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Morphology of the Guiana dolphin (*Sotalia guianensis*) off southeastern Brazil: growth and geographic variation

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Abstract: The objective of this study was to analyze the morphology of Guiana dolphin (*Sotalia guianensis*) to evaluate the existence of geographical variation along southeastern Brazil. Body length and 39 cranial variables were measured of specimens stranded or accidentally captured to consider ontogenetic and geographic variations. The areas studied were Espírito Santo (ES; 18º30'S-20º40'S), northern Rio de Janeiro (NRJ; 21º35'S-22º25'S), southern Rio de Janeiro (SRJ; 23º00'S-23º07'S) and São Paulo (SP; 23º30'S-25º30'S). Body length at age zero predicted by a non-linear Gompertz model for the Guiana dolphin was 148.3cm for area ES, 108.97cm for area NRJ, 98.4cm for area SRJ and 90.9cm for area SP. Asymptotic values were reached at about six years of age for total body length and cranial variations. These results indicate that Guiana dolphins reach adult size and sexual maturity simultaneously at six to seven years of age, when specimens cease to grow. The growth pattern for body and skull size indicated that there is variation between geographic areas. Guiana dolphins found in São Paulo are smaller than those analyzed in northern Rio de Janeiro and Espírito Santo, which implies a different growth rate. A canonical discriminant analysis of the cranial metric characters indicated significant differences between the four geographic areas. Differences between areas NRJ, SRJ and SP were responsible for 54% (axis 1) and 34% (axis 2) of the variation, respectively. The third axis depicted a difference between the area ES and the others. A partial overlap between geographic areas was observed in the projection of the species on the canonical axes, suggesting parapatry. Geographic variation recorded in this study is likely to be related to environmental adaptations. One of the areas that could play a role in the distribution of Guiana dolphin in the surveyed area is the central coast of Rio de Janeiro, which is characterized by the absence of river discharges, a narrowing of the continental shelf and upwelling influence that might be limiting the species occurrence in this area.

Resumo: O objetivo do presente estudo foi analisar a morfologia do boto-cinza (*Sotalia guianensis*) para avaliar a existência de variação geográfica no sudeste do Brasil. O comprimento do corpo e 39 variáveis cranianas foram medidas em animais encalhados ou capturados acidentalmente em rede de pesca para analisar a variação ontogênica e geográfica. As áreas estudadas foram Espírito Santo (ES) (18º30'S-20º40'S), norte do Rio de Janeiro (NRJ) (21º35'S-22º25'S), sul do Rio de Janeiro (SRJ) (23º00'S-23º07'S) e São Paulo (SP) (23º30'S-25º30'S). O comprimento do corpo na idade zero, predito pela curva de crescimento de Gompertz para o boto-cinza foi 148,3cm para a área ES, 108,97cm para a área NRJ, 98,4cm para a área SRJ e 90,9cm para a área SP. Os valores assintóticos foram alcançados aproximadamente aos seis anos de idade para o comprimento do corpo e variáveis cranianas. Esses resultados indicam que o boto-cinza alcança o tamanho adulto e a maturidade sexual simultaneamente aos seis a sete anos de idade, quando os espécimes param de crescer. Os padrões de crescimento para o tamanho corpóreo e craniano indicaram que há uma variação entre áreas geográficas. Os espécimes de botos-cinza encontrados em São Paulo são menores do que aqueles analisados no norte do Rio de Janeiro e Espírito Santo, o que implica em uma taxa de crescimento diferenciada. A análise discriminante canônica para os caracteres métricos do crânio indicou diferença significativa entre as quatro áreas geográficas. Diferenças entre as áreas NRJ, SRJ e SP foram responsáveis por 54% (eixo 1) e 34% (eixo 2) da variação. A diferença entre a área ES das demais áreas foi responsável pelos 12% restantes (eixo 3). Uma sobreposição parcial entre as áreas geográficas foi observada na projeção das espécies nos eixos canônicos, sugerindo parapatria.. A variação geográfica registrada neste estudo pode ser um reflexo de adaptações ambientais. Uma área que pode ser considerada crítica para a distribuição do boto-cinza é a costa central do Rio de Janeiro, a qual é caracterizada pela ausência de rios, plataforma continental estreita e influência de ressurgência. Estas características ambientais podem ser limitantes para a ocorrência da espécie nesta área.

Keywords: *Sotalia guianensis*, geographic variation, distribution, southeastern Brazil.

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Introduction

The Guiana dolphin (*Sotalia guianensis*) (Cetacea: Delphinidae) occurs along the Atlantic coast of South America as well as in the Caribbean, as far north as Honduras (~15˚N), and as far south as the State of Santa Catarina (~27˚S), southern Brazil (Simões-Lopes, 1988; da Silva and Best, 1996; da Silva *et al.*, 2010 this volume).

Knowledge on reproduction and growth of the species in Brazil comes from specimens stranded and accidentally captured in fishing nets (*e.g.* Schmielelow, 1990; Ramos *et al.*, 2000a; Rosas, 2000; Rosas *et al.*, 2003; Santos *et al.*, 2003). However this information is not available throughout most of the species' range.

Growth and reproduction parameters have been analyzed for specimens stranded or accidentally captured in northern Rio de Janeiro (~21˚20'-22˚20'S) (Ramos *et al.*, 2000a) and for specimens stranded along northern São Paulo and southern Paraná (~25˚00'-26˚00'S) (Rosas, 2000; Rosas *et al.*, 2003; Santos *et al.*, 2003). The estimated size and age at attainment of sexual maturity were similar between these regions. On the other hand, asymptotic lengths of the specimens from São Paulo and Paraná were lower than those from Rio de Janeiro.

