

REPRODUCTION OF FEMALE FRANCISCANA (*PONTOPORIA BLAINVILLEI*) IN RIO GRANDE DO SUL, SOUTHERN BRAZIL

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Abstract – In this paper, the reproductive biology of female franciscanas (*Pontoporia blainvillei*) is described based on a sample of 97 individuals collected in Rio Grande do Sul, southern Brazil. Data were collected from dolphins incidentally by-caught by the commercial fleet of Rio Grande and Tramandaí or stranded in the northern coast of Rio Grande do Sul. Age was estimated by counting the growth layer groups present in the dentin and cementum of the teeth. The female reproductive status was determined through the analysis of the ovaries, mammary glands and uterus. The large majority of the recorded ovulations occurred in the left ovary (88%). There was no evidence that the corpus luteum (CL) increases its size as gestation progresses, and there is a considerable individual variation in CL size in females of different stages of pregnancy. The reproduction of the franciscana is markedly seasonal and the species present a typical birth-pulse pattern in Rio Grande do Sul. Births begin abruptly in October and decrease gradually until February. Length and weight at birth was estimated at 73.4cm and 6.1kg, respectively, and the gestation period lasts 11.2 months. Mating and conception should occur between November and March. Sexual maturity in females is attained between 2 and 5 years. Estimation of mean age at sexual maturity was calculated as 3.7 years (CI 95%=3.0–4.4 years) by the DeMaster method and 3.5 years by the logistic equation. Length and weight at sexual maturity were 138.9cm (CI 95%=132.8–145.1) and 32.8kg (CI 95%=29.9–35.7), respectively. Annual pregnancy rate in Rio Grande do Sul was estimated to be 0.66, with a calving interval of 1.5 years. Due to its low age at sexual maturity, short calving interval and brief lifespan, the franciscana is one of the cetacean species with the fastest life history traits. There is no evidence of reproductive senescence and franciscanas seem to remain reproductively active throughout life.

Resumo – Neste trabalho a biologia reprodutiva das fêmeas de franciscanas (*Pontoporia blainvillei*) é descrita com base em uma amostra de 97 indivíduos coletados no Rio Grande do Sul, sul do Brasil. Os dados foram obtidos de animais acidentalmente capturados pela frota comercial de Rio Grande e de Tramandaí ou encalhados no litoral norte do Rio Grande do Sul. A idade foi estimada através da contagem dos grupos das camadas de crescimento (“growth layer groups”) presentes na dentina e no cemento dos dentes. O estado reprodutivo das fêmeas foi determinado através da análise dos ovários, glândulas mamárias e útero. A maioria das ovulações registradas ocorreram no ovário esquerdo (88%). Não foi encontrada nenhuma evidência de que o corpo lúteo (CL) aumente de tamanho a medida que a gestação progride, havendo uma grande variabilidade individual no tamanho do CL em fêmeas de diferentes estágios de gestação. A reprodução da franciscana é caracteristicamente sazonal, apresentando um típico padrão de nascimentos em pulso no Rio Grande do Sul. Os nascimentos iniciam abruptamente em outubro e diminuem gradualmente até fevereiro. O tamanho e peso médio de nascimento foi estimado em 73.4cm e 6.1kg, respectivamente, e o período de gestação dura 11.2 meses. O acasalamento e a concepção devem ocorrer entre os meses de novembro e março. A maturidade sexual nas fêmeas é atingida entre os 2 e 5 anos de idade. A idade média de maturidade sexual foi estimada em 3.7 anos (IC 95%=3.0 – 4.4 anos) através do método de DeMaster e 3.5 anos através da equação logística. O comprimento e peso médio de maturidade sexual é de 138.9cm (IC 95%=132.8–145.1) e 32.8kg (IC 95%=29.9–35.7), respectivamente. A taxa de prenhez anual foi estimada em 0.66, com um intervalo reprodutivo de 1.5 anos. Nenhuma evidência de senescência reprodutiva foi encontrada, sugerindo que as franciscanas continuem reprodutivamente ativas até o final da vida.

Keywords: Franciscana, *Pontoporia blainvillei*, reproduction, life history, southern Brazil.

Introduction

The franciscana (*Pontoporia blainvillei*) is a dolphin endemic to the coastal waters of the Southwestern Atlantic Ocean. Its distribution ranges from Golfo Nuevo (42°35'S; 64°48'W), Chubut Province, Argentina (Crespo *et al.*, 1998) to Itaúnas (18°25'S; 30°42'W), Espírito Santo, southeastern Brazil (Siciliano *et al.*, 2002) (Figure 1).

The franciscana is susceptible to incidental catches in gillnets and trammel nets throughout most of its range (e.g. Praderi *et al.*, 1989; Ott *et al.*, 2002; Secchi *et al.*, 2003). The species has been considered the most impacted small cetacean in the Southwestern Atlantic Ocean (Pinedo and Barreto, 1997; Secchi *et al.*, 2002).

In the Rio Grande do Sul coast, southern Brazil, this

species has been experiencing an intense bycatch in gillnets for at least three decades (Secchi *et al.*, 1997; Moreno *et al.*, 1997; Ott, 1998; Ott *et al.*, 2002). The annual mortality of franciscanas in this region was estimated to be ranging from several hundreds up to around a thousand individuals (Secchi *et al.* 1997; Ott, 1998; Ott *et al.*, 2002). The estimated bycatch rates are likely unsustainable (Secchi, 1999; Secchi *et al.*, 2003). In this sense, it was agreed by the participants of the Fourth Workshop for the Coordinated Research and Conservation of the Franciscana Dolphin (*Pontoporia blainvillei*) in the Western South Atlantic (Porto Alegre, 2000) that the franciscana should be classified as Vulnerable (VU) instead of Data Deficient (DD) in the IUCN Red List of Threatened Species (Secchi *et al.*, 2002).

