

MORPHOLOGY OF THE FRANCISCANA (*PONTOPORIA BLAINVILLEI*) OFF SOUTHEASTERN BRAZIL: SEXUAL DIMORPHISM, GROWTH AND GEOGRAPHIC VARIATION

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Abstract – Variations in body and skull morphology may exhibit geographic differences evidencing distinct population stocks. The objectives of the present study were to analyze such variation to test the hypothesis of a disjunct distribution of the franciscana (*Pontoporia blainvillei*) off the southeastern coast of Brazil. Body length and 39 cranial variables were measured from bycaught animals to considered sexual, ontogenetic and geographic variations. The areas studied were Espírito Santo (ES) (18°30'S-19°40'S), northern Rio de Janeiro (NRJ) (21°35'S-22°25'S) and São Paulo (SP) (23°30'S-25°30'S). Franciscanas from NRJ and SP presented significant sexual dimorphism, with the means for the metric characters larger for females than for males. Sexual dimorphism for franciscanas from ES was not examined due to limited sample size. The growth pattern for body and skull did not indicate clinal variation. The asymptotic values obtained for franciscanas from SP were smaller than the values obtained for franciscanas from NRJ and ES. Canonical discriminant analysis of the cranial metric characters indicated significant differences among the three geographic areas. Differences between areas ES and NRJ accounted for 85% of the variation (axis 1). The remaining 15% (axis 2) was due to difference between the area SP from the others. The geographic variation supports the hypothesis stock division in southeast Brazil; allopatry might be present. Therefore, three franciscana stocks from the southeastern coast of Brazil should be considered distinct for conservation and management actions.

Resumo – Variações no padrão morfológico do corpo e do crânio podem apresentar diferenças geográficas evidenciando estoques populacionais distintos. O objetivo do presente estudo foi estudar tais variações para testar a hipótese de distribuição disjunta para a toninha (*Pontoporia blainvillei*) na costa sudeste do Brasil. Para tanto, o comprimento do corpo e 39 caracteres cranianos foram determinados, considerando-se as variações morfológicas sexual, ontogênica e geográfica. As áreas estudadas foram Espírito Santo (ES) (18°30'S-19°40'S), norte do Rio de Janeiro (NRJ) (21°35'S-22°25'S) e São Paulo (SP) (23°30'S-25°30'S). Toninhas do NRJ e SP, apresentaram dimorfismo sexual significativo, com as médias obtidas para os caracteres métricos maiores para as fêmeas do que para os machos. O dimorfismo sexual não pode ser testado para o ES devido a problemas amostrais. Os padrões de crescimento para o tamanho corpóreo e craniano indicaram que não há uma variação clinal para a espécie. Os valores assintóticos obtidos foram menores para os espécimens do SP em relação aos valores obtidos para os espécimens do NRJ e ES. A análise discriminante canônica para os caracteres métricos do crânio indicou diferença significativa entre as três áreas geográficas, sem sobreposição para os estoques analisados. Diferenças entre as áreas ES e NRJ foram explicadas por 85% da variação (eixo 1). O 15% restantes da variação (eixo 2) foram responsáveis pela diferença entre a área SP das demais áreas. A variação geográfica observada apoia a hipótese de distribuição disjunta no sudeste do Brasil; uma alopatria pode estar presente. Desta forma, os três estoques de toninhas na costa sudeste do Brasil devem ser considerados distintos para fins de conservação e manejo.

Keywords: *Pontoporia blainvillei*, franciscana, morphology, sexual dimorphism, growth, geographic variation, southeastern Brazil.

Introduction

The franciscana, *Pontoporia blainvillei* (Pontoporiidae), is restricted to the coastal Atlantic waters of South America from Itaúnas (18°30'S), Espírito Santo State, southeastern Brazil to Nuevo Gulf (42°35'S), Argentina (Siciliano, 1994; Crespo *et al.*, 1998).

Pinedo (1991) proposed at least two different forms of the franciscana based on osteological differences: one found to the north (smaller animals) and the other to the south (larger animals) of Santa Catarina State (~29°S). Ramos *et al.* (2000a) presented data on age and growth for franciscanas from Rio de Janeiro State (~22°S) and found asymptotic body lengths smaller than those found by Kasuya and Brownell (1979) for franciscanas from Uruguay (~34°S). This corroborates the study of Pinedo (1991) regarding the existence of at least two different phenotypic forms.

Analyses of the mtDNA from franciscanas of each of the geographic forms provided evidence of the existence of one genetic population involving dolphins from Rio Grande do Sul State (~33°S), Uruguay and Argentina (~42°S). No haplotypes from these locations were shared with dolphins from Rio de Janeiro State, supporting the hypothesis of at least two genetically distinct populations of franciscana (Secchi *et al.*, 1998; Lázaro and Lessa, 2000; Hamilton *et al.*, 2000).

Siciliano *et al.* (*in press*) proposed two gaps in the distribution of the northern population. The first gap is located between Regência (19°40'S), Espírito Santo State and Atafona (21°35'S), northern Rio de Janeiro State and the second between Macaé (22°25'S), Rio de Janeiro State and Ubatuba (23°30'S), northern São Paulo State. Growth data suggest differences in morphology within northern franciscanas. The asymptotic lengths obtained by Rosas (2000) for franciscanas from São Paulo and northern Paraná States were smaller than the growth

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parameters obtained by Ramos *et al.* (2000a, b) for franciscanas from northern Rio de Janeiro State. This difference provides evidence of possible existence of more than two distinct stocks. Considerable effort has been given globally to managing impacted populations of small cetaceans. The first step in this management is to define the populations involved. One tool for defining mammal population is the analysis of geographic variation in morphology (Perrin, 1984). Three relevant aspects should be considered. First, quantification of the degree of sexual dimorphism found within populations is advisable before studying geographic variation in order to avoid attributing significant morphometric differences to inappropriate factors (Hersh *et al.*, 1990). Second, knowledge of the differences in postnatal growth between distinct geographic areas helps in the identification of population plasticity (Calzada *et al.*, 1997). Finally, geographic variation provides a basis for the description of stock units used to assess and manage dolphins (Schnell *et al.*, 1986).

The objectives of the present study were to analyze variations in cranial morphology to test the hypothesis of stock division along the southeastern coast of Brazil. Body length and 39 cranial variables were analysed to consider sexual, ontogenetic and geographic variation.

Material and Methods

Study area and sample

The sampling areas were defined according to known occurrence of the franciscana off the southeastern coast of Brazil. Three areas were considered: AREA ES - Espírito Santo State, from Itaúnas to Regência (18°30'S-19°40'S); AREA NRJ - northern Rio de Janeiro State, from Atafona to Macaé (21°35'S-22°25'S); and AREA SP - São Paulo State, from Ubatuba to Cananéia, including the Baía de Paranaguá, in the extreme north of Paraná State (23°30'S-25°30'S) (Figure 1).

The study specimens were accidentally caught in gillnet fisheries or found stranded. A total of 262 franciscanas were examined from different collections; 14 from area ES, 143 from area NRJ and 105 from area SP.

Age estimation and morphometric characters

Age was estimated in 205 franciscanas by counting the number of growth layer groups (GLGs) in the dentine and cement. We adopted the GLG pattern described for the species by Pinedo and Hohn (2000) and Ramos *et al.* (2000a): one complete dentinal GLG was composed of one narrow unstained layer and a broad stained layer. A fine darkly

