Age and growth of franciscana dolphins, Pontoporia blainvillei (Cetacea: Pontoporiidae) incidentally caught off southern Brazil and northern Argentina

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Age and length data of 291 franciscana dolphins (Pontoporia blainvillei) incidentally captured on the coast of Rio Grande do Sul State (RS), southern Brazil, were used to fit growth curves using Gompertz and Von Bertalanffy growth models. A small sample of franciscanas (N=35) from Buenos Aires Province (BA), Argentina, were used to see if there are apparent growth differences between the populations. Male and female franciscana samples from both areas were primarily (78-85%) <4 years of age. The Von Bertalanffy growth model with a data set that excluded animals <1 year of age provided the best fit to data. Based on this model, dolphins from the RS population reached asymptotic length at 136.0 cm and 158.4 cm, for males and females, respectively. No remarkable differences were observed in the growth trajectories of males and females between the RS and BA populations.

Keywords: franciscana, Pontoporia blainvillei, growth, age estimation, South America, dolphin, Cetacea

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INTRODUCTION

The franciscana dolphin, *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844), is endemic to south-western Atlantic coastal waters, extending from Itaúnas (18°25′S) in Brazil to Golfo San Matias (~42°10′S) in Argentina (Crespo *et al.*, 1998; Siciliano *et al.*, 2002). Its occurrence is well documented due to extensive by-catch in coastal fisheries, especially gillnetting, throughout its range (Pérez Macri & Crespo, 1989; Monzón & Corcuera, 1991; Corcuera, 1994; Secchi *et al.*, 1997; Pinedo & Polacheck, 1999; Di Beneditto & Ramos, 2001; Bertozzi & Zerbini, 2002; Kinas, 2002; Ott *et al.*, 2002; Rosas *et al.*, 2002; Secchi *et al.*, 2003a; Cappozzo *et al.*, 2007). Its distribution is not continuous, with two hiatuses being reported: one in southern Espírito Santo State, and the other between Macaé (southern Rio de Janeiro State) and Ubatuba (northern São Paulo State) (Siciliano *et al.*, 2002).

Pinedo (1991, 1995) proposed the existence of two morphotypes, based on osteological characters: one found to the north (smaller animals) and the other to the south (larger animals) of Santa Catarina State (~27°S). Genetic studies

using individuals sampled from each geographical form supported the existence of at least two genetic populations (Secchi et al., 1998). Recently, Lázaro et al. (2004) suggested the existence of one genetic population encompassing animals from Rio Grande do Sul, Uruguay and Argentina clearly differentiated from animals collected off Rio de Janeiro to the north. Furthermore, the authors found that differences in haplotype frequencies increased with geographical distance. These authors and Ott (2002) also indicated that haplotypic frequencies of samples from Claromecó (in Argentina) were significantly different from the rest of the southern population. Mendez et al. (2007), however, reported that individuals from Claromecó are more similar to those from coastal oceanic areas, including those from Uruguay, than to those from the estuary-influenced Samborombon Bay. Thus, they suggest that ecological forces can be more relevant than geographical distance in determining population structuring, by regulating gene flow.

Barreto & Rosas (2006) found that asymptotic lengths of franciscanas from São Paulo and northern Paraná States were smaller than those found off Rio de Janeiro and Espírito Santo States (Ramos *et al.*, 2000, 2002), suggesting that these differences are not clinal but due to environmental variation. A study combining available information on distribution, population response, genetics and morphometrics revealed that probably more than two populations exist and

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led these authors to propose four Franciscana Management Areas (FMAs sensu Secchi et al., 2003b). FMA I comprises Rio de Janeiro and Espírito Santo States, Brazil; FMA II ranges from São Paulo to Santa Catarina States, Brazil; FMA III includes Rio Grande do Sul State, Brazil and Uruguay; and FMA IV covers the species range in Argentine waters (Figure 1). However, more data are needed in order to precisely describe stock boundaries, especially in FMA IV where data are scarce.