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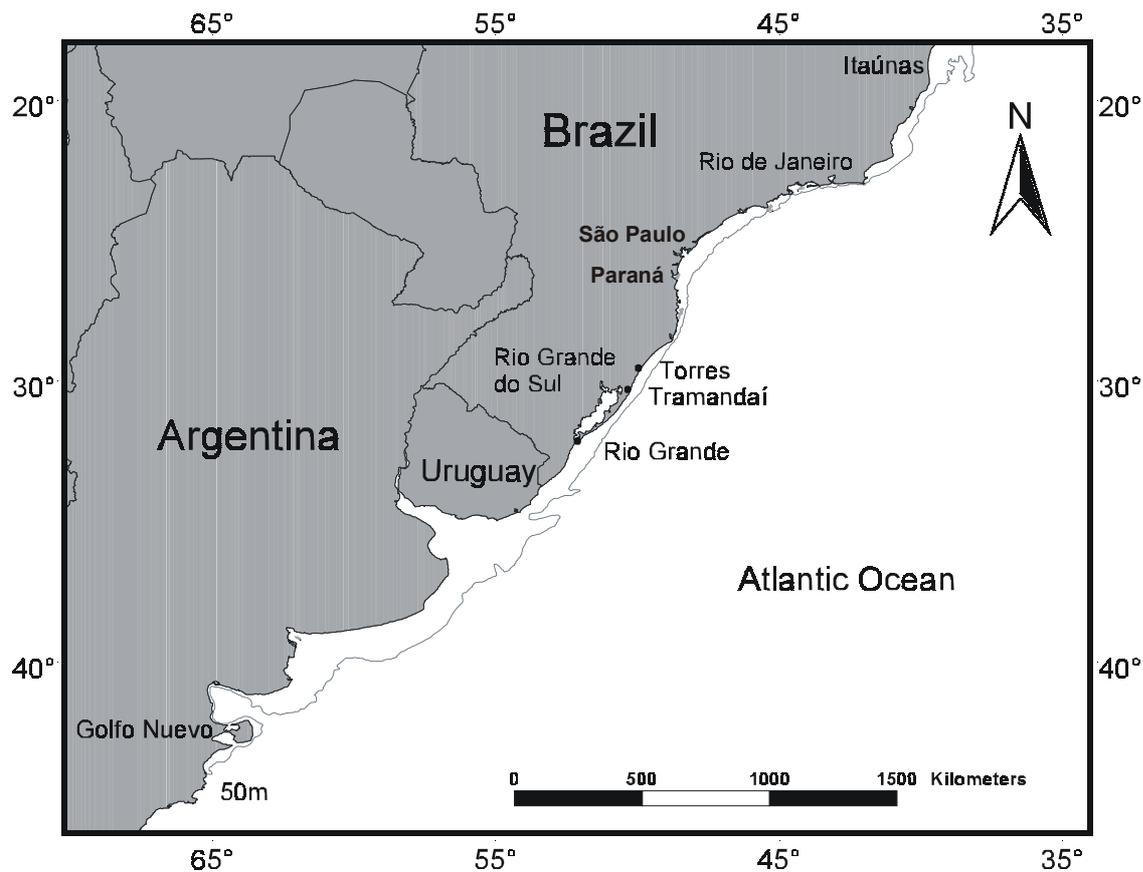


Figure 1. Map showing the distribution of franciscana, *Pontoporia blainvillei*, from Itaúnas, southeastern Brazil, to Golfo Nuevo, Argentina.

Reproductive studies of the franciscana are restricted to some localities of the species' range: Uruguay (Kasuya and Brownell, 1979; Harrison *et al.*, 1981), Rio Grande do Sul (Danilewicz, 2000; Danilewicz *et al.*, 2000; Danilewicz *et al.*, in press), southern coast of São Paulo and Paraná (Rosas and Monteiro-Filho, 2001) and Rio de Janeiro (Ramos, 1997; Ramos *et al.*, 2000). The first estimates of pregnancy rates and age at sexual maturity for female franciscanas off southern Brazil were published by Danilewicz *et al.* (2000), studying a sample of 50 animals from Rio Grande do Sul. The objective of this study was to describe the reproductive biology of female franciscanas from Rio Grande do Sul, yielding new estimates of age at sexual maturity and pregnancy rates based on a larger sample of animals. Furthermore, information on ovary characteristics, ovulation and mating time, gestation period, fetal growth, size at birth, and reproductive senescence is presented for franciscanas from this region.

Material and Methods

Sampling procedures

Data and samples collected from 97 specimens incidentally caught or stranded along the Rio Grande do Sul coast in the period 1992-1998 were used for the analysis. The sampling of incidentally caught animals was carried out

through the monitoring of the gillnet fishing fleet operating from Rio Grande (32°04'S; 52°04'W) and Tramandaí/Imbé (29°58'S; 50°07'W). Stranded dolphins were sampled from systematic beach surveys conducted in an area of an extension of 270km of sandy beaches, between Torres (29°19'S, 49°43'W) and Lagoa do Peixe (31°15'S, 50°54'W). Not all information could be collected from each carcass, so sample sizes vary between parameters. Standard length (n=97) was measured following the guidelines established by the American Society of Mammalogy (1961). The animals were weighed (n=81) and teeth were extracted and preserved dried or in 70% alcohol. Ovaries were removed and fixed in 10% formalin. The mammary glands were examined to determine whether a female was lactating or not. The uterus was carefully examined for the presence of a fetus; particularly when a corpus luteum was observed in one of the ovaries. The length and mass of the fetuses were also measured.

Age determination

Age estimates were obtained from counts of growth layer groups in thin, longitudinal sections of teeth (n=72). Franciscana teeth were decalcified in 5% nitric acid or in RDO (a commercial acid) and sectioned on a freezing microtome. Sections 15-20µm thick were stained with Mayer's hematoxylin and mounted on microscope slides

in Canadian balsam or in glycerin. Poor and off-center sections were discarded in favor of new preparations. Three readers counted the number of growth layer groups in the dentine and cementum independently. When estimates from the readers differed, the sections were reexamined together and agreed on a best estimate. In this paper, one GLG is considered to represent one year of age (Kasuya and Brownell, 1979; Pinedo, 1991; Pinedo and Hohn, 2000).

Reproduction

The ovaries were separated from the remains of the uterine horn and measured separately. After that, ovaries were examined externally for recording the presence or absence of corpus luteum, corpus albicans, and the largest follicles. To assure that all corpora resulting from an ovulation were recorded, the ovaries were sliced by hand to obtain sections 1-3mm thick. The largest corpora and follicles were measured in three planes and the arithmetic mean of these measurements was called mean diameter.