Cranial measurements of Guiana dolphin were analyzed by Schmiegelow (1990) for specimens from São Paulo (Ilha Comprida and Praia do Marujá) (~25˚00'-25˚30'S). Later on, Alves Jr. (1997) compared the cranial variable measurements for specimens from Ceará (~03˚01'-04˚50'S) with Schmiegelow's study and found that 67.5% of them were significantly different. The values from Ceará were larger than those from São Paulo; however, no geographic variation was determined for the species.

Based on these studies, Guiana dolphins found in São Paulo are smaller than those analyzed in northern Rio de Janeiro, which implies a different growth rate. So far, specimens from southern Rio de Janeiro and northern Espírito Santo, southeastern Brazil, have not been analyzed. It is unclear whether the growth rate in these regions is similar or not to the nearby area. Also, is the difference found between the northern Rio de Janeiro and São Paulo indicative of regional adaptations?

The objective of this study is to analyze the Guiana dolphin morphology to evaluate the existence of geographical variation along the southeastern Brazilian coast. Body length and cranial variables are analyzed to consider ontogenetic and geographic variation.

Material and Methods

Study area and sampling

The sampling areas were defined according to the known occurrence of Guiana dolphin off southeastern Brazil (Figure 1). Four areas were defined: AREA ES - Espírito Santo, from Itaúnas to Guarapari (18º30'S-20º40'S); AREA NRJ - northern Rio de Janeiro, from Atafona to Macaé (21º35'S-22º25'S); AREA SRJ - southern Rio de Janeiro, from Cabo Frio to Ilha Grande Bay (23º00'S-23º07'S) and AREA SP - São Paulo, from Ubatuba to Cananéia, including the Paranaguá Bay, in the extreme northern Paraná (23º30'S-25º30'S). The studied specimens were accidentally caught in gillnet fisheries or found stranded along the beach. A total of 311 Guiana dolphins were examined from different areas: 31 from ES, 125 from NRJ, 60 from SRJ and 95 from SP.

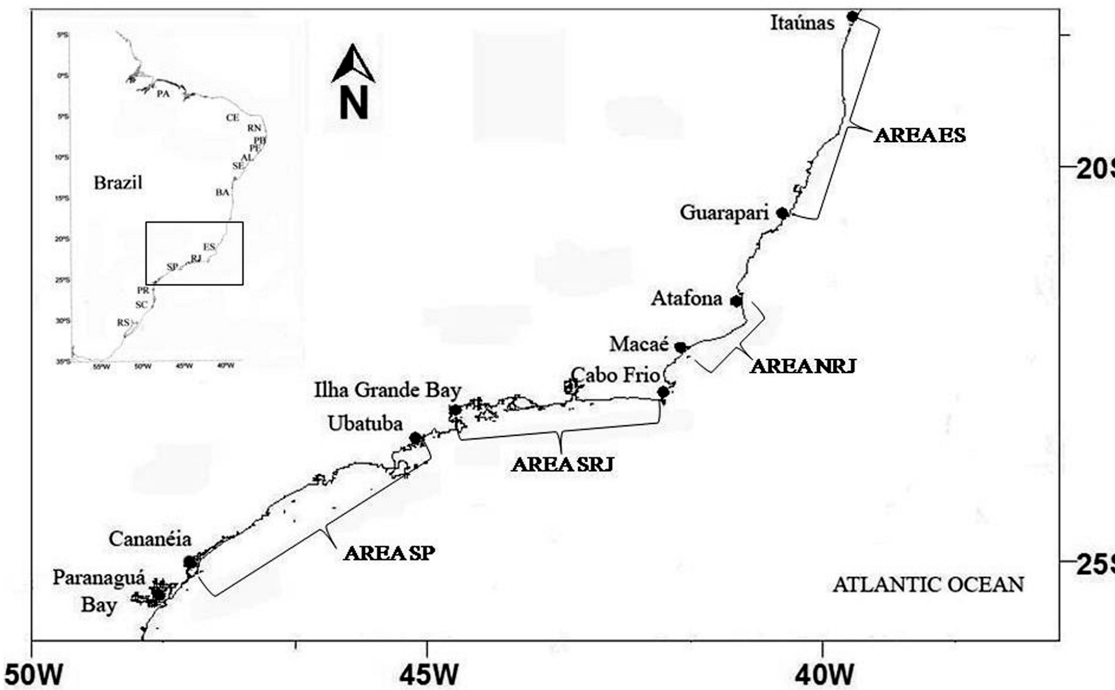

Figure 1. Study area, including sampling locations (northern-southern boundary of each area set in the filled circle).

Analyzes of cranial morphometrics performed by Borobia (1989) and of body length conducted by Ramos *et al.* (2000a), Rosas (2000) and Rosas *et al.* (2003) have indicated a lack of sexual dimorphism, so the analysis of growth and geographic variation were performed without consideration of sex.

Age estimation and morphometric characters

Age was estimated by one of the authors (RMAR) in 286 specimens by counting the number of growth layer groups (GLGs) in the dentine. We adopted the GLG pattern described by Ramos *et al*. (2000b): one complete dentinal GLG was composed of one narrow unstained layer and a broad stained layer. A fine darkly stained layer demarcated the boundary with unstained layer of the subsequent GLG. The method of preparation of decalcified thin and stained sections of the teeth for examination under an optical microscope was used following the recommendations of Perrin and Myrick (1980) and Hohn *et al*. (1989).

The body length (BL) of 202 specimens was measured along the longitudinal axis of the body, from the tip of the upper jaw to the notch of the flukes (Norris, 1961). A total of 311 skulls were examined by one of the authors (RMAR) for cranial metric characters following Perrin (1975) and Schnell *et al*. (1985).