Knowledge of growth patterns is an important part of understanding a species' life history strategy as it describes how individuals allocate resources to growth, reproduction and survival. Indeed, data on age-specific growth and reproductive rates, combined with survival rates, are essential for comparing life history strategies (Chivers, 2002a). Previous reports on growth of franciscanas from Rio Grande do Sul were based on stranded carcasses (Pinedo, 1991, 1995; Barreto & Rosas, 2006) and incidentally captured animals (Walter, 1997). Information about growth of franciscanas from Argentina consists of only some meeting abstracts showing preliminary results on length/age at physical maturity (Corcuera et al., 1990, 1996; Negri et al., 2004). Growth curves have not been published for animals from this area.

Fitting asymptotic sigmoidal growth curves to agedata facilitates growth comparisons at-length provides insights into the functioning of biological systems (Hammil et al., 1995). Among the sigmoidal family of growth curves, Gompertz and Von Bertalanffy models are the most commonly used to fit growth curves in cetaceans, for example, harbour porpoise Phocoena phocoena (Lockyer et al., 2001; Galatius, 2005), bottlenose dolphin Tursiops truncatus (Cockcroft & Ross, 1990; Read et al., 1993; Fernandez & Hohn, 1998; Stolen et al., 2002), Guiana dolphin Sotalia guianensis (Rosas et al., 2003), killer whale Orcinus orca (Clark et al., 2000) and common dolphin Delphinus delphis (Ferrero & Walker, 1995). Both models have been used to model growth of franciscanas but in different studies (Kasuya & Brownell, 1979; Walter, 1997; Ramos et al., 2000; Barreto & Rosas, 2006). However, a complete study on the age and growth of a species requires the application of multiple growth models (Carlson & Baremore, 2005) to determine which best fits the growth trajectory for that species.

The present study describes the age structure and growth of franciscanas incidentally caught off the coast of Rio Grande do Sul, Brazil, using the two growth models and considers the similarity in length at age of specimens incidentally caught off the coast of Buenos Aires, Argentina.

MATERIALS AND METHODS

We examined 291 franciscanas (157 males and 134 females) incidentally caught in fishing nets off the Rio Grande do Sul (RS) coast, southern Brazil (\sim 29°-33°S), from 1994 to 2005, and 35 franciscanas (20 males and 15 females) incidentally killed in nets off the Buenos Aires (BA) coast, Argentina (38°37′-38°47′S), from 1998 to 2007. The franciscana carcasses brought to port by fishermen were either stored on ice or frozen prior to necropsy. Recorded information included sex, weight and total length (TL). Sex was determined externally. TL was measured as a straight line from the tip of the rostrum to the fluke notch (American Society of Mammalogists, 1961).

Teeth were extracted from the centre of the left lower jaw for age estimation and processed following established procedures (Kasuya & Brownell, 1979; Pinedo & Hohn, 2000). Teeth were decalcified in RDO[©] (a commercially available decalcifying agent) and sectioned longitudinally on a freezing microtome at 25-µm thickness. Sections were stained with Mayer's haematoxylin and mounted on microscope slides in 100% glycerin. Age was estimated from the number of growth layer groups (GLGs; Perrin & Myrick, 1980) present in the dentine and cementum without reference to biological data. Although no direct validation exists, indirect evidence supports that one GLG represents one year of age (Kasuya & Brownell, 1979; Pinedo, 1991; Pinedo & Hohn, 2000).

The age structure of females and males from both areas was compared by the non-parametric Kolmogorov–Smirnov (K-S) test (Sokal & Rohlf, 1981).

Two models were fit to length-at-age data from the RS population. Growth curves were not calculated for BA data due to the small sample size. Thus, data from BA population were plotted over RS growth curves in order to visually explore if they roughly follow the same growth trajectory.

The Von Bertalanffy growth model (VBGM) (Von Bertalanffy, 1938) was fit to observed length-at-age data from the RS population following the equation

$$Lt = L_{\infty}(1 - e \exp(-k(t - t_0))),$$

where L_t corresponds to the length-at-age t;

 L_{∞} is the asymptotic length;

e is the base of the natural logarithm;

 t_o is a parameter for a better fit of the curve and represents the theoretical age when the animal's length equals zero; and k is a parameter of the curve that determines how fast the animal reaches L_{∞} .