The determination of the dolphin reproductive status followed the terminology recommended by the International Whaling Commission (Perrin and Donovan, 1984). Females with no corpora lutea (CL) or albicantia (CA) in the ovaries were classified as sexually immature. Females with at least one CL or CA in one ovary, denoting a past ovulation, were classified as sexually mature. Females were considered lactating if milk was detected in the mammary glands and the presence of a fetus in the uterus was used as criterion of pregnancy.

Gestation period and length at birth

Gestation period was estimated using the method of Huggett and Widdas (1951). This method utilizes the empirical concept that fetal growth in length is directly related to the gestation period and it is divided in two phases: a brief period of curvilinear growth (t_0) and a posterior period of linear growth until birth. The duration of t_0 can be derived from the equation provided by Calder (1982):

$$t_0 = 7.25 M^{0.19} \quad \text{equation [1]}$$

where M is the mean weight at birth (in grams). The linear phase is estimated applying the linear regression that describes the fetal growth.

To estimate the length at birth for the franciscanas, the mean length of the neonates collected only in October was calculated, since this is the month when births begin in the study region. Neonates were arbitrarily defined as animals smaller than 95.0cm long, considering the length of the largest recorded franciscana fetuses.

Attainment of sexual maturity

Mean age at sexual maturity (ASM) was estimated using two different methods: (A) the DeMaster method (1978) and (B) the age where 50% are mature as fitted by a logistic regression.

The DeMaster (1978) equation computes the mean as

$$ASM = \sum_{a=j}^k a (f_a - f_{a-1}) \quad \text{equation [2]}$$

where f_a is the fraction of sexually mature females with age a , j and k are the ages of the youngest sexually mature and the oldest sexually immature female, respectively.

The variance of the DeMaster method estimate is calculated as

$$\text{var (ASM)} = \sum_{a=j}^k [(f_a (1 - f_a) / N_a - 1)] \quad \text{equation [3]}$$

where N_a is the total number of animals aged a .

The logistic regression approach fits a sigmoid curve, representing the probability that a franciscana of age a is sexually mature, to the distribution of sexually mature and immature animals by age as

$$Y = 1 / (1 + e^{-x(b+a)}) \quad \text{equation [4]}$$

where x is the age of the dolphin, b is the slope of the regression and a is the intercept. To obtain the age when 50% of the animals are sexually mature ($Y=0.5$), the last equation is simplified as $ASM = -a/b$.

Mean length and weight at sexual maturity was also estimated by means of the DeMaster (1978) method, substituting age for length and weight, respectively. The method was slightly modified, as suggested by Ferrero and Walker (1993), and is represented as

$$LSM = \sum_{Cmin}^{Cmax} L (f_t - f_{t-1}) \quad \text{equation [5]}$$

where $Cmax$ is the length/weight class of the largest/heaviest sexually immature animal, $Cmin$ is the length/weight class of the smallest/lightest sexually mature animal, L is the lower value of the length/weight class t , and f_t is fraction of mature animals in the length/weight class t . The specimens were pooled in length and weight intervals of 4 cm and 4 kg, respectively.

The estimated variance of this method is also modified and is calculated as

$$\text{var (MS)} = w^2 \sum_{Cmin}^{Cmax} [(f_t (1 - f_t) / N_t - 1)] \quad \text{equation [6]}$$

where N_t is the number of specimens in the length/weight class t , and w in the interval width.

Annual pregnancy rate

The annual pregnancy rate (APR) is expressed as the proportion of sexually mature females that were pregnant adjusted by the gestation time in years (Perrin and Reilly, 1984).

The approximate variance in APR was estimated by

$$\text{var (APR)} = APR (1-APR) / n \quad \text{equation [7]}$$

where n is the number of reproductive females in the sample. The calving interval was calculated as the reciprocal of the pregnancy rate (Perrin and Reilly, 1984):

$$CI = 1 / APR \quad \text{equation [8]}$$

Ovulation time

The following criteria were utilized to detect a recent ovulation and to determine the ovulation time, as suggested by Harrison *et al.* (1981):

- a) Presence of a recently ruptured follicle or a CL in early development;
- b) Presence of a developed CL in a female carrying no embryo or fetus or with a distended uterus.

Results

Ovary characteristics

The weight of the ovary ranged from 0.08 to 1.25g in immature (mean=0.33g) and from 1.07 to 9.5g in mature females (mean=4.9g). The relationship between ovary weight and standard length in immature and mature animals is presented in Figure 2.

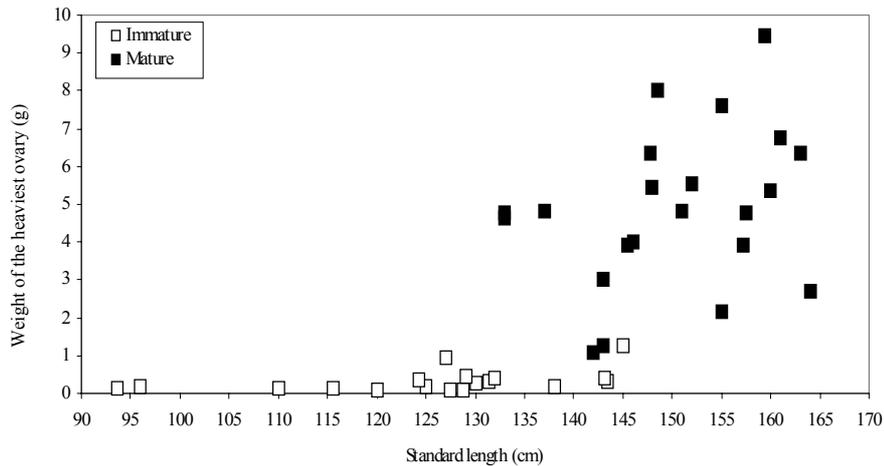
No difference was detected between the weight of the right and left ovary in immature females ($t=-0.31$;

$d.f.=24$; $P=0.76$). Nevertheless, the left ovary is heavier in 89% of the mature animals, and this difference is significant ($t=-6.16$; $d.f.=23$; $P>0.00001$). This is the reflection of the higher number of corpora present in the left ovary (88%). The majority of females (71%) possessed corpora only in the left ovary.