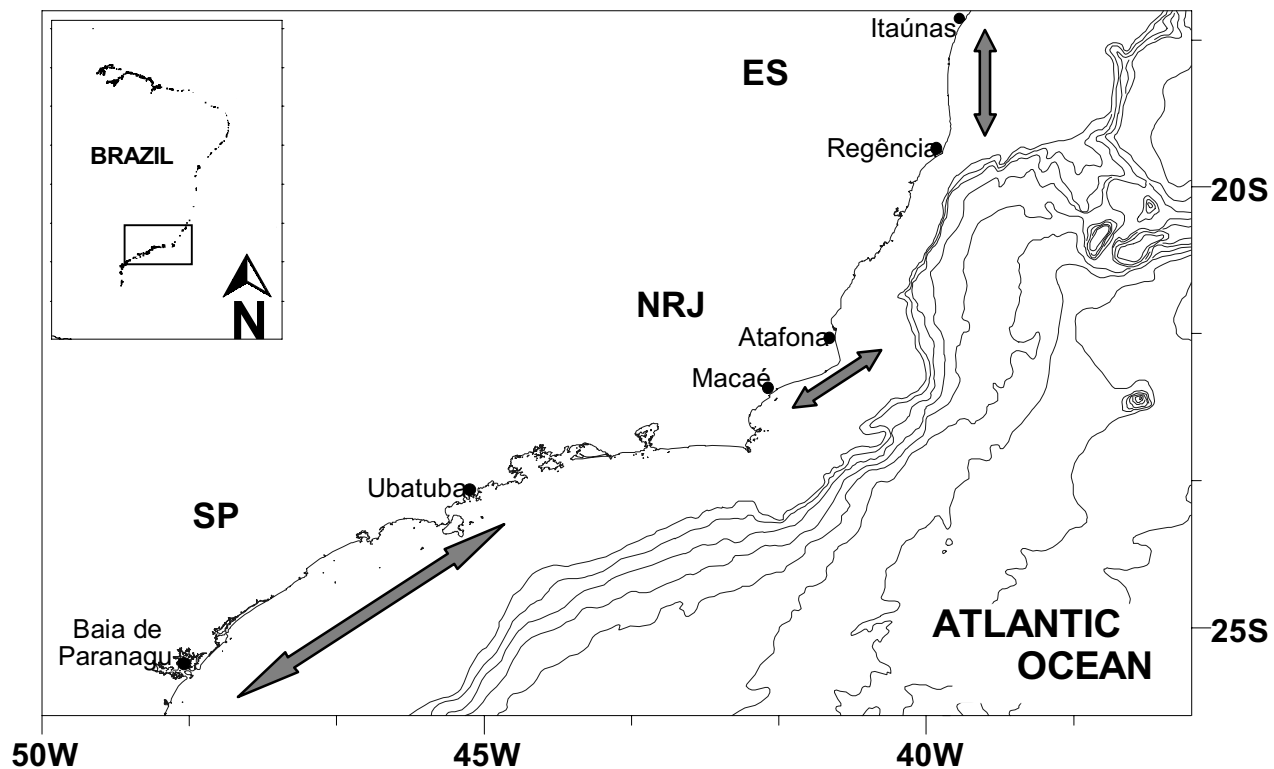


Figure 1. Areas of occurrence of *Pontoporia blainvillei* in southeastern Brazil. The arrows indicate the three geographic locations considered in the present study: area ES - Espírito Santo State, from Itaúnas to Regência (18°30'S-19°40'S); area NRJ - Northern Rio de Janeiro State, from Atafona to Macaé (21°35'S-22°25'S); and area SP - São Paulo State, from Ubatuba to Cananéia, including the Baía de Paranaguá, in the northernmost portion of Paraná State (23°30'S-25°30'S).

stained layer demarcated the boundary with unstained layer of the subsequent GLG. In the cementum, a complete GLG was composed of one narrow stained layer and a wide weakly stained layer. The method of preparation of decalcified thin and stained sections of the teeth for examination under an optical microscopy was used following the recommendations of Perrin and Myrick (1980) and Hohn *et al.* (1989).

Body length (BL) of 189 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 190 skulls from franciscanas were examined by one of the authors (RMAR) for cranial metric characters following Perrin (1975)

and Schnell *et al.* (1985) with some modifications (Table 1). Due to the small number of skulls for which widths of the rostrum could be measured, four variables were deleted from the analysis (WR1/4, WR1/2, WPMx1/2 and WR3/4). A total of 35 variables remained from the original 39. Acronyms are shown in Table 1.

The franciscanas were classified as immature or mature according to the relationship between age and body length. For franciscanas from northern Rio de Janeiro State, males were considered mature if age was ≥ 2 years and body length ≥ 113.0 cm; for females, the criteria were ≥ 3 years and ≥ 130.0 cm (Ramos *et al.*, 2000a). For franciscanas from São Paulo State, males were considered mature if body

Table 1. Cranial metric characters analysed in franciscanas (*Pontoporia blainvillei*) from southeastern Brazil.

N.º Cranial metric character	Acronym	Functional apparatus
1 Condylbasal length	CBL	B
2 Length of rostrum	LR	F
3 Width of rostrum at base	WRB	F
4 Width of rostrum at 1/4	WR1/4	F
5 Width of rostrum at 60 mm	WR60	F
6 Width of rostrum at midlength	WR1/2	F
7 Width of premaxillaries at midlength of rostrum	WPMx1/2	B
8 Width of rostrum at 3/4 length	WR3/4	F
9 Width of left premaxillary (midline nares)	WLPMx	B-S
10 Width of right premaxillary (midline nares)	WRPMx	B-S
11 Distance from tip of rostrum to external nares	DREN	B
12 Greatest preorbital width	GPreOW	B
13 Greatest postorbital width	GPostOW	B
14 Greatest width of external nares	GWEN	B-S
15 Greatest width at zygomatic process of squamosal	GWZS	B
16 Greatest width of premaxillaries	GWPMx	B
17 Greatest parietal width	GPW	B
18 Vertical external height of braincase	VEHB	B
19 Internal length of braincase	ILB	B
20 Greatest length of left posttemporal fossa	GLLPTF	B
21 Greatest width of left posttemporal fossa	GWLPTF	B
22 Major diameter of left temporal fossa proper	MaDLTF	B
23 Minor diameter of left temporal fossa proper	MiDLTF	B
24 Distance of supraoccipital crest	DSOC	B-S
25 Length of left orbit	LLO	V
26 Length of antorbital process of left lacrimal	LALL	V
27 Greatest width of internal nares	GWIN	B-S
28 Greatest length of left pterygoid	GLLP	B-S
29 Length of left tympanic cavity	LLTC	H
30 Length of right tympanic cavity	LRTC	H
31 Width of pterygobasioccipital sutures	WPS	H
32 Length of upper left tooth row	LULTR	F
33 Length of lower left tooth row	LLLTR	F
34 Greatest length of left ramus	GLLR	F
35 Greatest height of left ramus at right angles to greatest length	GHLR	F
36 Length of left mandibular fossa	LLMF	F
37 Greatest height of foramen magnum	GHFM	B
38 Greatest width of foramen magnum	GWFM	B
39 Distance from tip of rostrum to internal nares	DRIN	B

(B) braincase; (F) feeding; (B-S) breathing-sound; (V) vision; (H) hearing.

length was ≥ 112.0 cm and females, ≥ 122.0 cm, both with age ≥ 4 years (Rosas, 2000).

Sexual dimorphism

The franciscana has been considered a dimorphic species in body length and skull size, with females larger than males (Pinedo, 1991). Ramos *et al.* (2000a) verified that sexual dimorphism is significant only in mature franciscanas of three years or more of age.

Differences between mature males and females were examined here by a stepwise discriminant analysis using Statistic Program 5.5 for Windows. A discriminant score function was performed to ascertain the sex of franciscanas.

Growth

Growth was determined by fitting a non-linear Gompertz model, $Y = ae[-e(b-cx)]$, where Y is a metric character, a is asymptotic length, b is a correction factor, c is growth rate constant and, x is 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 sex and 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 and sex to variables not fitted by non-linear model.

An analysis of variance (ANOVA) was carried out to test interaction between sex and geographic area for each metric character using Statistic Program 5.5 for Windows. The Bonferroni correction was applied and only $P < 0.001$ was significant. The method of adjusting for sex differences described by Schenell *et al.* (1985) was applied. Correction terms were obtained to adjust measurements of the larger sex downward and the smaller sex upward, thus producing sex-adjusted or "zwitter" measurements. As a result, we were able to combine specimens for both sexes in an overall analysis of geographic variation.

A canonical discriminant analysis was applied to identify the subset of variables that, taken in linear combination, show the greatest degree of geographic variation (Afifi and Clarck, 1990). The method was applied with Statistic Program 5.5 for Windows.

Results

Sexual Dimorphism

Only one mature female was obtained for the area ES (Espírito Santo State), making inferences of sexual dimorphism impossible for franciscana in this area (Table 2).

In area NRJ (northern Rio de Janeiro State), females were larger than males for all the 36 variables (Table 3). The discriminant separation was significant (Wilks' Lambda = 0.04738; $\sim F_{36,16} = 8.9357$; $P < 0.001$). Four metric variables (BL, MaDLTF, WPS, GHFM) best showed the discriminant between the sexes. Of the 53 individuals in the analysis,

96.2% were correctly classified *a posteriori* using the classification function (Table 4). Because of this high reliability, we sexed two franciscanas of unknown sex with the classification function.

In area SP (São Paulo State), females were larger than males in 92.5% of the variables (Table 5). The discrimination was significant (Wilks' Lambda = 0.20333; $\sim F_{3,21} = 27.427$; $P < 0.001$). Three metric variables (BL, CBL, VEHB) best showed the discriminant between the sexes. All the 25 franciscanas were correctly classified *a posteriori* by the discriminant function (Table 4). Of the 20 franciscanas of unknown sex, 14 (70%) were classified by the discriminant function. Six franciscanas were not classified by the function due to absence of measured cranial variable used in the function (i.e. BL, CBL, VEHB).