The Gompertz growth model (GGM) (Ricker, 1975) was:

$$L(t) = L_{\infty}(\exp(-b\exp(-k)))$$

Growth equations were calculated separately for males and females due to sexual dimorphism in total length (Kasuya & Brownell, 1979; Pinedo, 1995). All growth-model parameters were estimated using the non-linear iterative Quasi-Newton method. The goodness-of-fit of each model was assessed by examining residual sum of squares (SQ), coefficient of determination (r^2), the level of significance (P < 0.05) and standard residual analysis.

RESULTS

Age

Franciscanas from RS ranged from 0 to 17 years old while animals from BA ranged from 0 to 13 years old. The oldest individuals in both areas were males. In BA, it was a 13 years-old male. In RS, it was the oldest male yet identified at 17 years old. The animal was >140 cm in total length (it could not be precisely measured because its rostrum was broken) and it weighed 29.1 kg.

Age distributions of males and females from both areas were primarily (78 to 85%) <4 years of age (Figure 2). The

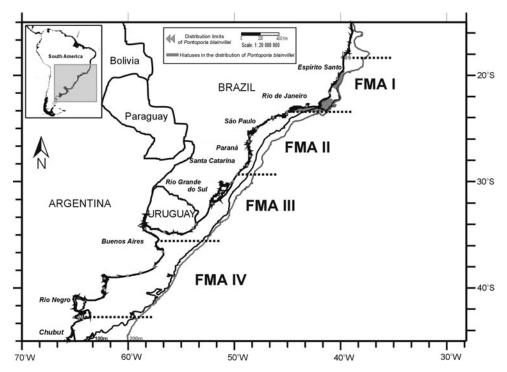


Fig. 1. Distribution of the franciscana, Pontoporia blainvillei and Franciscana Management Areas (FMA I-IV) (adapted from Secchi et al., 2003a).

modal age was 1 year in both sexes and areas (Table 1). There were no significant differences (K-S tests, P > 0.05) in age distributions between BA and RS including all individuals from each area, and for males and females separately. Male age distribution was not significantly different from females' in BA or in RS (K-S test, P > 0.05).

Growth

Total length of RS females and males ranged from 75 to 171 cm and from 76 to 147 cm, respectively. Female franciscanas from BA ranged from 73 to 158 cm in length whereas males ranged from 85 and 141 cm. The mean lengths-at-age between areas could not be tested due to the small sample

size of the BA data set. Lengths-at-age for franciscanas from BA were consistent with those from RS (Figure 3).

The VBGM and GGM models provided growth curves with a similar fit for males and for females from RS (VBGM and GGM: $\rm r^2=0.63$ and 0.48, for females and males, respectively) with similar estimates of asymptotic length. These two models, however, also provided similar but unrealistic 'lengths at birth' (i.e. predicted length at age zero) (109 and 104 cm for females and males, respectively). As a result, we re-fit the models excluding individuals less than 1 year old. No differences in asymptotic lengths were obtained with these new models (P > 0.05), and $\rm r^2$ values were almost the same. However, the sum of and trends in residuals indicated that the VBGM had a better fit to this new set of data

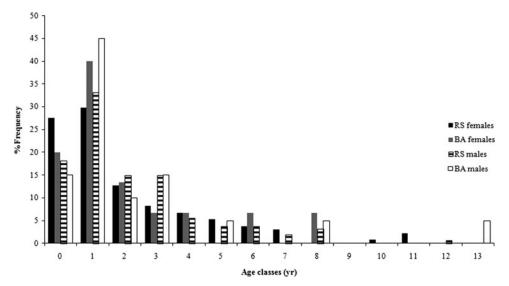


Fig. 2. Age distribution of franciscanas, Pontoporia blainvillei, incidentally captured from Rio Grande do Sul, Brazil (RS) and Buenos Aires, Argentina (BA).