The mean diameter of the CLs not associated with pregnancy (mean=13.5mm) was significantly smaller than the one associated with pregnancy (mean=19.0mm) ($t=2.87$, $d.f.=4$, $P=0.045$). Nevertheless, it was not possible to distinguish a gravid from a non-gravid CL based only on its morphology or size, as pointed out in several studies (e.g. Benirschke *et al.*, 1980, Iwasa and Atkinson, 1996).

There is no evidence that the CL increases its size as gestation progresses. Although the slope of the linear regression between mean diameter of CL and fetal length is slight positive (Figure 3), it is not significantly different from 0 ($b=0.071$; CI 95%= -0.066 to 0.21; $r^2=0.18$; $P=0.26$), and there is a considerable individual variation in CL size in females of different stages of pregnancy.

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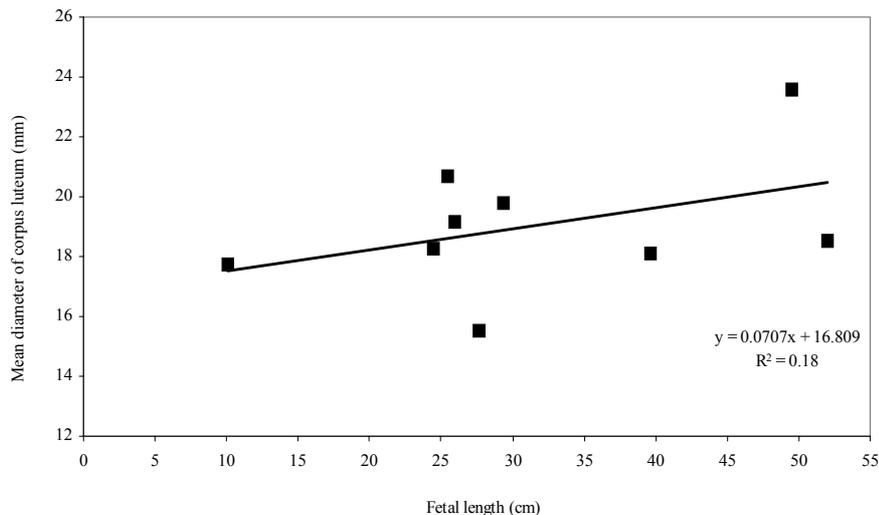


Figure 2. Relationship between standard length and weight of the heaviest ovary in immature and mature female franciscanas, *Pontoporia blainvillei*, from Rio Grande do Sul (n=40); figure 3. Relationship between mean diameter of corpus luteum and fetus length in franciscanas, *Pontoporia blainvillei*, from Rio Grande do Sul.

Gestation and births

The fetus growth in relation to the months of the year (Figure 4) is described by a linear regression (F=94.5, P<0.001, r²=0.86, n=18), represented by

$$y = 6.9445x - 9.1863 \quad \text{equation [9]}$$

where y is the fetus length (cm) and x represents the month of the year (January=1; December=12). Fetus growth in relation to the days of the year was also described by a linear regression (F=95.3, P<0.001, r²=0.86, n=18) and represented by

$$y = 0.2436x - 8.0574 \quad \text{equation [10]}$$

where y is the fetus length (cm) and x represents the day of the year (1 January=1; 31 December=365). In this manner, the fetal growth rate is estimated to be 6.94cm/month or 0.24cm/day. Two outlier fetuses (open boxes in Figure 4) were not included in the calculus of this regression.

The species presents a typical birth-pulse pattern. Every year, the first neonates were collected in October, with

the exception of an animal 67.0cm long collected in 6 September 1997. The frequency of franciscana births in Rio Grande do Sul does not show a normal distribution. Instead, births begin abruptly in October and decrease gradually until February (Figure 5). The distribution of the relative frequency of neonates smaller than 85.0cm suggests that about 75% of births occur from October to December.

The largest fetuses of the studied sample were 67.1, 75.0 and 84.0cm long, and were collected in October, December and January, respectively. The smallest neonates measuring 67.0, 67.5, and two 70.0cm long were collected in September, February and October (n=2), respectively. The mean length at birth was estimated to be 73.4cm.

The presence of remains of the umbilical cord still attached to the animal is an efficient indication that it is a newborn. In the studied sample, three neonates with standard length of 67.5, 70.0 and 70.0cm (mean = 69.2cm) were recorded with remains of the umbilical cord. It is important to note that former two were live stranded animals.