Thirty-five cranial metric characters were measured: condylobasal length (CBL); length of rostrum (LR); width of rostrum at base (WRB); width of rostrum at 1/4 (WR1/4); width of rostrum at 60mm (WR60); width of rostrum at midlength (WR1/2); width of premaxillaries at midlength of rostrum (WPMx1/2); width of rostrum at 3/4 length (WR3/4); width of left premaxillary (midline nares); (WLPMx); width of right premaxillary (midline nares); (WRPMx); distance from tip of rostrum to external nares (DREN); greatest preorbital width (GPreOW); greatest postorbital width (GPostOW); greatest width of external nares (GWEN); greatest width at zygomatic process of squamosal (GWZS); greatest width of premaxillaries (GWPMx); greatest parietal width (GPW); vertical external height of braincase (VEHB); internal length of braincase (ILB); greatest length of left posttemporal fossa (GLLPTF); greatest width of left posttemporal fossa (GWLPTF); major diameter of left temporal fossa proper (MaDLTF); minor diameter of left temporal fossa proper (MiDLTF); distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest (DSOC); length of left orbit (LLO); length of antorbital process of left lacrimal (LALL); greatest width of internal nares (GWIN); greatest length of left pterygoid (GLLP); length of left tympanic cavity (LLTC); length of right tympanic cavity (LRTC); width of pterygobasioccipital sutures (WPS); length of upper left tooth row (LULTR); length of lower left tooth row (LLLTR); greatest length of left ramus (GLLR); greatest height of left ramus at right angles to greatest length (GHLR); length of left mandibular fossa (LLMF); greatest height of foramen magnum (GHFM); greatest width of foramen magnum GWFM); and distance from tip of rostrum to internal nares (DRIN).

The specimens were classified as immature or mature according to the relationship between age and body length, considering as mature males at seven years old with a body length greater than or equal to 170.0cm, and females at six years old with body length greater than or equal to 164.0cm (Ramos *et al*., 2000a; Rosas, 2000; Rosas, 2003).

Growth

Growth was determined by fitting a non-linear Gompertz model,

$$Y = ae[-e\ (b-cx)],$$

where Y is a metric character, a is the asymptotic length, b is the correction factor, c is the growth rate constant and x is the age (Zullinger *et al*., 1984), using Curve Expert 1.3 for Windows. Mean values of body length and cranial metric characters were plotted against age by geographic area.

Geographic variation

Geographic variation in cranial morphology was examined for adult specimens only. Missing values in the data matrix were estimated with a non-linear Gompertz model or as the mean value by age class to variables not fitted by the non-linear model.

An ANOVA was carried out to test the interaction of geographic area for each metric character using the package Statistic 5.5 for Windows. The Bonferroni correction was applied and only $P < 0.001$ was considered significant. A canonical discriminant analysis was applied to identify the subset of variables that, taken in linear combination, showed the greatest degree of geographic variation (Afifi and Clark, 1990). The method was also applied with package Statistic 5.5 for Windows.

Results

In area ES, body length varied between 175.0 and 222.0cm for seven males and between 166.0 and 184.5cm for five females measured. For mature specimens the body length ranged between 167.0 and 222.0mm (n = 8; mean = 189.9mm; SD = 16.24mm and CV = 8.55). In area NRJ, the 64 males had body lengths ranging from 86.0 to 200.0cm and from 117.5 to 198.0cm for the 45 females. For mature specimens body length ranged between 161.0 and 200.0mm (n = 43; mean = 184.7mm; SD = 8.95mm and CV = 4.84). In area SRJ, length variation for 17 males and 17 females was from 92.5 to 210.0cm and from 84.0 to 198.0cm, respectively. For mature specimens body length ranged between 173.0 and 210.0mm (n = 24; mean = 185.8mm; SD = 8.97mm and CV = 4.83). Of the total of 22 males and 25 females in area SP, the smallest male and female were 120.0cm and 140.0cm long, respectively, and the largest male and female was 200.0cm long. For mature specimens body length ranged between 156.0 and 200.0mm (n = 41; mean = 180.2mm; SD = 10.89mm and CV = 6.05).

Growth

The mean, standard deviation (SD) and coefficient of variation (CV) were obtained for all metric variables. In area ES, the condylobasal length (CBL) ranged between 355.0 and 390.0mm (n = 10; mean = 373.3mm; SD = 10.83mm and CV = 2.90). In the area NRJ, the condylobasal length (CBL) ranged between 355.0 and 410.0mm (n = 41; mean = 384.8mm; SD = 11.62mm and CV = 3.02). In the area SRJ, the condylobasal length (CBL) ranged between 352.0 and 395.0mm (n = 30; mean = 379.0mm; SD = 13.08mm and CV = 3.45). And in the area SP, the condylobasal length (CBL) ranged between 348.0 and 396.0mm (n = 57; mean = 370.6mm; SD = 10.82mm and CV = 2.92).

Except for the distance of nasals to supraoccipital crest (DSOC), the coefficient of variation was below 20% in all the variables analyzed for the mature specimens from the four geographical areas. Thus, the average values of the cranial variables and the total body length were considered representative of the growth pattern analysis. The growth parameters are presented in Tables 1, 2, 3 and 4.

Table 1. Growth parameters obtained by the Gompertz model fitted to metric variables-at-age in Guiana dolphins (*Sotalia guianensis*) from Espírito Santo.

Variable*	Asymptotic value	Correction factor	Growth rate constant	Correlation coeficient (*r*)
BL	199.230 b	-1.220	0.228	0.46
CBL	374.730 a	-1.136	0.568	0.46
LR	224.640 a	-0.212	0.554	0.55
WRB	-	-	-	-
WR60	61.909 a	-1.078	0.258	0.58
WLPMx	-	-	-	-
WRPMx	31.037 a	-2.045	0.789	0.53
DREN	266.527 a	-1.146	0.511	0.69
GPreOW	143.263 a	-1.316	0.518	0.55
GPostOW	165.542 a	-0.906	0.559	0.61
GWEN	-	-	-	-
GWZS	171.701 a	-1.270	0.400	0.80
GWPMx	-	-	-	-
GPW	132.771 a	-2.689	0.342	0.58
VEHB	-	-	-	-
ILB	-	-	-	-
GLLPTF	88.321 a	-1.304	0.356	0.34
GWLPTF	66.174 a	-1.142	0.464	0.88
MaDLTF	49.459 a	-0.945	0.456	0.67
MiDLTF	33.365 a	-0.241	0.573	0.20
DSOC	-	-	-	-
LLO	48.494 a	-1.093	0.548	0.92
LALL	-	-	-	-
GWIN	-	-	-	-
GLLP	-	-	-	-
LLTC	-	-	-	-
LRTC	-	-	-	-
WPS	45.350 a	-0.082	0.388	0.77
LULTR	193.220 a	-1.275	0.438	0.66
LLLTR	192.075 a	-1.168	0.654	0.88
GLLR	323.906 a	-1.275	0.480	0.88
GHLR	70.011 a	-1.264	0.760	0.83
LLMF	106.210 a	-2.383	0.954	0.61
GHFM	-	-	-	-
GWFM	-	-	-	-
DRIN	253.174 a	-1.167	0.465	0.76