Table 1. Sample sizes in each age-class of *Pontoporia blainvillei* from Rio Grande do Sul, Brazil (RS) and Buenos Aires, Argentina (BA), incidentally caught from 1994 to 2008. Values in parentheses are percentage of the total number of samples.

Age	RS			BA		
	Females	Males	Total	Females	Males	Total
0-0.9	37 (28%)	29 (18%)	66 (22%)	3 (20%)	3 (15%)	6 (17%)
1-1.9	40 (30%)	53 (33%)	93 (32%)	6 (40%)	9 (45%)	15 (43%)
2-2.9	17 (13%)	24 (15%)	41 (14%)	2 (13%)	2 (10%)	4 (11%)
3-3.9	11 (8%)	24 (15%)	35 (12%)	1 (7%)	3 (15%)	4 (11%)
>4.0	29 (21%)	30 (19%)	59 (20%)	3 (20%)	3 (15%)	6 (18%)

(Table 2). Predicted values of length-at-age are presented in Table 3. No remarkable differences were observed in length-at-age for males and females from RS and BA (Figure 3).

Asymptotic length for females (158.40 cm) was greater than for males (135.97 cm) (t-test, P < 0.0001). Comparisons among predicted lengths-at-age in females resulted in significant differences between ages 1, 2, 3 and 4 (t-test, P < 0.05). However, predicted lengths between ages 4, 5, 6, 7 and 11 were not significantly different (t-test, P > 0.05). In males, we found significant differences in predicted lengths between ages 1, 2 and 3 (t-test, P < 0.05). Predicted lengths between ages 3 and older were not significantly different (t-test, t > 0.05). Approximate growth rates calculated as the difference in predicted lengths between two consecutive age-classes were plotted to compare the trends in females and males (Figure 4). These trends also suggest an extended period of growth for females.

DISCUSSION

Age distribution

More than 70–80% of the captures involved juveniles, as previously demonstrated in other studies on franciscana from several locations (Kasuya & Brownell, 1979; Corcuera *et al.*, 1994; Ramos *et al.*, 2000; Rosas *et al.*, 2002; Secchi *et al.*, 2003a; Danilewicz *et al.*, 2004) as well as for other small cetacean species such as harbour porpoises (Read & Hohn, 1995), Hector's dolphins (Slooten, 1991) and vaquitas (Hohn *et al.*,

1996). Nevertheless, the sample also included the oldest male (17 years) yet reported. The previous maximum observed age for males was 16 years (Kasuya & Brownell, 1979). This age distribution could represent the real structure of this population following many years of high levels of incidental mortality or it could be a result of the incidental captures being biased towards immature animals due to behavioural differences of young animals, making them more vulnerable to incidental catches. However, the stable age structure of the population is needed to confirm if the age distribution of this by-caught sample is a biased one of the true population age structure. Age-specific survival rates (Barlow, 1985; Barlow & Boveng, 1991) have been used to estimate stable age distributions (Barlow & Hohn, 1984; Chivers, 2002b). No information of an unexploited population of franciscanas is available to generate unbiased survival rates, however, and so the stable age structure of the franciscana remains unknown, as is the case of many other species (Chivers, 2002b).

Growth

Our estimates of asymptotic lengths using the VBGM model for franciscana dolphins incidentally caught off RS were higher than those reported by Barreto & Rosas (2006) for a smaller sample of individuals stranded along RS coast (females: 146.3 cm, N = 48; males:129.8 cm, N = 59). In addition, Walter (1997) estimated L_{∞} for a subsample of the data used in this work. Her estimates of asymptotic lengths were 138.4 cm for males and 161.9 cm for females which were slightly larger, but still similar to the current results, considering the error in the asymptotic lengths from this study. Techniques (e.g. age estimation), in both cases, were similar to ours. However, no statistical comparison was possible as those authors did not provide error measures for the estimated parameters. Thus, at this time, it is not possible to determine whether apparent differences in asymptotic length between the current study and that of Barreto & Rosas (2006) are real.