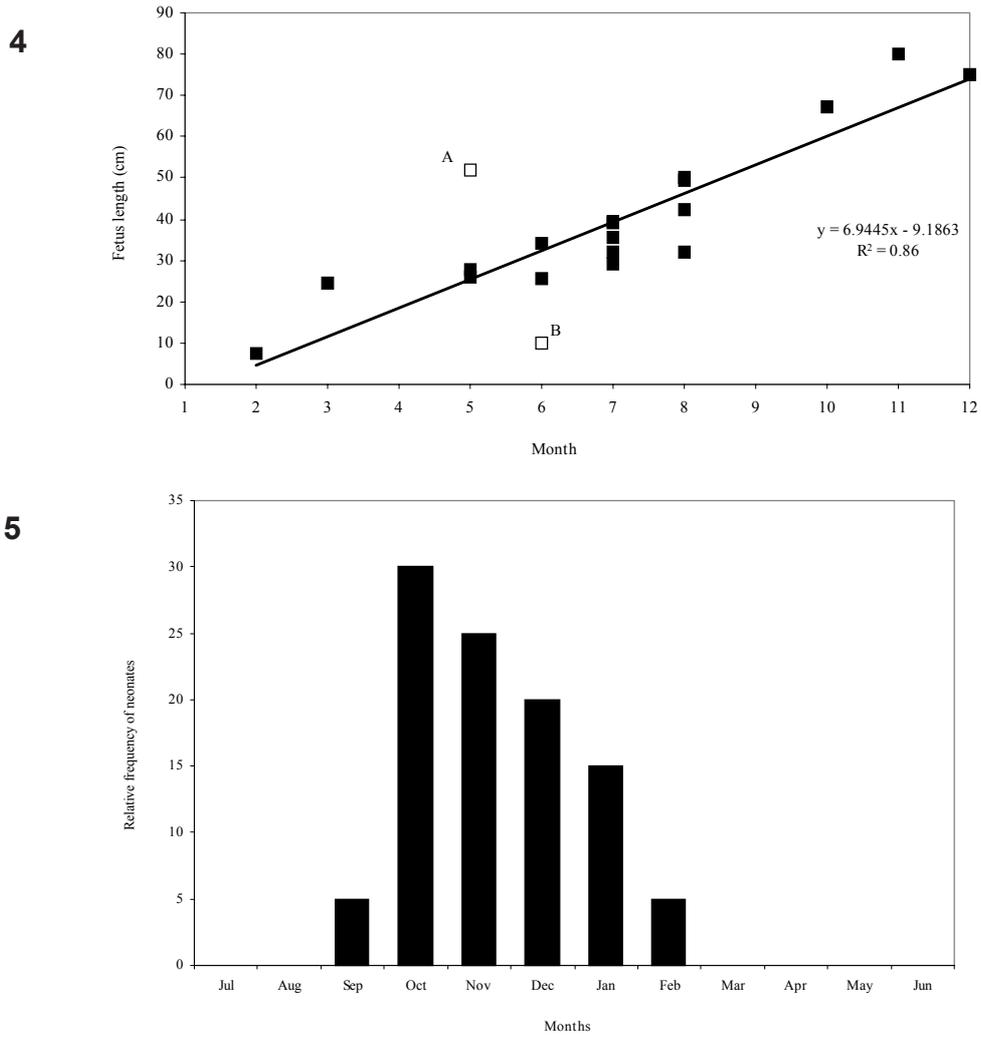


Figure 4. Linear regression of fetal length of franciscanas, *Pontoporia blainvillei*, by month from January (1) to December (12). Open boxes represent 'outliers'; figure 5. Relative frequency of franciscana neonates along the year in Rio Grande do Sul.

No multiplets were recorded (n=20). Although the fetal sex ratio was slightly towards males (1.3; 8 males and 6 females), it does not differ significantly from 1 ($X^2=0.29$, d.f.=1, $P<0.05$).

The exponential relationship between fetal length and weight ($r^2=0.99$) is shown in Figure 6 and is described by the equation

$$y = 0.0827e^{0.0586x} \quad \text{equation [11]}$$

From this equation, it is obtained a mean weight at birth of 6.1kg for the length at birth 73.4cm.

The nonlinear phase of gestation was estimated substituting the mean weight of birth (6.1kg) in the equation provided by Calder [1], and a period (to) of 38 days was obtained. In order to calculate the duration of the linear phase of gestation, equation [10] is solved for both date at birth (length at 73.4cm) and date at the start of linear growth (when fetal length is assumed to be 0), resulting in an estimate of 301 days. Thus, the entire duration of gestation is estimated to be 339 days (301 + 38) or 11.2 months. Considering that births occur between October and early February and that gestation lasts for approximately 11 months, mating and conception should occur between November and early March.

Although gestation and births of franciscanas in Rio Grande do Sul are characterized by seasonality, two outliers A and B (Figure 4) were recorded displaced from the fetal growth equation. Fetus A is displaced 3.5 months from fetal growth equation and its estimated conception and birth date are September 13 and August 19, respectively, while fetus B is displaced 3 months and its estimated conception and birth date are March 30 and March 4, respectively.

Sexual maturity

The sample of females with data on age and sexual maturity include 46 immature and 26 sexually mature dolphins. The oldest immature was 4 years old and the youngest mature were 3 years old, including some pregnant ones. Thus, sexual maturity is attained when females are between 2 and 5 years old (Table 1, see discussion). The mean age at onset of sexual maturity for females was calculated as 3.7 years (SD=0.36;

CI 95%=3.0 - 4.4 years) by the DeMaster method and 3.5 years by the logistic equation. The mean age of seven females with only one corpus in the ovaries (*i.e.*, collected in the year when they attained sexual maturity) was also 3.7 years (range= 3-6).

Table 1. Summary of information on age and reproduction of female franciscanas, *Pontoporia blainvillei*, in Rio Grande do Sul.

VARIABLE	AGE
Age interval of females without corpora	0-4
Youngest female with one corpus	3
Oldest female with one corpus	6
Youngest pregnant female	3
Oldest pregnant female	11
Youngest lactating female	5
Oldest lactating female	11
Oldest female of the sample	19

The sample of females with data on length and sexual maturity include 62 immature and 32 sexually mature dolphins. The largest immature female was 149.9cm long and the smallest mature was 133.0cm long. Mean length at attainment of sexual maturity was estimated in 138.9cm (SD=3.14; CI 95%=132.8 - 145.1 cm). The sample of females with data on weight and sexual maturity include 52 immature and 28 sexually mature dolphins. Mean weight at attainment of sexual maturity was estimated in 32.8kg (SD=1.48; CI 95%=29.9 - 35.7kg).

Annual reproductive rate and calving interval

Age-specific reproductive rates of franciscanas from Rio Grande do Sul are presented in Table 2. The estimated annual pregnancy rate was 0.66 (95% CI = 0.47 - 0.85), with a variance of 0.0086. The calving interval was estimate as 1.5 years (95% CI = 1.2 - 2.1 years).

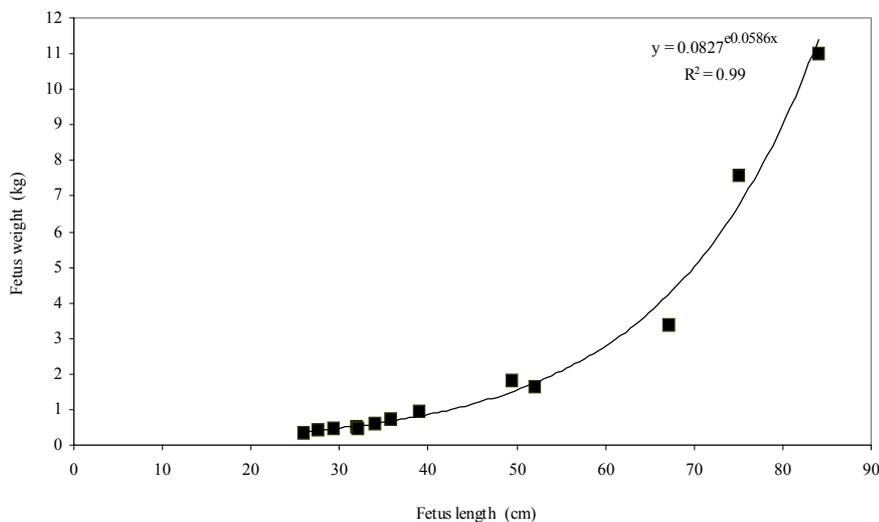


Figure 6. Relationship between length and weight of fetuses of franciscanas, *Pontoporia blainvillei*, in Rio Grande do Sul.