Growth

About 55% of the mean values for cranial variables were smaller for franciscanas from SP than franciscanas from ES and NRJ (Tables 2, 3 and 5). The coefficient of variation was smaller than 20% for all variables analysed. Therefore, the mean values of body length and cranial metric characters were considered suitable for growth pattern analysis. The growth parameters are presented in Tables 6, 7 and 8.

The growth curve for franciscanas from area ES was adjusted for males because only one female was obtained for this area (Table 6). The asymptotic value for body length (BL) was reached at about three years of age. One cranial variable of the feeding apparatus (WRB) reached asymptotic value earlier, at about four years. The other cranial variables reached asymptotic values at between five and six years (see Table 6). Only one variable of the feeding apparatus (MiDLTF) attained the asymptotic value after seven years. In area NRJ, the asymptotic value for females was larger than for males for all the variables analysed (Table 7). Males attained the asymptotic value earlier than females for 69% of the variables. Body length (BL) attained the asymptotic value at four years for males and five years for females. Most of the cranial variables of the braincase, breathing-sound and feeding apparatuses in males and females reached the asymptote at about six years (see Table 7). However, some variables of the breathing-sound and feeding apparatuses of the females reached the asymptote one year later, at seven years. In contrast, some variables of the breathing-sound and feeding apparatuses in males reached the asymptote one year earlier, at five years. The hearing apparatus (LLTC, LRTC and WPS) was the last to reach asymptotic values, at seven years in males and eight in females.

In area SP, the asymptotic values for females were larger than males for all the variables analysed (Table 8). Males attained the asymptote earlier than females in 65.4% of the variables. Body length (BL) reached the asymptotic value at four years for males and five years for females.

Most of the cranial variables of the braincase, breathing-sound, feeding and hearing apparatuses in males and females attained the asymptote at four years or at six years of age (see Table 8). Some variables of the breathing-sound and feeding apparatuses of females attained the asymptote at about seven years.

Table 2. Mean, standard deviation (SD) and coefficient of variation (CV) of metric variables for mature male and female franciscanas (*Pontoporia blainvillei*) from Espírito Santo State.

Variable ¹	n	Male			Female	
		mean	SD	CV	n	Value
BL	5	116.0	4.24	3.66	1	141.0
CBL	5	335.4	11.76	3.51	1	409.0
LR	5	239.6	7.83	3.27	1	302.0
WRB	5	34.8	1.12	3.21	1	37.6
WR60	5	15.2	1.35	8.86	1	18.6
WLPMx	5	15.2	0.50	3.31	1	17.2
WRPMx	5	16.9	0.84	4.98	1	18.5
DREN	5	268.8	9.78	3.64	1	340.0
GPreOW	4	71.5	1.57	2.19	1	78.8
GPostOW	4	84.6	1.78	2.10	1	93.6
GWEN	5	20.1	0.43	2.15	1	22.5
GWZS	5	102.0	2.84	2.78	1	111.3
GWPMx	5	38.0	1.70	4.49	1	40.0
GPW	5	82.4	1.03	1.25	1	86.6
VEHB	5	64.0	1.46	2.29	1	67.8
ILB	5	70.6	1.62	2.30	1	76.8
GLLPTF	5	63.5	1.31	2.06	1	68.9
GWLPTF	5	38.1	1.53	4.03	1	40.0
MaDLTF	5	29.0	1.73	5.96	1	28.4
MiDLTF	5	14.9	1.08	7.23	1	16.0
DSOC	4	31.2	2.52	8.09	1	29.0
LLO	5	25.2	0.79	3.13	1	26.8
LALL	5	9.2	1.48	16.07	1	10.6
GWIN	5	30.5	1.45	4.77	1	35.0
GLLP	4	40.0	2.83	7.07	1	41.2
LLTC	5	38.1	1.06	2.78	1	40.8
LRTC	5	37.8	1.44	3.81	1	41.4
WPS	5	28.1	1.24	4.42	1	28.6
LULTR	5	205.4	10.48	5.10	1	266.0
LLLTR	5	201.8	8.07	4.00	1	265.0
GLLR	5	297.6	12.65	4.25	1	372.4
GHLR	5	42.6	2.44	5.73	1	46.2
LLMF	5	73.9	2.64	3.57	1	85.0
GHFM	5	25.4	1.50	5.91	1	28.0
GWFM	5	25.1	1.38	5.51	1	27.2
DRIN	5	257.2	9.21	3.58	1	326.2

¹Acronyms in Table 1. Body size (BL) was measured in cm and the other variables in mm.

Table 3. Mean, standard deviation (SD) and coefficient of variation (CV) of metric variables for mature male and female franciscanas (*Pontoporia blainvillei*) from northern Rio de Janeiro State.

Variable ¹	Male				Female			
	n	mean	SD	CV	n	mean	SD	CV
BL	27	117.69	4.21	3.58	19	137.45	5.03	3.66
CBL	20	342.65	13.97	4.08	13	396.38	12.86	3.24
LR	18	248.25	14.53	5.85	13	295.42	10.09	3.42
WRB	29	36.19	1.92	5.31	22	38.43	1.68	4.38
WR60	27	17.19	1.01	5.87	20	20.12	1.58	7.87
WLPMx	29	16.19	1.03	6.36	21	16.98	1.11	6.55
WRPMx	29	17.84	0.96	5.39	23	18.67	0.76	4.06
DREN	18	279.12	13.73	4.92	13	328.16	11.17	3.40
GPreOW	25	72.84	2.91	3.99	14	78.02	2.19	2.81
GPostOW	24	87.74	2.60	2.97	17	93.03	2.91	3.13
GWEN	27	20.22	0.84	4.17	22	20.95	0.78	3.73
GWZS	27	98.57	4.73	4.79	16	104.64	3.23	3.08
GWPMx	29	39.86	1.33	3.34	22	41.21	1.31	3.19
GPW	29	85.82	1.96	2.28	21	87.41	3.17	3.63
VEHB	29	66.05	1.74	2.63	22	68.01	2.57	3.78
ILB	29	70.67	2.22	3.14	22	73.27	2.63	3.58
GLLPTF	28	62.54	2.24	3.58	18	65.59	2.25	3.43
GWLPTF	29	38.79	1.53	3.93	20	42.07	2.40	5.70
MaDLTF	29	26.72	1.19	4.45	21	29.20	1.29	4.42
MiDLTF	29	15.52	1.27	8.16	18	17.73	1.19	6.69
DSOC	29	30.10	1.73	5.73	23	30.21	2.17	7.19
LLO	26	24.58	2.44	9.91	17	26.80	3.83	14.28
LALL	25	8.17	0.96	11.70	17	8.61	1.12	12.97
GWIN	28	30.88	1.18	3.83	21	33.32	2.19	6.57
GLLP	21	29.68	3.86	12.99	12	33.95	4.52	13.31
LLTC	29	38.28	1.51	3.93	22	40.74	1.63	4.00
LRTC	29	38.14	1.38	3.61	22	40.91	1.51	3.70
WPS	29	28.72	1.70	5.92	22	31.01	2.00	6.44
LULTR	18	214.21	14.06	6.56	13	254.48	9.48	3.72
LLLTR	16	213.63	12.65	5.92	11	252.00	9.54	3.79
GLLR	16	308.11	15.82	5.13	11	357.63	10.97	3.07
GHLR	30	44.03	1.48	3.36	18	47.04	2.09	4.44
LLMF	30	75.21	2.90	3.86	19	82.28	3.06	3.72
GHFM	29	28.27	2.23	7.87	21	29.61	2.08	7.04
GWFM	29	25.86	1.76	6.79	22	27.24	1.95	7.16
DRIN	18	268.02	14.88	5.55	14	312.24	17.51	5.61

¹Acronyms in Table 1. Body size (BL) was measured in cm and the other variables in mm.

Body length at zero age predicted by the Gompertz model for male franciscanas was 71.0cm for area ES, 70.3cm for area NRJ and 68.5cm for area SP. For females, body length at zero age was predicted at 70.2cm for area NRJ and 67.3cm for area SP.

Geographic Variation

The analysis of variance (ANOVA) for geographic area demonstrated that 18 variables (51.4%) varied significantly ($P < 0.001$ - Bonferroni correction) (Table 9). ANOVA for sex demonstrated that 19 variables (54.3%) were significantly different ($P < 0.001$ - Bonferroni correction) (Table 9).

The ANOVA for the interaction between geographic variation and sex was significant for three variables only (8.6%): VEHB, GLLP and DRIN (Table 9). The interaction indicated that sexual dimorphism for these characters varied geographically and for this reason, these variables were excluded from analysis of geographic variation. Sexual dimorphism was independent of geographic variation for 91.4% of the variables (Table 9). The correction factor presented in Table 10 was subtracted from the values for males and added to the values for females. Therefore, males and females were analysed simultaneously.