As pointed out by Hammill et al. (1995), the choice of the growth model is less critical if the conclusions reached by a study are biologically robust. Age and growth parameters from longitudinal data from captive animals (Clark et al., 2000) or from a long-term study of identified individuals (Read et al., 1993) may provide significant insight into life

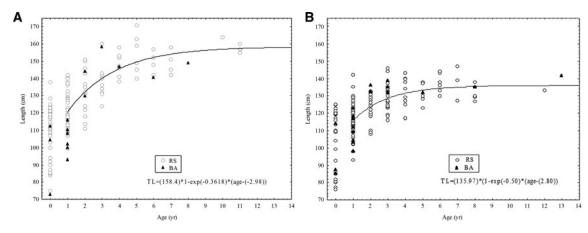


Fig. 3. Growth curves of female (A) and male (B) franciscana, *Pontoporia blainvillei*, from Rio Grande do Sul, southern Brazil (RS). Data from individuals from Buenos Aires, Argentina (BA) are plotted over the curve.

Table 2. Parameters values from the Von Bertalanffy (VBGM) and Gompertz growth models (GMM) fit to age-at-length data of male and female franciscanas, *Pontoporia blainvillei*, from Rio Grande do Sul, southern Brazil. Two set of samples were analysed: one with all data and one which excluded animals <1.0 year of age. TL, asymptotic length (cm); k, growth constant; t_o, theoretical age at which the length of the animal is zero; SQ, residual sum of squares; r², the variance in the data explained by the model. Values in parentheses are standard errors of the estimated parameters.

	TL ∞	k	t _o	SQ	r ²	N
Females			·			
VBGM						
All data	161.71 (6.17)	0.28 (0.07)	-3.98(0.78)	18401.38	0.63	134
<1 year excluded	158.40 (5.03)	0.36 (0.11)	-2.98 (0.98)	10046.12	0.61	97
GGM			- , - ,			
All data	160.16 (5.40)	0.38 (0.03)	0.34 (0.07)	18354.71	0.63	134
<1 year excluded	157.80 (4.66)	0.40 (0.03)	0.40 (0.03)	10038.65	0.61	97
Males						
VBGM						
All data	136.64 (3.11)	0.44 (0.10)	-3.24(0.78)	15596.75	0.48	156
<1 year excluded	135.97 (2.77)	0.50 (0.16)	-2.80 (1.08)	8380.75	0.45	130
GGM						
All data	136.27 (2.92)	0.26 (0.02)	0.50 (0.11)	15581.97	0.48	156
<1 year excluded	135.85 (2.66)	0.27 (0.03)	0.53 (0.16)	8373.93	0.45	130

history, including 'real' growth trajectories. In the case of franciscanas, as in many other cetaceans, no such studies have been conducted thus far. Therefore, all studies have relied on cross-sectional data. As summarized by Leberg *et al.* (1989), such data show some intrinsic biases and errors, all of which typically occur in franciscana data. As pointed out earlier, stranding and by-catch data are very unlikely to be a random sample of the population. In addition, substantial variation in length-at-age data within age-classes, especially in earlier ages, was observed in this as well as in other

Table 3. Length-at-age (cm) of franciscanas, *Pontoporia blainvillei*, from Rio Grande do Sul, Brazil (RS). Predicted values are derived from Von Bertalanffy growth models fit to a data set that excluded animals <1 year of age. Age o animals are from o – o.9 years of age.