Table 2. Age-specific reproductive rates of female franciscanas, *Pontoporia blainvillei*, in Rio Grande do Sul. n = sample size.

AGE	N	MATURE	PROPORTION OF MATURE	PREGNANT	PROPORTION OF PREGNANT
0	7	0	---	0	---
1	23	0	---	0	---
2	11	0	---	0	---
3	12	8	0.67	5	0.63
4	3	2	0.67	2	1.00
5	3	3	1.00	2	0.67
6	4	4	1.00	4	1.00
7+	9	9	1.00	3	0.33
Total	72	26	0.36	16	0.62

The low proportion of lactating females and of simultaneously pregnant and lactating females is contradictory to the high annual pregnancy rate found in this study. When the females experiencing their first pregnancy and that consequently could not be lactating are subtracted from the sample, the proportion of lactating and of simultaneously pregnant and lactating females is 0.3 and 0.1, respectively.

The proportion of lactating females in the population is proportional to the time expended in the lactation (Perrin and Reilly, 1984), or:

$$L_p = G_p \times (L/P) \quad \text{equation [12]}$$

where L_p is lactation period in months, G_p is gestation period in months, L is the proportion of sexually mature females that are lactating and P is the proportion of sexually mature females that are pregnant.

In this manner, considering a lactation period of 9 months (Harrison *et al.*, 1981), the proportion of pregnant females and the gestation period found in this study, it would be expected a proportion of 0.5 lactating franciscanas in the sample.

Ovulation time

Five females presenting ovaries with evidences of recent ovulation were collected in January, February (n=2), June and August.

Longevity and reproductive senescence

The maximum age recorded for females in this study was 19 years. Evidence of reproductive senescence has been reported for some cetacean species by the observation of atrophic ovaries (*i.e.*, ovaries of small size, with no recent ovulation and with atretic follicles) in old females, according to Perrin *et al.* (1976) and Marsh and Kasuya (1984). No animal analyzed in this study presented such characteristics. Some older females (two 10 yr-old, one 11 yr-old, and one 19 yr-old) were still reproductively active.

Discussion

The tendency of a much higher activity of the left ovary has been well documented in *P. blainvillei* (*e.g.* Harrison *et al.*,

1981, Brownell, 1984). In Uruguay, no mature female studied (n=43) presented corpora in both ovaries simultaneously, and only two of them had corpora in the right ovary (Brownell, 1984). Interestingly, no ovulation polarity was observed in franciscanas from the southern coast of São Paulo and Paraná, with both right and left ovaries being functional (Rosas and Monteiro-Filho, 2001).

Although in some marine mammal species the corpus luteum increases its size as gestation progress (*e.g.* Boyd, 1984), there is not a clear pattern among cetaceans. It was demonstrated that in the pantropical spotted dolphin, *Stenella attenuata*, and in the striped dolphin, *S. coeruleoalba*, the CL decreases during gestation (Perrin *et al.*, 1976; Miyazaki, 1977), and in the short-finned pilot whale it does not suffer significant changes in size during gestation (Marsh and Kasuya, 1984). Data from this study does not indicate an increase of the CL as the franciscana gestation progresses, and CL size alone must not be used as an indicator of gestation time. Harrison *et al.* (1981) analyzed a larger sample (n=33) of pregnant females and also recognized a high individual variation of CL in relation to gestation time. Nevertheless, a slight increase in its size during the gestation could be noticed.

Gestation period is one of the reproductive parameters with less intraspecific variation among mammals (Kiltie, 1982). In most cetacean species gestation lasts about 10-12 months (Lockyer, 1984; Perrin and Reilly, 1984). As exceptions, the following could be cited: the sperm whale, *Physeter macrocephalus* (16-17 months, Harrison, 1969), the Baird's beaked whale, *Berardius bairdii* (17 months, Kasuya, 1977), the pilot whales, genus *Globicephala* (15 months (Kasuya and Marsh, 1984) and the killer whale, *Orcinus orca* (15 months, Perrin and Reilly, 1984). The gestation period estimation of 11.2 months obtained for the franciscana in this study is very similar to those estimated in other study sites. In Uruguay, Harrison *et al.* (1981) estimated a gestation period of 10.5-12 months (probably closer to 10.5 months), and Kasuya and Brownell (1979) studied the same sample and estimated it as 10.8-11 months. Along the Brazilian coast, gestation was calculated to last 10.6 months in Paraná/southern São Paulo (Rosas and Monteiro-Filho, 2001) and 10.2-10.4 months in Rio de

Janeiro (Ramos, 1997). These last values are the smallest for the species and may be influenced by the estimator: the linear regression given Perrin *et al.* (1977) and applied by Ramos tends to produce shorter estimations of gestation length than the Huggett and Widdas (1951) method, even when the same values of length at birth are used in the calculation.

The fetal growth rate of the linear phase of gestation is higher in Rio de Janeiro (7.6cm/month) than in Rio Grande do Sul (6.94cm/month). This difference is also likely the result of using distinct methods to calculate gestation length rather than a reflection of real differences in fetus growth pattern.

It is considered here that the mean length and weight at birth of 73.4cm and 6.1kg, respectively, are the most accurate for the population of franciscanas from Rio Grande do Sul, since it considers only the neonates collected in the first month of parturition in the region (October), and decreases the probability of including older animals in the calculation.

Adult franciscanas from Rio Grande do Sul are remarkably larger than those from Paraná, São Paulo and Rio de Janeiro. While asymptotic lengths of males and females from the former region range from 129.8-136.4cm and 146.4-161.9cm, respectively, the asymptotic lengths of males and females from the later regions range from 113.3-117.1cm and 128.9-144.7cm (Kasuya and Brownell, 1979; Walter, 1997; Ramos *et al.*, 2000; Rosas and Monteiro-Filho, 2001). Thus, it could be expected that length at birth would also be larger in Rio Grande do Sul. However, length at birth in Rio de Janeiro (71.0cm) and Paraná/southern São Paulo (71.2cm) is almost the same as in Rio Grande do Sul and very similar to the values for Uruguay found by Harrison *et al.* (1981) (closer to 70.0cm) and Kasuya and Brownell (1979) (70.0 - 75.0cm), demonstrating the birth size does not present variation in this species. The smallest neonate reported for Rio de Janeiro was 66.0cm long, while in Rio Grande do Sul the smallest neonate measured 67.0cm in length. On the other hand, the largest fetus in Rio de Janeiro measured 65.0cm, while in Rio Grande do Sul it measured 80.0cm. This marked difference may suggest that the range of length at birth is considerably wider in Rio Grande do Sul.

