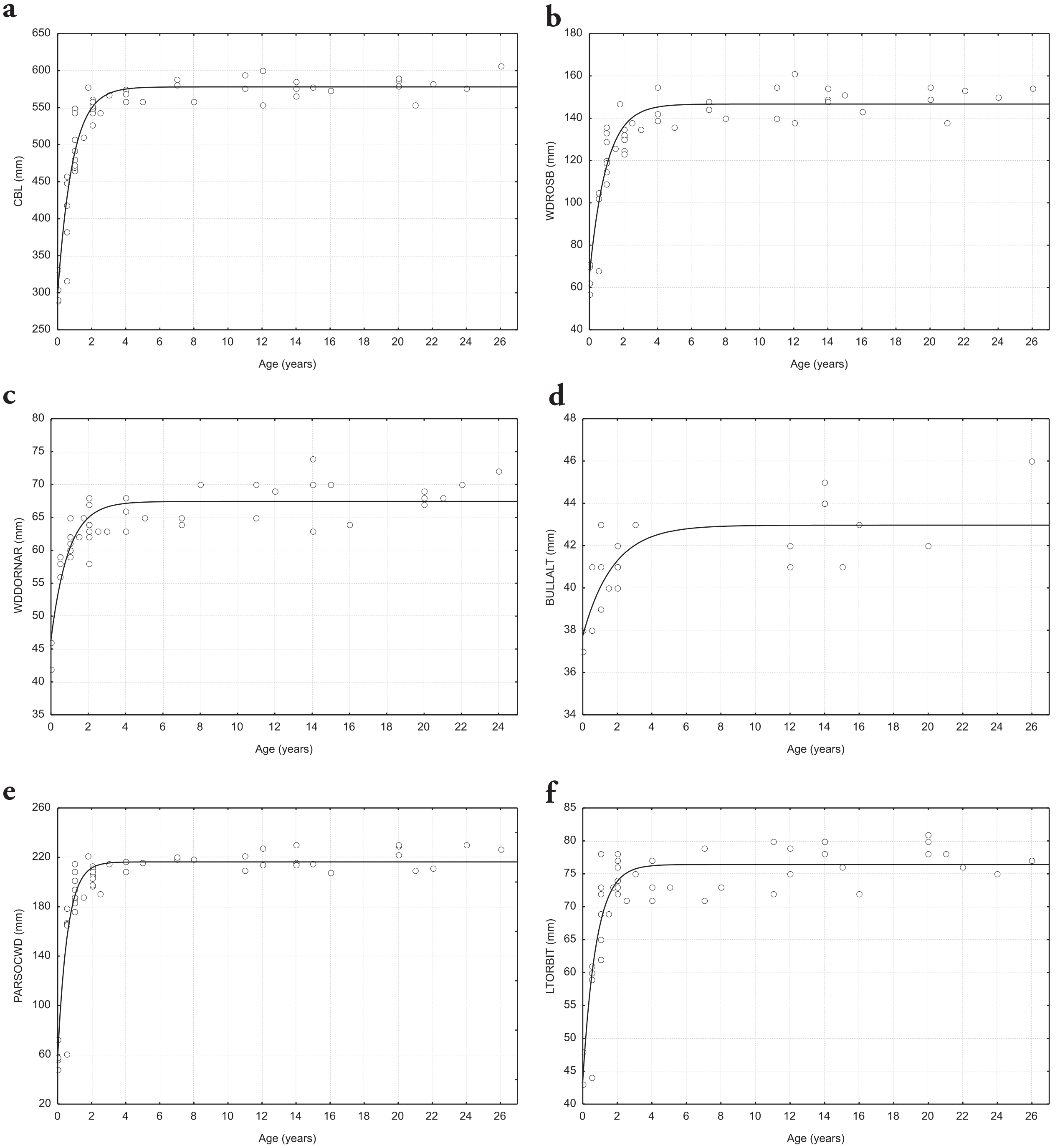

Figure 3. Growth of selected measurements of bottlenose dolphin *Tursiops truncatus* skull, exemplifying the trajectories of the different functional apparatuses: (a) condylo-basal length; (b) width of rostrum at base (feeding); (c) greatest width of dorsal nares (breathing and sound); (d) greatest length of bulla (hearing); (e) width of parietal at the supraoccipital (braincase) and (f) length of orbital (vision).