The canonical discriminant analysis of the 32 cranial variables uncovered a significant difference among geographic areas (Wilks' Lambda = 0.0428917; $F_{64,100} \cong 5.982051$; $P < 0.001$). The discriminant function classified correctly *a posteriori* one hundred percent of the 84 specimens analysed (Table 11).

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 of the breathing-sound (DREN), braincase (CBL) and feeding (GPostOW, GLLPTF, LLLTR) apparatuses (Table 11). Discriminant axis 1 explained 85% of the variance among the geographic areas, representing mainly the difference between areas ES and NRJ. Discriminant axis 2 explained the remaining 15% of variance, representing the difference between area SP and the other areas. Figure 2 presents the projection of the 84 specimens in the canonical axes. No overlap occurred among the three geographic areas.

Discussion

Sexual dimorphism

The sexual dimorphism observed in the present study, with values for females larger than for males in all variables analysed for three geographic areas, corroborates other studies that considered the species highly dimorphic (Pinedo, 1991; Ramos *et al.*, 2000a).

Females larger than males are also observed in other species of small cetaceans, such as the harbour porpoise (*Phocoena phocoena*) and the vaquita (*P. sinus*) (Hohn *et al.*, 1996; Read and Tolley, 1997). Sexual dimorphism can be manifested in a variety of ways, from the possession of secondary sexual characters to differences in size (Ralls, 1977).

Sexual dimorphism has been associated with a differential investment of energy in growth, reflecting divergent reproductive strategies in the two sexes (Calzada *et al.*, 1997).

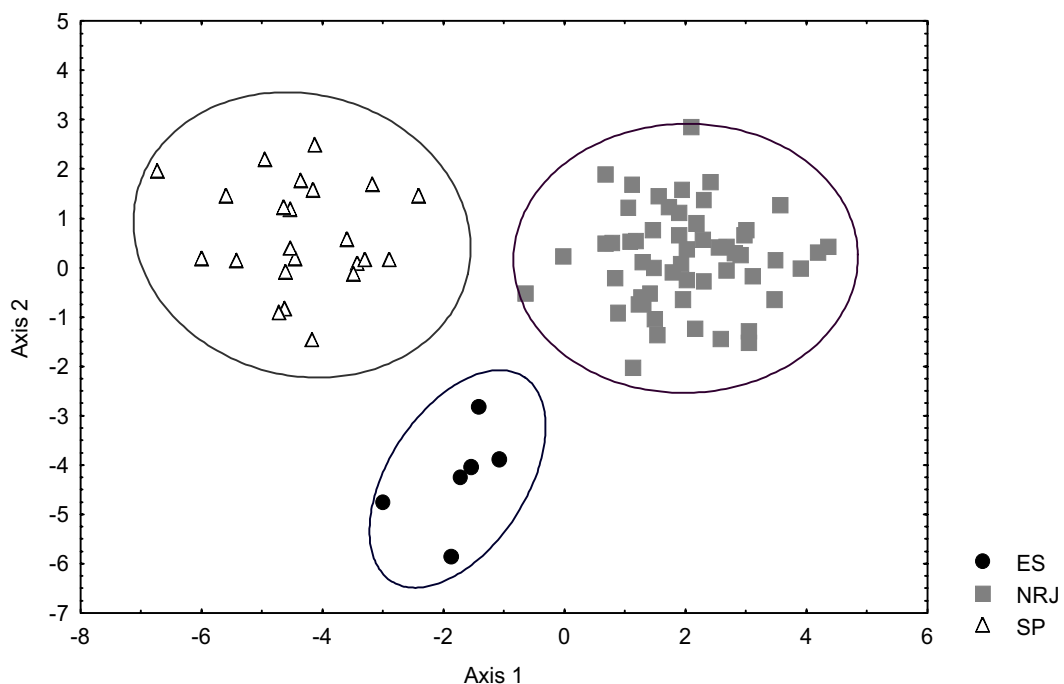


Figure 2 - Axis projection of canonical discriminant analysis for cranial metric variables in franciscanas (*Pontoporia blainvillei*) from Espírito Santo (ES), northern Rio de Janeiro (NRJ) and São Paulo (SP) states, southeastern Brazil (Ellipses represent 80%).

Table 4. Classification function from discriminant analysis of mature male and female franciscanas (*Pontoporia blainvillei*) from northern Rio de Janeiro (NRJ) and São Paulo (SP) states.

Variable ¹	NRJ		Variable ¹	SP	
	male	female		male	female
BL	3.10931	3.62154	BL	9.007913	9.766454
MaDLTF	16.32607	17.63560	CBL	3.888905	4.121325
WPS	7.32019	7.64222	VEHB	15.36025	15.89918
GHFM	8.47198	8.90233			
Constant	-628.29834	-752.21497	Constant	-1716.66	-1929.4

¹Acronyms in Table 1.**Table 5.** Mean, standard deviation (SD) and coefficient of variation (CV) of metric variables for mature male and female franciscanas (*Pontoporia blainvillei*) from São Paulo State.

Variable ¹	Male				Female			
	n	mean	SD	CV	n	mean	SD	CV
BL	13	116.04	5.08	4.77	10	131.50	5.25	3.74
CBL	4	332.75	9.81	4.13	4	369.75	17.50	3.61
LR	4	231.50	13.03	6.09	3	263.87	13.99	3.86
WRB	5	36.50	0.80	4.45	4	38.43	1.62	5.05
WR60	5	17.20	1.21	5.58	4	19.33	0.79	4.89
WLPMx	5	15.30	0.69	6.12	4	15.85	1.72	7.54
WRPMx	5	16.84	0.48	5.97	4	17.68	1.28	5.31
DREN	4	261.50	12.69	5.66	3	299.50	15.90	3.92
GPreOW	4	74.95	2.30	3.56	4	78.50	3.73	4.45
GPostOW	4	85.80	1.67	2.78	4	91.33	5.38	4.63
GWEN	5	20.20	0.89	6.05	4	19.38	1.44	6.80
GWZS	5	99.52	4.03	3.10	4	105.70	5.48	4.59
GWPMx	5	38.50	1.75	5.68	4	40.05	2.91	5.37
GPW	5	84.84	2.50	3.69	3	89.27	0.93	2.05
VEHB	5	65.94	0.54	4.52	3	72.50	4.36	5.04
ILB	5	71.80	1.32	4.34	4	73.45	3.51	5.76
GLLPTF	5	64.86	3.02	4.37	4	69.10	2.53	3.79
GWLPTF	5	37.08	1.81	3.69	4	40.78	5.28	8.72
MaDLTF	4	28.75	2.56	6.80	4	30.73	2.97	8.84
MiDLTF	4	15.85	2.54	11.09	4	18.20	1.59	9.91
DSOC	5	29.14	1.19	6.06	3	30.93	2.39	9.74
LLO	4	24.98	1.34	9.76	4	25.85	2.27	9.87
LALL	5	9.30	2.42	18.60	4	9.38	1.20	12.32
GWIN	4	29.65	1.67	4.95	2	32.15	2.33	7.38
GLLP	0	-	-	-	1	35.20	0.00	6.59
LLTC	5	40.36	1.15	3.91	4	42.35	2.12	4.20
LRTC	5	39.78	0.60	4.57	4	41.15	2.00	4.49
WPS	5	27.80	1.61	7.45	3	29.10	2.01	7.74
LULTR	4	202.25	10.05	6.52	3	225.93	15.76	4.90
LLLTR	4	201.75	9.81	7.21	4	223.95	15.65	5.79
GLLR	4	293.90	14.57	5.81	4	330.75	15.40	4.40
GHLR	5	43.90	1.41	3.25	4	47.38	3.25	5.30
LLMF	5	73.44	2.54	4.07	4	83.20	3.49	3.57
GHFM	5	26.02	0.81	5.41	4	26.55	3.72	9.94
GWFM	5	23.70	0.47	6.94	4	25.38	2.45	10.36
DRIN	4	253.75	12.47	5.11	2	288.50	24.75	5.44

¹Acronyms in Table 1. Body size (BL) was measured in cm and the other variables in mm.

Other possible selective factors are female dominance over males, the reduction of inter-sexual competition for food, more intense competition for some resource, such as food, by females than by males, and the fact that a big mother is often a better mother. The factors are clearly not mutually exclusive: more than one of them may affect a single species (Ralls, 1976). The sexual dimorphism observed in franciscanas might be related to reproductive strategies or availability of resources.

Growth

No differentiation of growth pattern among the functional apparatuses was observed, suggesting that the braincase, breathing-sound and feeding apparatuses present a similar development with age. An exception was observed for the hearing apparatus development in franciscanas from northern Rio de Janeiro State, which presented a late physical

Table 6. Growth parameters obtained by Gompertz model fitted to metric variables-at-age of male franciscanas (*Pontoporia blainvillei*) from Espírito Santo State.