Body size (BL) was measured in cm and the other variables in mm (asymptotic value attained at 6yr (a) or 10yr (b)).

In area ES, the Gompertz model fitted the metric data for 24 variables (66.7%) (Table 1). Given the limited number of specimens from this area and the absence of specimens aged zero. Asymptotic values were reached at about six years for the cranial variables. The total body length did not display good fit by the model and an asymptote was only reached at about ten years of age.

The Gompertz model fitted the metric data for 27 variables (75.0%) in area NRJ, 33 (91.7%) in area SRJ and 29 (80.6%) in area SP (Tables 2, 3 and 4). In these areas, asymptotic values were reached at about six years of age for total body length and cranial variations.

Body length at age zero predicted by the Gompertz model for the Guiana dolphin was 148.3cm for area ES, 108.97cm for area NRJ, 98.4cm for area SRJ and 90.9cm for area SP.

Table 2. Growth parameters obtained by the Gompertz model fitted to metric variables-at-age in Guiana dolphins (*Sotalia guianensis*) from northern Rio de Janeiro.

Variable*	Asymptotic value	Correction factor	Growth rate constant	Correlation coeficient (*r*)
CT	190.057 a	-0.586	0.366	0.94
CCB	382.767 a	-1.318	0.550	0.72
CR	225.858 a	-0.965	0.615	0.64
LRb	-	-	-	-
LR60	60.721 a	-1.636	0.382	0.36
LPMxE	-	-	-	-
LPMxD	-	-	-	-
DRNE	268.898 a	-1.033	0.606	0.43
LpreO	144.672 a	-1.226	0.574	0.71
LposO	164.529 a	-1.126	0.527	0.83
LNE	39.489 a	-1.916	0.397	0.41
LPZE	172.921 a	-1.561	0.521	0.58
LPMx	62.941 a	-2.391	0.533	0.26
LP	133.485 a	-2.214	0.767	0.20
ACC	111.299 a	-2.381	0.415	0.42
CICC	-	-	-	-
CFPTE	89.920 a	-1.411	0.427	0.69
LFPTE	70.015 a	-1.176	0.547	0.49
MaDFTE	48.818 a	-1.333	0.449	0.67
MeDFTE	35.107 a	-0.960	0.364	0.66
DCSO	-	-	-	-
COD	48.630 a	-1.221	0.673	0.46
CPLE	-	-	-	-
LNI	-	-	-	-
CPE	48.151 a	-1.697	0.293	0.45
CCTE	57.738 a	-1.267	0.595	0.69
CCTD	57.770 a	-2.553	0.319	0.25
LSP	45.336 a	-1.243	0.299	0.69
CFDSE	194.497 a	-0.766	0.574	0.71
CFDIE	195.798 a	-0.753	0.602	0.72
CMdE	327.375 a	-0.831	0.639	0.71
AMdE	72.566 a	-1.139	0.486	0.88
CFMdE	107.944 a	-1.263	0.891	0.67
AFM	-	-	-	-
LFM	-	-	-	-
DRNI	258.406 a	-1.542	0.427	0.56

*Body size (BL) was measured in cm and the other variables in mm (asymptotic value attained at 6yr (a)).

Geographic Variation

The ANOVA for the geographic areas demonstrated that 27 variables (77%) varied significantly ($P < 0.001$) (Table 5). The canonical discriminant analysis of the 35 cranial variables uncovered a significant difference among geographic areas (Wilks' Lambda = 0.04731; $F_{105.32} = 5.3661$; $P < 0.001$) (Table 6). Of the 144 specimens analyzed, the discriminant function classified correctly *a posteriori* 137 specimens (95%; Table 7).

Evaluation of the standard coefficients of the canonical discriminant analysis indicated that five variables best represented the difference among the geographic areas. These variables were: the condylobasal length (CBL) and those associated with the feeding apparatus (LR, GLLR, GWZS and MiDLTF) (Table 8). Discriminant axes 1 and 2 explained 54% and 34% of the variance among the geographic areas, respectively, representing mainly the difference between area NRJ and areas SRJ and SP. Discriminant axis 3 explained the remaining 12% of variance, representing the difference of area ES with respect to the other areas. Figure 2 presents the projection of the 144 specimens in the canonical axes, showing a partial overlap between the ellipses.

Table 3. Growth parameters obtained by the Gompertz model fitted to metric variables-at-age in Guiana dolphins (*Sotalia guianensis*) from southern Rio de Janeiro.