to the pterygoids (PTERLT, PTERWD and PPPTERWD), and their growth patterns were probably intermediate between the feeding and hearing apparatuses. The smallest values found for the lengths of the bulla (BULLALT) and tympanoperiotic (PERIOTLT), from animals less than one year of age, were respectively 83.9% and 84.6% of their asymptotic lengths, similar to what was observed for *S. attenuata*, *S. longirostris* and *P. blainvillei*. Thus, the inclusion of the same set of measurements used by Perrin (1975) and Pinedo (1991) for the hearing apparatus might not be adequate, since it exhibited a slower growth than was expected by the observed length increase of the bulla and tympanoperiotic bones.

In pantropical spotted dolphins the hearing apparatus is the first apparatus to reach maturity, together with some components of the breathing and sound production apparatuses, followed by vision, braincase, other elements of breathing and sounds and the feeding apparatus, in this order (Perrin, 1975). In spinner dolphins the development of the skull is more precocious than in pantropical spotted dolphins but follows the same pattern (Perrin, 1975). In Guiana dolphins *Sotalia fluviatilis* (= *guianensis*), Borobia (1989) and Schmiegelow (1990) also found that the feeding apparatus is the last apparatus to reach maturity. In franciscana dolphins the hearing apparatus is the first to develop, followed by breathing and sounds, vision, braincase and feeding, in this order (Pinedo, 1991).

However, the present study defined cranial maturity differently (change in character length in one year being less than 1% of the asymptotic size), in contrast to the criteria used by Perrin (1975), Borobia (1989), Schmiegelow (1990) and Pinedo (1991) (visual analysis of the growth curves). Other than the variation among species, a different methodology might be partially responsible for the differences observed in cranial growth patterns. Furthermore, allocation of some measurements in each apparatus was different among these studies, and since none of the previous studies used the von Bertalanffy growth equation to define age at maturity, differences between studies are expected.

This study used animals stranded or incidentally caught along a relatively large area, from southern Brazil to northern Argentina, encompassing approximately 1300km. Even though all specimens were classified as belonging to a single population unit (the 'southern' morphotype - Barreto 2000; see also Ott *et al.*, 2016 Workshop Report on Taxonomy and Stock Identity, this volume) the possibility of having individuals from coastal and offshore bottlenose dolphins populations mixed on the analyzed sample should not be discarded, as there are several coastal resident populations along the sampled area and sightings of bottlenose dolphins further offshore (Zerbini *et al.*, 2004; see Lodi *et al.*, 2016 Workshop Report on Distribution, this volume). It has been shown that growth patterns can be different between populations/stocks of cetaceans (*e.g.* Barreto and Rosas, 2006) and therefore a reanalysis of the growth patterns of bottlenose dolphins in Southwest Atlantic Ocean in the future would enhance our understanding of such variations, if skulls from each population can be identified.

Nonetheless, even if future studies separate the sample used here, probably the general pattern observed will hold, since previous and current studies all indicate a late development of the feeding apparatus as a general growth pattern for odontocetes. This very likely reflects a higher energy investment in other apparatuses with a postponement of the maturation of the feeding apparatus. In bottlenose dolphin this could be possibly explained by the relatively long period of lactation, of approximately two years (Cockcroft and Ross, 1990*b*; Mead and Potter, 1990), and to the utilization of a wide range of prey sizes (Pinedo, 1982; Cockcroft and Ross, 1990*c*; Barros and Odell, 1990). By having at its disposal a food source (milk) which does not require the full development of the feeding apparatus, and by feeding on prey of smaller size while the feeding apparatus is underdeveloped, the animal would be able to invest more energy on other functional units of relatively greater importance for its survival.

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Appendix 1. List of specimens used in the present study. Collection acronyms: 'UFSC' – Laboratório de Mamíferos Aquáticos (LaMAq), Universidade Federal de Santa Catarina, Brazil; 'LMM' – Laboratório de Mamíferos Aquáticos, Universidade Federal de Rio Grande (FURG), Brazil; 'MDLP' – Museu de La Plata, Argentina; 'FCM' – Facultad de Ciências de Montevideo, Uruguay. 'Lat' and 'Lon' are the approximate latitude and longitude where the specimens were collected.