Variable ¹	Asymptotic value	Correction factor	Growth rate constant	Correlation coefficient (<i>r</i>)
BL	116.134 a	-0.709	2.028	0.99
CBL	385.118 c	-0.535	0.348	0.98
LR	272.500 c	-0.251	0.434	0.97
WRB	35.503 b	-2.145	0.490	0.87
WR60	-	-	-	-
WLPMx	15.659 c	-1.350	0.611	0.99
WRPMx	-	-	-	-
DREN	285.709 c	0.061	0.764	0.99
GPreOW	74.688 c	-1.046	0.519	0.99
GPostOW	86.645 c	-0.950	0.771	0.98
GWEN	-	-	-	-
GWZS	-	-	-	-
GWPMx	-	-	-	-
GPW	83.397 c	-2.973	0.321	0.93
VEHB	-	-	-	-
ILB	-	-	-	-
GLLPTF	66.059 c	-1.438	0.422	0.99
GWLPTF	38.280 c	-1.815	0.585	0.91
MaDLTF	30.390 c	-0.814	0.532	0.99
MiDLTF	17.297 d	-0.441	0.385	0.97
DSOC	-	-	-	-
LLO	-	-	-	-
LALL	-	-	-	-
GWIN	-	-	-	-
GLLP	-	-	-	-
LLTC	-	-	-	-
LRTC	-	-	-	-
WPS	-	-	-	-
LULTR	223.816 c	0.257	0.741	0.99
LLLTR	-	-	-	-
GLLR	-	-	-	-
GHLR	-	-	-	-
LLMF	74.992 c	-1.024	0.967	0.98
GHFM	-	-	-	-
GWFM	-	-	-	-
DRIN	271.805 c	0.196	0.847	0.99

¹Acronyms in Table 1. Body size (BL) was measured in cm and the other variables in mm. Asymptotic value attained at 3-years (a), 4-years (b), 5-6-years (c) or 7-years (d).

maturity in comparison to the other functional apparatuses. The early development of the hearing and visual apparatuses observed in the franciscana could be related to the preference of the species for estuarine areas with high turbidity.

The results on growth pattern of body size and cranial characters for franciscanas in the present study do not indicate that there is a clinal variation for the species. Initially, the hypothesis of clinal variation was suggested

by Pinedo (1991) and supported by Ramos *et al.* (2000a) based on data obtained for the extremes of the species geographic distribution. Rosas (2000) and Ramos *et al.* (2000b) presented the first evidence that the variation is not clinal. The asymptotic values for body size in franciscanas from São Paulo (113.3cm for males and 128.9cm for females; Rosas, 2000) were smaller than values obtained for franciscanas from northern Rio de Janeiro (117.1cm for males and 144.7cm for females; Ramos *et al.*,

Table 7. Growth parameter values obtained by Gompertz model fitted to metric variables-at-age of male and female franciscanas (*Pontoporia blainvillei*) from northern Rio de Janeiro State.

Variable ¹	Male				Female			
	Asymptotic value	Correction factor	Growth rate constant	Correlation coefficient (r)	Asymptotic value	Correction factor	Growth rate constant	Correlation coefficient (r)
BL	121.961 a	-0.595	0.881	0.99	140.853 b	-0.361	0.608	0.99
CBL	361.225 c	-0.709	0.593	0.99	422.464 c	-0.396	0.459	0.98
LR	262.950 c	-0.394	0.659	0.99	316.236 d	-0.115	0.505	0.98
WRB	37.137 c	-1.925	0.503	0.98	38.283 c	-1.681	0.599	0.95
WR60	18.172 c	-1.010	0.605	0.98	19.967 c	-0.713	0.733	0.94
WLPMx	16.967 b	-1.610	0.518	0.98	17.247 c	-1.530	0.481	0.77
WRPMx	18.100 c	-1.724	0.828	0.97	18.530 c	-1.577	0.760	0.92
DREN	295.445 c	-0.491	0.633	0.99	350.803 d	-0.207	0.494	0.99
GPreOW	75.559 c	-1.573	0.503	0.96	80.821 d	-1.259	0.416	0.98
GPostOW	91.420 c	-1.608	0.466	0.97	100.177 d	-1.222	0.322	0.99
GWEN	-	-	-	-	-	-	-	-
GWZS	101.642 c	-1.442	0.624	0.99	108.111 c	-1.202	0.491	0.99
GWPMx	40.270 c	-2.244	0.748	0.96	40.680 c	-2.109	0.949	0.93
GPW	86.223 c	-2.498	0.679	0.98	89.244 c	-2.141	0.375	0.98
VEHB	-	-	-	-	-	-	-	-
ILB	-	-	-	-	-	-	-	-
GLLPTF	63.957 c	-1.798	0.595	0.97	68.650 d	-1.426	0.385	0.99
GWLPTF	39.357 c	-2.369	0.462	0.91	42.139 c	-1.723	0.466	0.76
MaDLTF	27.271 c	-1.818	0.646	0.99	29.034 c	-1.428	0.568	0.86
MiDLTF	16.497 c	-1.206	0.429	0.97	18.317 d	-0.827	0.443	0.96
DSOC	30.186 b	-2.751	0.920	0.78	30.472 c	-2.631	0.553	0.90
LLO	-	-	-	-	-	-	-	-
LALL	-	-	-	-	-	-	-	-
GWIN	31.120 c	-2.457	0.732	0.92	34.146 d	-1.632	0.368	0.70
GLLP	28.094 b	-1.744	1.355	0.99	35.989 d	-0.845	0.396	0.85
LLTC	39.709 d	-2.239	0.299	0.99	44.209 e	-1.507	0.224	0.99
LRTC	40.101 d	-2.047	0.269	0.96	43.493 e	-1.507	0.297	0.92
WPS	30.891 d	-1.443	0.357	0.99	31.860 e	-1.262	0.429	0.95
LULTR	228.139 c	-0.342	0.632	0.99	270.760 d	-0.088	0.518	0.99
LLLTR	231.831 c	-0.277	0.618	0.99	279.821 d	-0.042	0.478	0.99
GLLR	336.990 c	-0.444	0.551	0.99	396.424 d	-0.198	0.450	0.99
GHLR	44.207 b	-1.825	1.027	0.99	46.960 c	-1.481	0.674	0.87
LLMF	75.366 b	-1.557	1.187	0.99	81.631 c	-1.220	0.742	0.93
GHFM	-	-	-	-	-	-	-	-
GWFM	-	-	-	-	-	-	-	-
DRIN	283.247 c	-0.453	0.656	0.99	337.130 d	-0.191	0.504	0.99

¹Acronyms in Table 1. Body size (BL) was measured in cm and the other variables in mm. Asymptotic value attained at 4-years (a), 5-years (b), 6-years (c), 7-years (d) or 8-years (e).

2000b) and from Uruguay (133.3cm for males and 153.0cm for females; Kasuya and Brownell, 1979). The differences observed in the asymptotic values and size at birth between the geographic areas in the present study are consistent with these conclusions. Franciscanas may present different characteristics within population stocks independent of latitudinal distribution.

The franciscana also exhibits geographic variation in reproductive strategy. The northern franciscanas

reproduce year round, while southern franciscanas have seasonal reproduction (Harrison *et al.*, 1981; Pinedo *et al.*, 1989; Danilewicz, *et al.*, 2000; Ramos *et al.*, 2000a). The results of the present study suggest that there is a difference in reproductive investment in the northern franciscanas. The variation in resource allocation between somatic and reproductive investment might cause alteration in reproductive periodicity, as well as morphological differentiation (Stearns, 1992).

Table 8. Growth parameter values obtained by Gompertz model fitted to metric variables-at-age of male and female franciscanas (*Pontoporia blainvillei*) from São Paulo State.