Variable*	Asymptotic value	Correction factor	Growth rate constant	Correlation coeficient (*r*)
CT	187.594 a	-0.437	0.463	0.83
CCB	378.090 a	-0.661	0.634	0.94
CR	221.752 a	-0.413	0.603	0.90
LRb	88.220 a	-0.850	0.651	0.86
LR60	58.640 a	-0.658	0.550	0.86
LPMxE	24.500 a	-1.409	0.710	0.56
LPMxD	29.498 a	-1.781	2.089	0.52
DRNE	264.876 a	-0.354	0.717	0.90
LpreO	143.104 a	-1.059	0.706	0.81
LposO	160.832 a	-1.181	0.483	0.76
LNE	38.397 a	-1.496	0.332	0.67
LPZE	171.589 a	-1.028	0.607	0.85
LPMx	61.617 a	-1.456	0.640	0.81
LP	133.801 a	-2.082	0.702	0.67
ACC	110.690 a	-1.631	0.519	0.67
CICC	115.456 a	-1.979	0.579	0.61
CFPTE	86.354 a	-1.537	0.298	0.48
LFPTE	70.449 a	-1.395	0.246	0.72
MaDFTE	48.370 a	-1.301	0.358	0.83
MeDFTE	32.304 a	-0.887	0.450	0.66
DCSO	-	-	-	-
COD	48.077 a	-1.435	0.630	0.83
CPLE	34.279 a	-1.293	0.532	0.55
LNI	42.283 a	-1.169	4.065	0.71
CPE	46.769 a	-0.778	0.441	0.74
CCTE	58.510 a	-1.371	0.662	0.76
CCTD	58.118 a	-1.546	0.551	0.77
LSP	44.649 a	-0.827	0.435	0.86
CFDSE	190.263 a	-0.493	0.534	0.86
CFDIE	195.353 a	-0.561	0.607	0.88
CMdE	321.930 a	-0.581	0.739	0.88
AMdE	72.545 a	-0.592	0.836	0.90
CFMdE	106.014 a	-0.739	2.038	0.81
AFM	-	-	-	-
LFM	-	-	-	-
DRNI	252.417 a	-0.425	0.517	0.87

*Body size (BL) was measured in cm and the other variables in mm (asymptotic value attained at 6yr (a)).

Discussion

Growth

Body length at age zero predicted by the Gompertz model for the study areas resulted in the lowest value for SP, gradually increasing to SRJ, NRJ and ES. However, it is important to emphasize that the estimated length for the ES was too high for the species, probably due to the limited number of specimens analyzed from this area.

Age at sexual maturity has been estimated at six years old for males and females from northern Rio de Janeiro (Ramos *et al.*, 2000a), and between six and seven years for females and seven years for males from São Paulo and Paraná (Rosas, 2000; Rosas *et al.* 2003). At São Paulo and Paraná, Rosas (2000) and Rosas *et al.* (2003) observed that males reach the sexual maturity at 170.0cm and females at 164.0cm. In northern Rio de Janeiro, males were 180.0cm length and females 160.0cm upon reaching the sexual maturity (Ramos *et al.*, 2000a).

The asymptotic body and cranial values were reached at about six years old in the four geographic areas, indicating that adult size does not vary among areas. These results are similar to those already reported in the literature. Growth data presented by Borobia (1989)

Table 4. Growth parameters obtained by the Gompertz model fitted to metric variables-at-age in Guiana dolphins (*Sotalia guianensis*) from São Paulo.

Variable*	Asymptotic value	Correction factor	Growth rate constant	Correlation coeficient (*r*)
CT	181.207 a	-0.371	0.591	0.86
CCB	370.578 a	-0.855	0.738	0.90
CR	219.023 a	-0.508	0.852	0.90
LRb	-	-	-	-
LR60	57.332 a	-1.035	0.469	0.72
LPMxE	-	-	-	-
LPMxD	30.742 a	-1.298	1.041	0.58
DRNE	258.479 a	-0.562	0.900	0.90
LpreO	140.715 a	-0.973	0.778	0.90
LposO	163.537 a	-0.967	0.746	0.92
LNE	37.287 a	-1.185	1.052	0.84
LPZE	168.289 a	-0.990	0.841	0.88
LPMx	59.920 a	-1.425	1.272	0.56
LP	-	-	-	-
ACC	117.730 a	-1.360	0.355	0.44
CICC	-	-	-	-
CFPTE	87.449 a	-1.431	0.376	0.62
LFPTE	69.111 a	-1.579	0.270	0.79
MaDFTE	46.450 a	-1.821	0.279	0.46
MeDFTE	30.956 a	-1.655	0.308	0.20
DCSO	-	-	-	-
COD	47.005 a	-1.145	1.143	0.92
CPLE	32.976 a	-0.927	0.480	0.81
LNI	41.580 a	-1.745	0.608	0.37
CPE	45.463 a	-0.926	0.469	0.67
CCTE	57.350 a	-1.613	0.452	0.50
CCTD	57.479 a	-1.906	0.368	0.49
LSP	45.274 a	-0.779	0.289	0.90
CFDSE	188.437 a	-0.516	0.741	0.92
CFDIE	190.184 a	-0.663	0.698	0.90
CMdE	314.421 a	-0.770	0.817	0.90
AMdE	70.561 a	-0.911	0.674	0.92
CFMdE	106.014 a	-1.143	1.285	0.83
AFM	-	-	-	-
LFM	-	-	-	-
DRNI	248.850 a	-0.558	0.777	0.88

Body size (BL) was measured in cm and the other variables in mm (asymptotic value attained at 6yr (a)).

for the Guiana dolphin and the tucuxi (*S. fluviatilis*) showed that at five years old both species had reached adult size for all the cranial features analyzed. Santos *et al.* (2003) estimated asymptotic values at seven years of age for the specimens from São Paulo. Schmiegelow (1990) estimated the asymptotic values at six years old for males and females along the São Paulo coast. These results indicate that Guiana dolphins reach adult size and sexual maturity simultaneously at six to seven years of age, when specimens cease to grow.

In contrast, the attainment of cranial and post-cranial maturity appears to be slow, displaying considerable individual variation between the ages of five and ten years.

Geographic variation

The ANOVA for geographic areas indicated variation in which the skulls in adults are smaller at higher latitudes in the study area. The variables that best represented geographic variation, corresponding to the cranial and feeding apparatuses, may be indicative of selection pressure related to feeding behavior and functional morphology.