Many mammalian species exhibit a reproductive seasonality, presenting a well-defined period for mating and births. This seasonality is generally associated with a higher offspring survival from females that give birth within the reproductive peak than those who give birth outside the peak (Majluf, 1992). The franciscana reproduction in Rio Grande do Sul (29°-32°S) is characteristically seasonal. Although births extend for five months, 75% of them take place between October and December. Very similar birth periods were found for franciscanas in Uruguay (33°-34°S) (November and December) (Harrison *et al.*, 1981; Brownell, 1984) and in Paraná/southern São Paulo (25°S) (October to December) (Rosas and Monteiro-Filho, 2001). On the other hand, Ramos (1997) noted the absence of seasonality in Rio de Janeiro (21°S), where births take place year around.

Among the factors that may influence the timing of

reproduction in mammals are the availability and quality of food, variation in the predation pressure and variation in the environment temperature and photoperiod (*e.g.* Dobson and Kjelgaard, 1985; Rutberg, 1987; Bronson, 1989, 1995). Thus, the regional variance in franciscana reproductive seasonality may be the reflection of local differences in these factors. Although all these biotic and abiotic factors have the capacity to shape the seasonality of the franciscana reproduction, the available information on most of them is still scanty to allow a comparison between areas.

However, surface water temperature is a well-documented variable. The waters of Rio Grande do Sul experience considerable fluctuations in temperature (Figure 7), remaining around 15-16°C in the winter, rising to 20°C in mid spring, when the first calves are recorded, and reaching 26°C during the summer. Thus, franciscana parturition takes place during the months when the waters are warmer and more suitable for the birth and first months of growth of a calf, suggesting that the observed seasonality may have evolved, at least in part, as a response to the fluctuations of the environmental temperature. Oppositely, the fluctuation of the water temperature in the Rio de Janeiro coast is much less noteworthy. Sea-surface temperature variation along all the year in that region (22-26°C) (Ramos, 1997) corresponds to the same range of temperatures that occur during the parturition months in Rio Grande do Sul (20-26°C). In this sense, the energetic cost of maintaining the body heat is certainly reduced in franciscana calves from Rio de Janeiro, which allows the births to take place even during autumn and winter months. Further comparative analyses on other variables that can potentially influence the franciscana reproductive seasonality (*e.g.* food availability) are encouraged.

Collectively, the franciscana can be considered one of the cetaceans with fastest life history traits, mainly due to its remarkably low age at sexual maturity, short reproductive interval and short life span. Its age at sexual maturity is one of the earliest among the group (Danilewicz *et al.*, 2000), resembling only those of the phocoenids harbour porpoise, *Phocoena phocoena* (Read and Hohn, 1995), Dall's porpoise, *Phocoenoides dalli* (Ferrero and Walker, 1999) and vaquita, *Phocoena sinus* (Hohn *et al.*, 1996), and it is considerably lower than the ASMs of delphinids, even those with similar maximum observed age (*e.g.* *Cephalorhynchus hectori* - Slooten, 1991).

The ASM estimated here was the same as the one calculated by Danilewicz *et al.* (2000) for a smaller sample from Rio Grande do Sul. The youngest mature females were 3 years old, the same age of the youngest pregnant females (n=5). This might suggest that some animals could have attained sexual maturity when they were 2 years old, although no females with this age in the sample (n=11) were mature. When the conception dates of the fetuses of these females were estimated, it could be noticed that one female was fertilized before October, suggesting that this animal was still 2 years old when conceiving. Pinedo (1994) analyzed the age structure of animals from Rio Grande do Sul and Uruguay and also noticed one pregnant female aged 2 years.

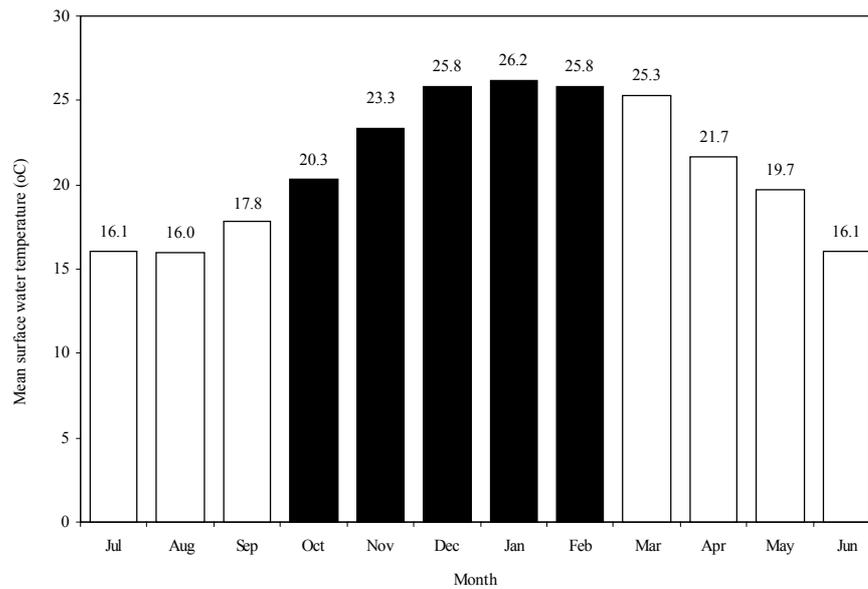


Figure 7. Monthly variation of the mean water surface temperature in the coast of Rio Grande do Sul (1994-1995). Black bars indicate the period when births of franciscanas, *Pontoporia blainvillei*, take place in the region.