Variable ¹	Male				Female			
	Asymptotic value	Correction factor	Growth rate constant	Correlation coefficient (r)	Asymptotic value	Correction factor	Growth rate constant	Correlation coefficient (r)
BL	120.510 a	-0.572	0.747	0.99	134.000 b	-0.373	0.634	0.97
CBL	338.740 c	-0.694	0.614	0.96	383.720 c	-0.436	0.518	0.96
LR	238.020 c	-0.295	0.740	0.94	271.580 b	0.060	0.728	0.94
WRB	35.628 a	-1.838	1.101	0.94	37.804 a	-1.490	0.778	0.90
WR60	17.956 b	-0.744	0.525	0.93	19.182 d	-0.558	0.590	0.87
WLPMx	15.128 a	-1.282	1.399	0.97	15.628 a	-1.159	1.220	0.91
WRPMx	16.703 a	-1.442	1.177	0.98	18.026 a	-1.135	0.847	0.89
DREN	269.694 c	-0.379	0.642	0.97	309.726 d	-0.145	0.606	0.96
GPreOW	74.055 a	-1.402	1.128	0.98	77.587 c	-1.207	0.962	0.92
GPostOW	85.803 a	-1.107	1.399	0.99	89.678 c	-0.974	1.139	0.96
GWEN	-	-	-	-	-	-	-	-
GWZS	101.141 c	-1.411	0.809	0.97	105.924 c	-1.189	0.874	0.90
GWPMx	37.564 a	-2.397	2.972	0.84	39.679 a	-1.901	1.074	0.84
GPW	83.416 a	-2.213	1.570	0.91	88.049 c	-1.805	0.682	0.99
VEHB	-	-	-	-	-	-	-	-
ILB	-	-	-	-	-	-	-	-
GLLPTF	63.727 c	-1.770	0.782	0.91	67.844 c	-1.413	0.623	0.88
GWLPTF	37.037 c	-2.080	0.841	0.87	39.960 d	-1.598	0.348	0.86
MaDLTF	28.942 c	-1.156	0.714	0.92	29.121 c	-1.117	0.759	0.90
MiDLTF	16.781 a	-0.474	1.150	0.96	17.013 a	-0.426	1.286	0.87
DSOC	-	-	-	-	-	-	-	-
LLO	-	-	-	-	-	-	-	-
LALL	-	-	-	-	-	-	-	-
GWIN	29.018 a	-1.991	1.650	0.74	31.908 c	-1.431	0.716	0.96
GLLP	-	-	-	-	-	-	-	-
LLTC	-	-	-	-	41.472 c	-2.266	0.291	0.83
LRTC	38.401 a	-2.540	2.141	0.73	39.581 a	-2.197	1.137	0.87
WPS	27.813 c	-1.654	0.776	0.85	29.788 c	-1.318	0.527	0.91
LULTR	202.771 c	-0.132	0.777	0.96	235.753 b	-0.044	0.627	0.96
LLLTR	202.017 c	-0.164	0.781	0.96	248.303 d	0.050	0.527	0.98
GLLR	301.702 c	-0.434	0.666	0.97	351.913 d	-0.193	0.536	0.97
GHLR	43.438 a	-1.448	1.291	0.98	46.121 c	-1.238	0.727	0.98
LLMF	75.086 c	-1.119	0.872	0.99	82.288 c	-0.858	0.660	0.97
GHFM	-	-	-	-	-	-	-	-
GWFM	-	-	-	-	-	-	-	-
DRIN	256.444 c	-0.392	0.834	0.92	298.455 d	-0.337	0.457	0.98

¹Acronyms in Table 1. Body size (BL) was measured in cm and the other variables in mm. Asymptotic value attained at 4-years (a), 5-years (b), 6-years (c) or 7-years (d).

Table 9. Analysis of variance of the metric variables for areas, for sexes and for interaction between area and sex in franciscanas (*Pontoporia blainvillei*) from southeastern Brazil.

Variable ¹	Area (df 2)			Sex (df 1)			Area * Sex (df 2)		
	MS	F	P	MS	F	P	MS	F	P
CBL	3055.203	14.585	0.00000 ***	19866.435	94.841	0.00000 ***	633.880	3.026	0.05423
LR	3443.958	19.125	0.00000 ***	14807.587	82.232	0.00000 ***	449.976	2.498	0.08873
WRB	5.862	1.936	0.15109	36.807	12.157	0.00081 ***	0.152	0.050	0.95076
WR60	5.813	4.338	0.01635 *	42.157	31.463	0.00000 ***	2.136	1.594	0.20954
WLPMx	12.422	12.553	0.00002 ***	7.444	7.522	0.00755 **	0.991	1.001	0.37198
WRPMx	8.328	10.450	0.00010 ***	8.612	10.806	0.00152 **	0.228	0.286	0.75133
DREN	3689.412	18.463	0.00000 ***	18048.839	90.326	0.00000 ***	446.095	2.232	0.11407
GPreOW	0.313	0.048	0.95238	169.037	26.310	0.00000 ***	13.399	2.085	0.13110
GPostOW	49.015	6.254	0.00292 **	275.755	35.414	0.00000 ***	8.207	1.054	0.35343
GWEN	12.239	15.081	0.00000 ***	6.964	8.581	0.00445 **	2.326	2.867	0.06288
GWZS	55.638	3.750	0.02784 *	317.849	21.426	0.00001 ***	3.938	0.265	0.76750
GWPMx	26.158	10.480	0.00009 ***	18.340	7.347	0.00825 **	0.588	0.235	0.79055
GPW	15.881	2.745	0.07044	67.569	11.680	0.00101 **	10.34857	1.788	0.17393
VEHB	15.787	2.766	0.06908	99.242	17.389	0.00008 ***	29.300	5.134	0.00804 **
ILB	20.487	2.798	0.06700	98.108	13.403	0.00046 ***	4.215	0.575	0.56456
GLLPTF	31.807	6.100	0.00345 **	125.428	24.058	0.00000 ***	4.178	0.801	0.45236
GWLPTF	32.662	8.149	0.00061 ***	50.400	12.575	0.00066 ***	0.758	0.189	0.82796
MaDLTF	20.757	8.380	0.00050 ***	8.450	3.411	0.06852	4.417	1.783	0.17482
MiDLTF	2.469	1.391	0.25479	11.043	6.223	0.01472 *	4.001	2.255	0.11163
DSOC	8.732	2.093	0.13010	0.975	0.233	0.63005	3.200	0.767	0.46770
LLO	0.325	0.043	0.95724	14.437	1.941	0.16743	5.907	0.794	0.45541
LALL	14.329	10.602	0.00008 ***	2.895	2.142	0.14733	0.517	0.382	0.68327
GWIN	20.575	8.359	0.00051 ***	62.903	25.556	0.00000 ***	1.829	0.743	0.47883
GLLP	229.002	28.898	0.00000 ***	24.831	3.133	0.08061	43.599	5.501	0.00582 **
LLTC	3.384	1.447	0.24150	38.299	16.377	0.00012 ***	0.300	0.128	0.87968
LRTC	0.454	0.191	0.82579	41.116	17.364	0.00008 ***	6.784	2.865	0.06298
WPS	10.744	2.998	0.05566	18.420	5.139	0.02615 *	1.438	0.401	0.67073
LULTR	3126.126	18.818	0.00000 ***	11921.692	71.764	0.00000 ***	446.432	2.687	0.07436
LLLTR	3132.618	17.926	0.00000 ***	12277.858	70.260	0.00000 ***	448.675	2.567	0.08319
GLLR	3360.244	12.028	0.00003 ***	19292.210	69.058	0.00000 ***	510.400	1.827	0.16771
GHLR	2.181	0.702	0.49854	60.092	19.347	0.00003 ***	0.269	0.086	0.91704
LLMF	5.372	0.654	0.52252	406.035	49.468	0.00000 ***	8.089	0.985	0.37781
GHEM	73.563	17.406	0.00000 ***	22.198	5.252	0.02461 *	0.453	0.107	0.89840
GWEM	48.571	14.646	0.00000 ***	8.537	2.574	0.11265	3.515	1.059	0.35140
DRIN	4814.680	21.345	0.00000 ***	13831.069	61.318	0.00000 ***	1371.886	6.082	0.00351 **

¹Acronyms in Table 1. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Table 10. Correction factor for sexual differences of franciscanas (*Pontoporia blainvillei*) from Espírito Santo (ES), northern Rio de Janeiro (NRJ) e São Paulo (SP) states.

Variable ¹	Correction factor		
	ES	NRJ	SP
CBL	-36.95	-28.05	-20.45
LR	-31.30	-24.55	-18.10
WRB	-1.45	-1.15	-1.05
WR60	-1.75	-1.30	-0.90
WLPmX	-1.00	-0.45	-0.20
WRPMx	-0.85	-0.45	-0.50
DREN	-35.75	-25.55	-20.30
GPreOW	-3.65	-2.70	-1.45
GPostOW	-4.45	-3.15	-2.35
GWEN	-1.20	-0.35	0.00
GWZS	-4.65	-3.20	-2.90
GWPMx	-1.05	-0.65	-0.90
GPW	-2.10	-0.90	-2.05
VEHB	-1.90	-1.05	-3.00
ILB	-3.10	-1.45	-1.40
GLLPTF	-2.75	-1.75	-2.35
GWLPTF	-1.00	-1.65	-1.55
MaDLTF	0.25	-1.20	-0.80
MiDLTF	-0.60	-1.10	-0.40
DSOC	1.05	-0.10	-0.30
LLO	-0.80	-1.10	-0.35
LALL	-0.80	-0.20	-0.20
GWIN	-2.30	-1.15	-1.35
GLLP	-1.05	-2.25	0.15
LLTC	-1.35	-1.30	-1.10
LRTC	-1.85	-1.45	-0.60
WPS	-0.25	-1.10	-1.20
LULTR	-30.50	-20.85	-15.20
LLTR	-31.70	-20.20	-15.35
GLLR	-37.60	-26.15	-20.65
GHLR	-1.85	-1.40	-1.45
LLMF	-5.60	-3.30	-3.35
GHFM	-1.35	-0.75	-0.70
GWFM	-1.10	-0.70	0.05
DRIN	-34.65	-24.05	-12.20

¹Acronyms in Table 1.