In northern Rio de Janeiro, Di Beneditto *et al*. (2001) analyzed the feeding habits of Guiana dolphin and verified that the cutlassfish (*Trichiurus lepturus*) was the most representative prey in its diet. Studies on the feeding habits of this species conducted in other areas

Table 5. Analysis of variance (ANOVA) of metric variables between the geographic areas for Guiana dolphins (*Sotalia guianensis*) in southeastern Brazil.

Variable	G.L.	SQ	MQ	*F*	*P*
CBL	3	5123.21356	1707.73785	13.29974	0.00000 ***
LR	3	1264.26318	421.42106	5.64390	0.00111 **
WRB	3	1259.45102	419.81701	24.67510	0.00000 ***
WR60	3	331.35393	110.45131	13.09781	0.00000 ***
WLPMx	3	12.85354	4.28451	1.41924	0.23975
WRPMx	3	64.98000	21.66000	9.30129	0.00001 ***
DREN	3	3194.07224	1064.69075	11.02922	0.00000 ***
GPreOW	3	302.57697	100.85899	3.36401	0.02054 *
GPostOW	3	1083.63321	361.21107	8.99054	0.00002 ***
GWEN	3	96.69500	32.23167	5.96110	0.00075 ***
GWZS	3	877.17468	292.39156	9.24264	0.00001 ***
GWPMx	3	229.78763	76.59588	13.73418	0.00000 ***
GPW	3	4179.39846	1393.13282	21.13179	0.00000 ***
VEHB	3	3122.55988	1040.85329	16.78498	0.00000 ***
ILB	3	686.64847	228.88282	10.63605	0.00000 ***
GLLPTF	3	509.38896	169.79632	9.70414	0.00001 ***
GWLPTF	3	179.95457	59.98486	6.85954	0.00024 ***
MaDLTF	3	196.37733	65.45911	15.88552	0.00000 ***
MiDLTF	3	367.42021	122.47340	19.88620	0.00000 ***
DSOC	3	1390.19505	463.39835	21.81108	0.00000 ***
LLO	3	46.75488	15.58496	5.06637	0.00232 **
LALL	3	235.26021	78.42007	14.35172	0.00000 ***
GWIN	3	89.01554	29.67185	9.42801	0.00001 ***
GLLP	3	162.58329	54.19443	6.18527	0.00056 ***
LLTC	3	127.61258	42.53753	9.45963	0.00001 ***
LRTC	3	64.53191	21.51064	5.57437	0.00122 **
WPS	3	0.03303	0.01101	0.00196	0.99988
LULTR	3	1528.80890	509.60297	7.37417	0.00013 ***
LLLTR	3	1774.89396	591.63132	10.35805	0.00000 ***
GLLR	3	6085.24641	2028.41547	20.20930	0.00000 ***
GHLR	3	243.01726	81.00575	16.02030	0.00000 ***
LLMF	3	97.93940	32.64647	1.65835	0.17881
GHFM	3	60.09746	20.03249	3.09201	0.02911 *
GWFM	3	84.46485	28.15495	6.51542	0.00037 ***
DRIN	3	3154.17079	1051.39026	12.27759	0.00000 ***

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

also report the importance of the cutlassfish (Barros *et al.*, 1998[11]; Borobia and Barros, 1989; Schmiegelow, 1990). Analysis of nine stomach contents of Guiana dolphin in the Cananéia Estuary, in southern São Paulo, indicated that sciaenid fishes were the most representative prey in its diet (Santos *et al.*, 2002). The authors linked the diet of Guiana dolphin to the abundance of fish of the Sciaenidae family in that estuary. The differences in the prey size among geographic areas, requiring differing feeding strategies, may result in variation in the functional morphology. However, information on the diet of Guiana dolphin along its distributional range is still incipient to verify this hypothesis. The diet of Guiana dolphin throughout its geographical distribution must be compared to verify whether there exists a significant difference in the size of the preferred prey, leading to different feeding strategies that might, in turn, result in variation in morphological function or metabolic rates.

Table 6. Classification function of the canonical discriminant analysis in Guiana dolphins (*Sotalia guianensis*) for Espírito Santo (ES), northern Rio de Janeiro (NRJ), southern Rio de Janeiro (SRJ) and São Paulo (SP), southeastern Brazil.

Variable	ES	NRJ	SRJ	SP
CBL	0.59044	0.73079	0.65776	0.48805
LR	1.17079	1.03517	1.36948	1.49207
WRB	-1.69285	-0.96136	-0.79069	-1.22261
WR60	-2.91464	-3.43623	-3.91136	-3.75502
WLPMx	1.66382	1.93597	2.38041	2.59896
WRPMx	10.30654	9.46328	8.90571	9.26140
DREN	-1.16310	-0.88452	-0.79056	-1.06070
GPreOW	1.16398	0.74714	1.05450	1.09541
GPostOW	0.54097	0.25274	0.12413	0.53630
GWEN	4.28710	4.60887	4.69368	4.50596
GWZS	-2.10682	-2.21015	-2.23777	-1.84392
GWPMx	-1.33787	-1.10839	-1.45287	-1.74527
GPW	3.72524	3.78252	3.79324	3.76764
VEHB	2.17611	2.61757	2.51008	2.47659
ILB	4.21340	4.31728	4.14421	4.24839
GLLPTF	1.60745	1.64822	1.22353	1.58789
GWLPTF	3.56887	4.53908	4.73995	4.28383
MaDLTF	-1.34367	-2.26780	-2.56209	-2.86150
MiDLTF	-0.77974	-0.22273	-0.67895	-1.05910
DSOC	0.97038	1.10471	0.95032	0.81635
LLO	3.69643	3.31487	3.60127	3.39873
LALL	-2.78086	-2.26420	-2.65517	-2.83622
GWIN	10.34756	10.04337	9.46967	9.16883
GLLP	-1.83532	-2.26691	-2.12369	-2.36767
LLTC	-1.79110	-1.77065	-1.37380	-1.39795
LRTC	6.09536	6.00158	6.93875	6.86186
WPS	1.11612	1.15741	1.59982	1.59803
LULTR	-2.91035	-3.36673	-3.85681	-3.30250
LLLTR	1.48503	1.52765	1.85031	1.69381
GLLR	1.11747	1.20763	0.93974	0.90802
GHLR	1.35426	1.52388	2.45664	2.09483
LLMF	3.29052	3.46417	3.25283	3.51279
GHFM	2.94907	2.73027	3.43759	3.26882
GWFM	-0.09166	-0.14548	-0.62813	-0.91754
DRIN	1.13485	1.26039	1.20748	1.14977
Constant	-1683.77173	-1771.75085	-1739.40186	-1698.21826