Collection	Catalog number	Lat	Lon	Age	Sex
FCM	1332	36°49'01"S	55°19'01"W	22.0	F
LMM	#E	-	-	0.0	-
LMM	GEPH	-	-	20.0	-
LMM	#B	-	-	7.0	-
LMM	57	32°15'29"S	52°13'59"W	2.0	-
LMM	60	32°07'44"S	52°05'17"W	1.0	-
LMM	61	32°07'44"S	52°05'17"W	1.0	F
LMM	70	32°11'31"S	52°10'59"W	14.0	F
LMM	73	32°02'31"S	52°04'01"W	3.0	F
LMM	78	31°29'46"S	51°25'30"W	21.0	-
LMM	81	31°58'44"S	51°54'47"W	0.5	-
LMM	82	31°58'44"S	51°54'47"W	2.0	-
LMM	94	32°09'29"S	52°04'59"W	20.0	F
LMM	95	32°00'29"S	51°56'31"W	2.0	M
LMM	114	32°08'31"S	52°04'44"W	0.0	M
LMM	115	32°02'46"S	51°58'59"W	0.0	M
LMM	454	32°11'31"S	52°10'59"W	16.0	M
LMM	459	32°02'46"S	51°58'59"W	0.5	M
LMM	466	32°04'01"S	52°00'14"W	4.0	F
LMM	525	31°55'44"S	51°50'17"W	1.0	-
LMM	538	32°03'47"S	52°04'30"W	12.0	F
LMM	677	32°07'01"S	52°03'29"W	4.0	M
LMM	680	32°06'29"S	52°02'60"W	1.0	-
LMM	690	31°55'59"S	51°51'00"W	8.0	-
LMM	802	32°09'29"S	52°04'59"W	4.0	M
LMM	820	32°09'29"S	52°04'59"W	0.0	-
LMM	877	32°07'16"S	51°54'47"W	20.0	F
LMM	910	32°35'17"S	52°24'14"W	15.0	-
LMM	923	32°03'29"S	51°59'46"W	1.0	-
LMM	1044	31°58'44"S	51°55'01"W	2.0	M
LMM	1045	31°59'17"S	51°55'30"W	1.0	M
LMM	1056	30°25'16"S	50°17'46"W	24.0	-
LMM	1100	33°39'14"S	53°15'29"W	14.0	-
LMM	1188	32°03'29"S	51°59'46"W	11.0	M

Appendix 1 (cont.)

Collection	Catalog number	Lat	Lon	Age	Sex
LMM	1310	31°55’44”S	51°51’29”W	26.0	M
LMM	1337	32°02’46”S	51°58’01”W	2.0	F
LMM	1405	30°40’16”S	50°25’59”W	2.0	M
LMM	1420	30°45’00”S	50°30’47”W	12.0	M
LMM	1439	30°37’44”S	50°25’30”W	2.0	-
LMM	1584	32°12’14”S	52°10’01”W	2.0	-
LMM	1604	32°32’60”S	52°23’31”W	1.5	-
LMM	1846	32°36’29”S	52°25’1”W	2.0	-
LMM	2047	32°08’24”S	52°04’37”W	2.5	-
MDLP	1505	-	-	14.0	-
UFSC	1044	27°34’59”S	48°34’01”W	1.0	F
UFSC	1077	27°34’59”S	48°34’01”W	7.0	M
UFSC	1081	27°34’59”S	48°34’01”W	1.8	F
UFSC	1089	28°28’59”S	48°46’59”W	11.0	F
UFSC	1105	27°34’59”S	48°34’01”W	0.5	M
UFSC	1106	27°34’59”S	48°34’01”W	1.0	-
UFSC	1110	27°34’59”S	48°34’01”W	0.5	M
UFSC	1116	27°34’59”S	48°34’01”W	5.0	-
UFSC	1123	27°38’38”S	48°38’59”W	0.5	M