Geographic variation

The geographic variation in cranial morphology observed in the present study confirms the hypothesis that the species has more than two population stocks. The following management subdivision has been proposed by Secchi *et al.* (in press): i) northern population - occurring to the north of Santa Catarina State, Brazil - i.1) from Espírito Santo to northern Rio de Janeiro States (~18°S-22°S) and i.2) from São Paulo to Santa Catarina States (~24°S-29°S); ii) southern population - occurring to the south of Santa Catarina State, Brazil - ii.1) from Rio Grande

do Sul State, south of Brazil to Uruguay (~33°S-34°S) and ii.2) from Argentina (~42°S). The results of the present study support this scheme.

The geographic variation revealed here is consistent with the hypothesis of disjunct distribution in southeastern Brazil. The areas may not overlap (see Figure 2). The hypothesis of a disjunct distribution for the northern population was proposed by Siciliano *et al.* (in press) based on two gaps in the distribution in southeastern Brazil. The authors related these gaps mainly to two factors: lack of fluvial drainage, which would increase the abundance of trophic resources and narrowing of the continental shelf decreasing habitat areas.

The preference of the franciscana for estuarine areas with high turbidity can be related to optimal conditions for feeding (Siciliano and Santos, 1994, Crespo *et al.*, 1998). The franciscana can be considered specialists in trophic terms, obtaining greater success in areas that present favorable conditions for its feeding (Di Benedetto, 2000). The trophic specialization can act to limit the habitat occupied (Crespo *et al.*, 1998).

The franciscana is characteristically coastal, living within 30 nautical miles of the coast and up to depths of 30m (Praderi *et al.*, 1989). Water depth might also be considered a factor limiting its distribution (Secchi and Ott, 2000). Thus, in areas where the continental shelf is wider, the species will have more extensive habitat and, possibly, trophic resource. In contrast, in the area of Arraial do Cabo and southern Espírito Santo State, a narrowing of the continental shelf and an increase in water clarity are present (Szpilman, 1992; Muehe and Valentini, 1998). These factors may cause the gaps in the occurrence pattern of franciscana off the southeastern coast of Brazil (Siciliano *et al.*, in press).

The two gaps observed in franciscana distribution may prevent gene flow, favoring the isolation of populations and perceptible morphologic variation. Variation in body size in cetaceans separated by little geographic distance has been observed in several species, such as the harbour porpoise and striped dolphin (*Stenella coeruleoalba*) (Perrin, 1984; Calzada and Aguilar, 1995; Gao and Gaskin, 1996). The factors that cause this morphological variation may include reproductive isolation due to a fragmentation of the species distribution.

The geographic variation observed in the present study supports the hypothesis of disjunct distribution of the franciscana in southeastern Brazil. Understanding of phenotypic variation is important in the formulation of conservation strategies, particularly in relation to coastal species, which present limitations in the preferred habitat and greater vulnerability to activities such as fishing operations and to pollution (Borobia *et al.*, 1991; Secchi *et al.*, in press). The results of the present study suggest that the franciscana stocks off the southeastern coast of Brazil should be considered distinct for conservation and management actions.

Table 11. Classification function and standard coefficients of the canonical discriminant analysis of franciscanas (*Pontoporia blainvillei*) for three geographic areas, Espírito Santo (ES), northern Rio de Janeiro (NRJ) and São Paulo (SP) states, southeastern Brazil. The bold values indicate the variables that best showed the differences between geographic areas.

Variable ¹	Classification function			Standard coefficients	
	ES	NRJ	SP	Axis 1	Axis 2
CBL	9.36128	8.81962	9.56681	-1.69641	-0.29103
LR	-3.34587	-3.44954	-3.58885	0.25076	-0.51687
WRB	-5.13565	-4.50547	-5.71372	0.32309	-0.03171
WR60	2.96646	5.06677	3.99226	0.21887	0.34952
WLPMx	-31.65259	-31.07853	-33.72588	0.39241	-0.20546
WRPMx	3.55817	5.50679	3.21549	0.32472	0.10803
DREN	5.17386	5.54241	4.72318	1.76706	-0.34615
GPreOW	-0.85402	-1.41388	-0.29933	-0.43360	0.05387
GPostOW	-3.30641	-0.93767	-3.06653	0.96650	0.63492
GWEN	21.10513	18.25035	17.14567	0.10515	-0.65322
GWZS	7.12693	6.29476	7.09740	-0.49968	-0.28220
GWPMx	18.41056	18.06371	19.18782	-0.26710	0.10490
GPW	12.43375	13.40507	13.40743	0.03530	0.48306
ILB	10.08836	9.20894	9.85371	-0.29071	-0.27698
GLLPTF	18.06019	16.63805	18.65688	-0.72102	-0.10445
GWLPTF	-13.02791	-11.41003	-12.66043	0.41476	0.36155
MaDLTF	-8.59163	-9.21444	-9.00667	-0.06277	-0.16221
MiDLTF	-8.16536	-7.58722	-5.59813	-0.37407	0.48450
DSOC	-12.58283	-12.45414	-13.76200	0.39302	-0.27367
LLO	1.89015	1.20410	2.35153	-0.48462	-0.00212
LALL	12.52905	9.00472	12.04576	-0.57872	-0.41231
GWIN	-8.69119	-8.75493	-10.11847	0.30994	-0.28327
LLTC	10.78812	9.28118	12.01493	-0.64408	0.03743
LRTC	-15.09727	-14.03606	-15.48062	0.34907	0.06428
WPS	16.03862	16.80089	17.00652	-0.03437	0.34575
LULTR	-10.08552	-9.82884	-10.23225	0.80851	0.04472
LLLTR	-2.17260	-2.33885	-1.72527	-1.21463	0.54185
GLLR	0.15068	0.22982	0.01483	0.58826	-0.18185
GHLR	3.52408	3.57393	3.88050	-0.07732	0.08447
LLMF	13.35313	12.35335	12.94100	-0.28936	-0.38458
GHFM	6.22894	6.91800	5.37498	0.48388	-0.09698
GWFM	1.23929	0.97979	1.12238	-0.21308	-0.31022
Constant	-2814.83276	-2733.61938	-2779.13721		
Eigenvalue				8.29659	1.50786
Cumulative proportion				0.84621	1.00000

¹Acronyms in Table 1.

Acknowledgements

We thank Jamilce Ribeiro Pedra and Silvana Ribeiro Gomes for help during the collection of data; João Alves de Oliveira of the Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ) and Dr. Mário de Vivo of the Museu de Zoologia, Universidade de São Paulo (USP); Leandro Rabello Monteiro of Universidade Estadual do Norte Fluminense (UENF) for statistical assistance and useful suggestions to improve the manuscript; Fundação Estadual do Norte Fluminense (FENORTE) for a fellowship, and Universidade Estadual do Norte Fluminense (UENF) for institutional support. Oliver Boisseau, William Perrin and Koen Van Waerebeek provided very important suggestions to improve the manuscript.