[11] Barros, N.B., Zanelatto, R.C., Oliveira, M.R., Rosas, F.C.W., Simões-Lopes, P.C. (1998) Hábitos alimentares do boto cinza, *Sotalia fluviatilis*, no extremo sul de sua distribuição. Page 21 *in* Abstracts, 8ª Reunião de Trabalho de Especialistas em Mamíferos Aquáticos da América do Sul, 25-29 October 1998, Olinda, PE, Brasil.

Ramos *et al*. (2002) studied geographic variation in franciscanas in southeastern Brazil and reported that it was consistent with the disjunct distribution hypothesis. This hypothesis was proposed by Siciliano *et al*. (2002) based on two gaps in its distribution along this region. These authors related the gaps to two factors: the lack of fluvial drainage, which would increase the abundance of trophic resources, and the narrowing of the continental shelf, which decreases available habitat. The preference of the franciscana for estuarine areas with high turbidity can be related to optimal conditions for feeding

Table 7. *A posteriori* classification of Guiana dolphins (*Sotalia guianensis*) based on the canonical function for Espírito Santo (ES), northern Rio de Janeiro (NRJ), southern Rio de Janeiro (SRJ) and São Paulo (SP), southeastern Brazil.

	Classification *a posteriori* (%)	ES	NRJ	SRJ	SP
ES	100.00	10	0	0	0
NRJ	92.68	0	38	2	1
SRJ	91.67	0	1	33	2
SP	98.25	0	0	1	56
Total	95.14	10	39	36	59

Table 8. Standard coefficients of the canonical analysis for Guiana dolphins (*Sotalia guianensis*) from southeastern Brazil.

Variable	Axis 1	Axis 2	Axis 3
CBL	**0.63176**	-0.27059	0.09216
LR	**-0.92865**	-0.20171	-0.25461
WRB	0.18284	-0.64282	0.38171
WR60	0.26651	0.43010	-0.21386
WLPMx	-0.29576	-0.12434	0.14046
WRPMx	0.10946	0.33411	-0.17134
DREN	0.35534	-0.75417	0.14735
GPreOW	-0.39536	0.00183	-0.60742
GPostOW	-0.39832	0.63704	0.06111
GWEN	0.03854	-0.16231	0.09437
GWZS	**-0.49650**	0.35490	0.25851
GWPMx	0.35283	-0.01311	0.05396
GPW	0.01676	-0.08759	0.07182
VEHB	0.16689	-0.26271	0.84584
ILB	0.05981	0.13445	0.24629
GLLPTF	0.04590	0.44650	0.40721
GWLPTF	0.10618	-0.55737	0.42808
MaDLTF	0.35209	0.21581	-0.53194
MiDLTF	**0.46790**	-0.08176	0.23118
DSOC	0.30765	-0.02827	0.08016
LLO	-0.01328	-0.05212	-0.25299
LALL	0.29072	-0.03440	0.26881
GWIN	0.39558	0.15110	-0.17065
GLLP	0.11524	-0.02092	-0.46176
LLTC	-0.19244	-0.14280	-0.04407
LRTC	-0.40295	-0.28797	-0.17129
WPS	-0.25614	-0.17541	-0.03374
LULTR	-0.04677	1.59695	0.11140
LLLTR	-0.30601	-0.56029	-0.26274
GLLR	**0.70240**	0.28795	0.30916
GHLR	-0.31704	-0.46803	-0.16456
LLMF	-0.08297	0.20705	0.44235
GHFM	-0.31263	-0.27657	-0.30910
GWFM	0.39621	0.09585	-0.07926
DRIN	0.21689	-0.10965	0.21503
Eigenvalue	3.13508	1.99689	0.70563
Cumulative proportion	0.53705	0.87912	1.00000

Bold values indicate the variables that captured the greatest differences between geographic areas.

(Siciliano and Santos, 1994[12], Crespo *et al.*, 1998). The franciscana obtains greater success in areas that present favorable conditions for their feeding and its trophic specialization can act to limit the habitat occupied (Crespo *et al.*, 1998; Di Beneditto *et al.*, 2001).

The *a posteriori* classification of the discriminant function correctly classified 95% of the specimens analyzed. Only two specimens were collected in Cabo Frio (SRJ area). This probably indicates that the specimens might be coming from the surroundings of Macaé (NRJ area). Over two years, Hassel *et al.* (2001)[13] recorded cetacean sightings in Cabo Frio and frequently recorded groups of common dolphins (*Delphinus* sp.) and Atlantic spotted dolphins (*Stenella frontalis*), but Guiana dolphins were never observed.