Age	Sex	N	Range	Mean (SE)	Predicted
0	Female	37	75-138	110 (1.96)	
	Male	26	76-125	105 (2.01)	
1	Female	40	99-142	121 (1.89)	121
	Male	53	93-142	116 (1.41)	116
2	Female	17	111-151	132 (2.89)	132
	Male	24	108-132	122 (2.09)	124
3	Female	11	124-160	137 (3.60)	140
	Male	23	116-146	130 (2.13)	129
4	Female	9	138-158	148 (3.98)	146
	Male	9	117-143	132 (3.41)	131
5	Female	7	140-171	155 (4.51)	149
	Male	6	123-138	131 (4.18)	134
6	Female	5	142-157	148 (5.34)	152
	Male	6	130-144	137 (4.18)	134
7	Female	4	142-158	149 (5.97)	154
	Male	3	127-147	138 (5.91)	135
8	Female	0			
	Male	5	127-138	132 (4.58)	135
9	Female	0			
	Male	0			
10	Female	1	164		157
	Male	0			
11	Female	3	155-160	157 (6.89)	157
	Male	0			
12	Female	0			
	Male	1	133		136

franciscana studies (Kasuya & Brownell, 1979; Pinedo, 1991; Walter, 1997; Ramos et al., 2000; Barreto & Rosas, 2006). It is also typical for many other cetaceans such as bottlenose dolphins, Tursiops truncatus (Read et al., 1993; Stolen et al., 2002), harbour porpoises, Phocoena phocoena (Lockyer et al., 2001), humpback whales, Megaptera novaeangliae (Stevick, 1999), Dall's porpoises, Phocoenoides dalli (Ferrero & Walker, 1999) and short-beaked common dolphins, Delphinus delphis (Danil & Chivers, 2007). This variation potentially affects the predicted length-at-age and, consequently, the fit of the growth curve (Moreau, 1987).

The present study provides the first insight into a possible somatic growth trajectory for the BA population inasmuch as it seems similar to franciscanas from RS. Because life history traits (i.e. growth rates, size and age at sexual maturity) vary among franciscana populations from different management areas (Secchi et al., 2003b), growth parameters might also be expected to differ accordingly. Although franciscanas from RS and BA are currently defined to belong to two different management stocks (FMA III and FMA IV respectively), it seems that both populations may follow the same somatic growth trajectories. Increased sample sizes from BA are needed in order to fit a growth curve. The evidence for

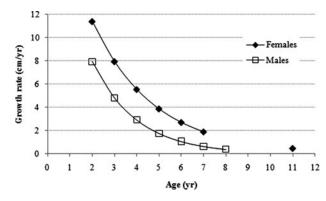


Fig. 4. Rates of growth in length of female and male franciscanas (*Pontoporia blainvillei*) from Rio Grande do Sul, Brazil (RS), calculated from predicted lengths-at-age derived from Von Bertalanffy growth models fit to a data set that excluded animals <1 year of age.

splitting franciscanas from Argentina, Uruguay and Rio Grande do Sul (southern Brazil) into two management stocks was considered weak (Secchi *et al.*, 2003b), so the addition of precise information on growth parameters might help to better define whether or not these management areas should be split.

Information on patterns of growth is available for the other two management stocks (Ramos et al., 2000; Barreto & Rosas, 2006). Results from our study differed markedly from those of Ramos et al. (2000) for northern Rio de Janeiro (FMA I) and Barreto & Rosas (2006) for southern São Paulo/Paraná (FMA II), although no statistical test was possible as those authors fail to provide any measure of parameter error. Ramos et al. (2000) reported asymptotic lengths of 117.1 cm for males (N = 39) and 144.7 cm for females (N = 43). Barreto & Rosas (2006) indicated that asymptotic lengths in FMA II are even smaller (113.3 cm, N = 23 and 129.1 cm, N = 18, for males and females, respectively). These differences in asymptotic lengths among franciscana dolphins are not clinal and, therefore, might have resulted from a variety of factors beyond environmental conditions, including historical genetic characteristics (Ramos et al., 2000).

This study reported asymptotic somatic lengths of franciscanas from the RS population of FMA III, based on a greater sample size than previous published works, and demonstrated that individuals from this population attain greater sizes than animals from the two northernmost management units. Asymptotic length values from the BA population in FMA IV could not be calculated due to the small sample size from this southernmost area but the lengths-at-age for the small sample available suggest that they may be a similar size to the RS animals. Further studies in this area should put effort on increasing sample sizes in order to get accurate somatic growth parameters.

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