References

- Afifi, A.A. and Clark, V. (1990) *Computer - Aided Multivariate Analysis*. Second edition, Chapman & Hall, New York, London.
- Borobia, M., Siciliano, S., Lodi, L. and Hoek, W. (1991) Distribution of the South American dolphin *Sotalia fluviatilis*. *Canadian Journal Zoology* 69: 1025-1039.
- Calzada, N. and Aguilar, A. (1995) Geographic variation of body size in the Mediterranean striped dolphin. *Zeitschrift für Säugetierkunde* 60: 257-264.
- Calzada, N., Aguilar, A., Lockyer, C. and Grau, E. (1997) Patterns of growth and physical maturity in the western Mediterranean striped dolphin, *Stenella coeruleoalba* (Cetacea: Odontoceti). *Canadian Journal Zoology* 75:632-637.
- Crespo, E.A., Harris, G. and González, R. (1998) Group size and distributional range of the franciscana, *Pontoporia blainvillei*. *Marine Mammal Science* 14(4): 845-849.
- Danilewicz, D.S., Secchi, E.R., Ott, P.H., and Moreno, I.M. (2000) Analysis of the age at sexual maturity and reproductive rates of franciscana (*Pontoporia blainvillei*) from Rio Grande do Sul, southern Brazil. *Comunicações do Museu de Ciências e Tecnologia, PUCRS* 13: 89-98.
- Di Benedetto, A.P. (2000) *Ecologia Alimentar de Pontoporia blainvillei e Sotalia fluviatilis (Cetacea) na costa Norte do Estado do Rio de Janeiro, Brasil*. Doctoral Thesis. Universidade Estadual do Norte Fluminense, Campos dos Goytacazes. 128pp.
- Gao, A. and Gaskin, D.E. (1996) Geographical variation and sexual dimorphism in metric skull characters among proposed subpopulations and stocks of harbour porpoise, *Phocoena phocoena*, in the western North Atlantic. *Marine Mammal Science* 12(4): 516-527.
- Hamilton, H., Rosemberg, A., Corcuera, J., Monzon, F. and Brownell, R.L. (2000) Secuencias de la region control del ADN mitocondrial de la franciscana, *Pontoporia blainvillei*: comparacion entre poblaciones de Brasil y Argentina. Page 56 in Abstract, IX Reunión de Trabajo de Especialistas en Mamíferos Acuáticos da América del Sur. Buenos Aires.
- Harrison, R.J., Bryden, M.M., McBrearty, D.A. and Brownell, R.L. (1981) The ovaries and reproduction in *Pontoporia blainvillei* (Cetacea: Platanistidae). *Journal of Zoology* 193: 563-580.
- Hersh, S.L., Odell, D.K. and Asper, E.D. (1990) Sexual dimorphism in bottlenose dolphins from the East Coast of Florida. *Marine Mammal Science* 6(4): 305-315.
- Hohn, A.A., Scott, M.D., Wells, R.S., Sweeney, J.C. and Irvine, A.B. (1989) Growth layers in teeth from known age, free-ranging bottlenose dolphins. *Marine Mammal Science* 5(4): 315-342.
- Hohn, A.A., Read, R.J., Fernandez, S., Vidal, O. and Findley, L.T. (1996) Life history of the vaquita, *Phocoena sinus* (Phocoenidae, Cetacea). *Journal of Zoology* 239: 235-251.
- Kasuya, T. and Brownell Jr., R.L. (1979) Age determination, reproduction and growth of the franciscana dolphin, *Pontoporia blainvillei*. *The Scientific Reports of the Whales Research Institute* 31: 43-67.
- Lázaro, M. and Lessa, E.P. (2000) Variacion de la region de control del ADN mitocondrial en franciscanas (*Pontoporia blainvillei*) de la costa Uruguaya. Page 68 in Abstract. IX Reunión de Trabajo de Especialistas en Mamíferos Acuáticos da América del Sur. Buenos Aires.
- Muehe, D. and Valentini, E. (Eds.) (1998) *O litoral do Estado do Rio de Janeiro: uma caracterização Físico-Ambiental*, Fundação de Estudos do Mar - FEMAR, Rio de Janeiro. 99p.
- Norris, K.S. (1961) Standardized methods for measuring and recording data on the smaller cetaceans. *Journal of Mammalogy* 42(4): 471-476.
- Perrin, W.F. (1975) Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. *Bulletin of the Scripps Institution of Oceanography of the University of California* 21: 1-206.
- Perrin, W.F. (1984) Patterns of geographical variation in small cetaceans. *Acta Zoologica Fennica* 172: 137-140.
- Perrin, W.F. and Myrick Jr. A.C. (Eds) (1980) Report of the workshop on Age Determination. In: Age determination of toothed whales and sirenians. *Report of the International Whaling Commission*, 3, 229pp.
- Pinedo, M.C. (1991) *Development and variation of the franciscana, Pontoporia blainvillei*. PhD Thesis - University of California, Santa Cruz. 406pp.
- Pinedo, M.C. and Hohn, A.A. (2000) Growth layer patterns in teeth from the franciscana, *Pontoporia blainvillei*: Developing a model for precision in age estimation. *Marine Mammal Science* 16(1): 1-27.
- Pinedo, M.C., Praderi, R. and Brownell Jr., R. (1989) Review of the biology and status of the franciscana *Pontoporia blainvillei*. Pages 46-51 in Perrin, W.F., Brownell, R.L., Kaiya, Z. and Jiankang, L. (Eds) *Biology and Conservation of the River Dolphins*. Occas. pap. IUCN SSC 3. Gland.
- Praderi, R., Pinedo, M.C. and Crespo, E.A. (1989) Conservation and management of *Pontoporia blainvillei* in Uruguay, Brazil and Argentina. Pages 52-56 in Perrin, W.F., Brownell, R.L., Kaiya, Z. and Jiankang, L. (Eds) *Biology and Conservation of the River Dolphins*. Occas. pap. IUCN SSC 3. Gland.
- Ralls, K. (1976) Mammals in which females are larger than males. *The Quarterly Review of Biology* 51: 245-276.
- Ralls, K. (1977) Sexual dimorphism in mammals: avian models and unanswered questions. *The American Naturalist* 111: 917-938.
- Ramos, R.M.A., Di Benedetto, A.P. and Lima, N.R.W. (2000a) Growth parameters of *Pontoporia blainvillei* and *Sotalia fluviatilis* (Cetacea) in northern Rio de Janeiro, Brazil. *Aquatic Mammals* 26(1): 65-75.
- Ramos, R.M.A., Di Benedetto, A.P., Siciliano, S., Santos, M.C., Zerbini, A.N., Bertozzi, C., Vicente, A., Zampiroli, E., Siqueira, F., De Vivo, M. and Lima, N.R.W. (2000) Informações sobre idade e crescimento de *Pontoporia blainvillei* no litoral sudeste do Brasil Technical Paper WP12 presented to the IV Workshop para a Coordenação da Pesquisa e Conservação da Franciscana, Pontoporia blainvillei, no Atlântico Sul Occidental. 05-09 November. Porto Alegre.
- Ready, A.J. and Tolley, K.A. (1997) Postnatal growth and allometry of harbour porpoises from the bay of fundy. *Canadian Journal of Zoology* 75: 122-130.
- Rosas, F.C.W. (2000) Interações com a pesca, mortalidade, idade, reprodução e crescimento de *Sotalia guianensis* e *Pontoporia blainvillei* (Cetacea, Delphinidae e Pontoporiidae) no litoral sul do Estado de São Paulo e litoral do Estado do Paraná, Brasil. Doctoral Thesis. Universidade do Paraná, Curitiba. 145pp.
- Schnell, G.D., Douglas, M.E. and Hough, D.J. (1985) Sexual dimorphism in spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. *Marine Mammal Science* 1: 1-14.

- Schnell, G.D., Douglas, M.E. and Hough, D.J. (1986) Geographic patterns of variations in offshore spotted dolphins (*Stenella attenuata*) of the eastern tropical Pacific Ocean. *Marine Mammal Science* 2(3): 186-213.
- Secchi, E.R. and Ott, P.H. (2000) A profundidade como um fator determinante da distribuição de toninhas, *Pontoporia blainvillei*, conforme indicado pelos índices de CPUE. Pages 55-57 in UNEP/CMS (Eds) *Report of the Third Workshop for Coordinated Research and Conservation of the Franciscana Dolphin (Pontoporia blainvillei) in the Soutwestern Atlantic*. UNEP/CMS, Bonn.
- Secchi, E.R., Wang, J.Y., Murray, B.W., Rocha-Campos, C.C. and White, B.N. (1998) Population differentiation in the franciscana (*Pontoporia blainvillei*) from two geographic locations in Brazil as determined from mitochondrial DNA control region sequences. *Canadian Journal of Zoology* 76(9): 1622-1627.
- Secchi, E.R., Danilewicz, D. and Ott, P.H. (in press) Applying the phylogeographic concept to identify franciscana dolphin stocks: implications to meet management objectives. *Journal Cetacean Research Management*.
- Siciliano, S. (1994) Review of small cetaceans and fishery interactions in coastal waters of Brazil. *Report of the International Whaling Commission* 15: 241-250.
- Siciliano, S. and Santos, M.C.O. (1994) *Considerações sobre a distribuição da franciscana Pontoporia blainvillei no litoral sudeste do Brasil*. Paper presented in II Encontro de Trabalho sobre a Coordenação de Pesquisa e Conservação da Franciscana, Florianópolis.
- Siciliano, S., Di Benedetto, A.P.M. and Ramos, R.M.A. (in press) A toninha *Pontoporia blainvillei* nos Estados do Rio de Janeiro e Espírito Santo, costa sudeste do Brasil: caracterização dos habitats e fatores de isolamento das populações. *Boletim do Museu Nacional, N. S., Zoologia*, 476: 1-15.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford, University Press, New York.
- Szpilman, M. (1992) *Aqualung Guide to Fishes. A practical Guide to the Identification of Brazilian Coastal Fishes*. Ed. Aqualung. 307pp.
- Zullinger, E.M., Ricklefs, R.E., Redford, K.H. and Mace, G.M. (1984) Fitting sigmoidal equations to mammalian growth curves. *Journal of Mammalogy* 65(4): 607-636.

Received 6 December 2001. Accepted 25 May 2002.