The water temperature seems to influence the distribution of Guiana dolphins. Borobia *et al.* (1991) have suggested that water temperature may act as a thermal barrier for the species, since it does not occur beyond ~27°S, where temperature may reach 15°C. In Cabo Frio, due to local upwelling, temperature may reach low values during the spring-summer seasons (Valentin and Monteiro-Rivas, 1993), around 15 to 18°C (Fagundes-Netto and Gaelzer, 1991). For this reason, this region is likely to be unfavorable for Guiana dolphins. In southern Espírito Santo there are atypical characteristics for the occurrence

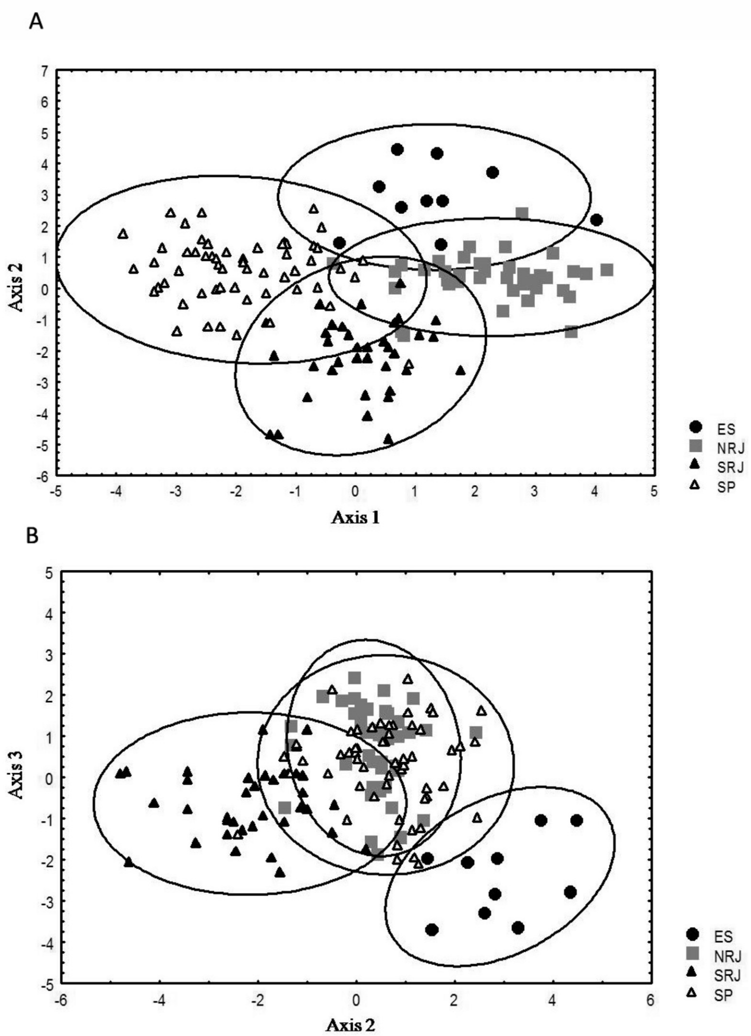

Figure 2. Projection of axes 1 and 2 (a) and axes 2 and 3 (b) of a canonical discriminant analysis of cranial metric variables in Guiana dolphins (Sotalia guinanesis) from Espírito Santo (ES), northern Rio de Janeiro (NRJ), southern Rio de Janeiro (SRJ) and São Paulo (SP), southeastern Brazil.

[12] Siciliano, S. and Santos, M.C.O. (1994) Considerações sobre a distribuição da franciscana *Pontoporia blainvillei* no Litoral Sudeste do Brasil. *In Segundo Encontro de Trabalho sobre a Coordenação de Pesquisa e Conservação da Franciscana* - Florianópolis, Brasil, 1994. (EF/2/DT6).

[13] Hassel, L.B., Fernandes, T., Demari e Silva, E. and Siciliano, S. (2001) Pequenos cetáceos associados a ressurgência de Arraial do Cabo, RJ. Page 39 *in* Abstracts, *Congresso Brasileiro de Mastozoologia,* 6-9 September 2001, Porto Alegre, RS, Brazil.

of coastal cetacean species, such as the absence of heavy-flowing rivers and the narrowing of the continental shelf. However, the limited observation effort in this region prevents a more accurate definition of Guiana dolphin occurrence.

A partial overlap between geographic areas was observed in the projection of the species on the canonical axes (Figure 2), which suggests that the Guiana dolphin is parapatric in southeastern Brazil.

Many cetaceans have a wide distribution in one or more oceans, and in some species, individuals migrate over an extensive range, such as baleen whales. Some species, in contrast, range over relatively finite geographic areas, as for example, local populations of the common bottlenose dolphin (*Tursiops truncatus*). Other odontocetes such as killer whales (*Orcinus orca*) have a very wide distribution in the oceans, though both proximate and distant populations can become genetically differentiated (Hoelzel, 1998). In parapatry there is no specific extrinsic barrier to gene flow. Differences may happen because of reduced gene flow within the population and varying selection pressures across the population's range. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the common bottlenose dolphin was studied by Hoelzel *et al.* (1998). The results of the authors are consistent with local differentiation based on habitat or resource specialization in the western North Atlantic, and suggest differences in the character of the nearshore/offshore distinction. The habitats used by the nearshore and offshore forms of bottlenose dolphin differ in a number of ways including water temperature, depth, prey diversity and prey species composition. The differential use of these habitats may be a consequence of resource specialization based on one or more of these characteristics. Intraspecific variation correlated with habitat use or resource use has been described for a number of delphinid species (Hoelzel, 1998).

Geographic variation recorded in this study may be related to environmental adaptations. One of the areas that could be considered critical to the Guiana dolphin distribution is the central coast of Rio de Janeiro, which is characterized by the absence of river discharges, narrowing of the continental shelf and upwelling influence. These environmental features might be limiting the species occurrence in this area.

Although molecular studies have shown that Guiana dolphins are represented by one stock found from Santa Catarina (27°S) to Rio de Janeiro (Cunha *et al.*, 2005; Caballero *et al.*, 2007), the use of other tools such as contaminant loads (see Laílson-Brito *et al.*, 2010) and skeletal morphology (present study) have identified significant differences in populations of the quoted stock. Additional tools such as the use of stable isotopes could address further differences in populations found in Guiana dolphins in southern and in southeastern Brazil.

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