The reproductive rates presented here are also very similar to those given by Danilewicz *et al.* (2000) for a smaller sample from Rio Grande do Sul. The APR found in this study indicates that about half of the mature females are reproducing annually, while other half are reproducing biannually [(0.5 mature females \times 1 year) + (0.5 mature females \times 2 years) = 1.5]. Consequently, the proportion of lactating (0.30) and simultaneously pregnant and lactating females (0.10) found here is lower than the expected for a mean calving interval of 1.5 years (0.5 lactating and 0.39 simultaneously pregnant and lactating). This low proportion of lactating females may be caused by sampling bias due to lower vulnerability to bycatch. Segregation in the geographic distribution between lactating and pregnant animals in Rio Grande do Sul may also affect the results. Further investigation on large- and small-scale habitat use of the franciscana in Rio Grande do Sul will assist in clarifying the effect of the species distribution on these parameter's estimations.

Amongst the five females with evidences of recent ovulation, two were collected in months (June and August) out of the main mating period (November to early March). Similarly, Danilewicz *et al.* (in press) did not found any regression in testis mass of mature males in non-reproductive months, concluding that males are able to produce spermatogonia and reproduce year-round. The presence of two fetuses displaced of the fetal growth curve indicates that some franciscanas mate and conceive out of the main mating period, although the viability of these calves potentially decreases.

There was no indication that female franciscanas experience reproductive senescence, as observed in some extended life span cetaceans, such as pilot whales (Marsh and Kasuya, 1984). The oldest known female and male franciscanas from Rio Grande do Sul and Uruguay are 21 and 15 years old, respectively (Pinedo, 1994), which led this author to comment that females seem to have a higher longevity than

males. However, from the 374 franciscanas with known age and sex studied by Pinedo (1994), the proportion of the animals older than 12 years was 6.3% for the males and 3.0% for the females. Thus, it seems unlikely that there is a sex-differential mortality for *P. blainvillei*.

Although there is evidence that some franciscanas are able to live until they are 20 years old, the large majority of animals do not seem to live more than 13-14 years. The high mortality in gillnets mainly of juveniles, together with the natural mortality by diseases and predation (Praderi, 1985; Ott and Danilewicz, 1998) indicates it is unlikely that adult franciscanas will reach maximum potential longevity. Similarly, Brownell (1984) suggests that the longevity of franciscana should be considered 15 years. Considering this information, and taking account the ASMs and the calving intervals presented here, it is suggested the one female franciscana may have 5-10 calves per lifetime (see Table 3).

Table 3. Suggested offspring size of franciscana, *Pontoporia blainvillei*, in Rio Grande do Sul, considering a life expectancy of 14 years, an age at sexual maturity of 3.7 (95% CI = 3.0 - 4.4) and a calving interval of 1.5 (95% CI = 1.2 - 2.1).

AGE AT SEXUAL MATURITY	CALVING INTERVAL	OFFSPRING SIZE
3.0	1.2	10
3.0	1.5	8
3.0	2.1	6
3.7	1.2	10
3.7	1.5	7
3.7	2.1	5
4.4	1.2	9
4.4	1.5	6
4.4	2.1	5

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References

- American Society of Mammalogists. (1961) Standardized methods for measuring and recording data on the smaller cetaceans. *Journal of Mammalogy* 42: 471-476.
- Benirschke, K., Johnson, M.L. and Benirschke, R.J. (1980) Is ovulation in dolphins, *Stenella longirostris* and *Stenella attenuata*, always copulation-induced? *Fishery Bulletin* 782:507-528.
- Boyd, I.L. (1984) Development and regression of the corpus luteum in the grey seal (*Halichoerus grypus*) ovaries and its use in determining fertility rates. *Canadian Journal of Zoology* 62: 1095-1100.
- Brownell, R.L., Jr (1984) Review of reproduction in platanistid dolphins. *Report of the International Whaling Commission* (special issue) 6: 149-158.
- Bronson, F.H. (1989) *Mammalian Reproductive Biology*. The University of Chicago Press, Chicago.
- Bronson, F.H. (1995) Seasonal variation in human reproduction: environmental factors. *Quarterly Review of Biology* 70 (2): 141-164.
- Calder, W.A. (1982) The pace of growth: an allometric approach to comparative embryonic and post-embryonic growth. *Journal of Zoology* 198: 215-225.
- Crespo, E.A., Harris, G. & González, R. (1998) Group size and distribution range of the franciscana, *Pontoporia blainvillei*. *Marine Mammal Science* 14 (4): 845-849.
- Danilewicz, D., Claver, J.A., Pérez-Carrera, A.L., Secchi, E.R. and Fontoura, N.F. (in press) Reproductive biology of male franciscanas (*Pontoporia blainvillei*) (Mammalia: Cetacea) from Rio Grande do Sul, southern Brazil. *Fishery Bulletin*.
- Danilewicz, D., Secchi, E.R., Ott, P.H. and Moreno, I.B. (2000) Analyses of the age at sexual maturity and reproductive rates of franciscanas (*Pontoporia blainvillei*) from Rio Grande do Sul, southern Brazil. *Comunicações do Museu de Ciências e Tecnologia da PUCRS. Série Zoologia* 13: 89-98.
- DeMaster, D. P. (1978) Calculation of the average age of sexual maturity in marine mammals. *Journal of Fisheries and Research Board of Canada* 35 (6):912-15.
- Dobson, F.S. and Kjelgaard, J.D. (1985) The influence of food resources on life history in Columbian ground squirrels. *Canadian Journal of Zoology* 63: 2105-2109.
- Ferrero R.C. and Walker, W.A. (1993) Growth and reproduction of the northern right whale dolphin, *Lissodelphis borealis*, in the offshore waters of the North Pacific Ocean. *Canadian Journal of Zoology* 71 (12): 2335-2344.
- Ferrero, R.C. and Walker, W.A. (1999) Age, growth, and reproductive patterns of Dall's porpoise (*Phocoenoides dalli*) in the central North Pacific ocean. *Marine Mammal Science* 15 (2): 273-313.
- Harrison, R.J. (1969). Reproduction and reproductive organs. In Andersen, H.T. (ed.). *The biology of marine mammals*. Academic Press.
- Harrison, R.J., Bryden, M.M., McBrearty, D.A. and Brownell, R.L., Jr. (1981) The ovaries and reproduction in *Pontoporia blainvillei* (Cetacea:Platanistidae). *Journal of Zoology* 193: 563-580.
- Hohn, A.A., Read, A., Fernandez, F., Vidal, O. and Findley, L.T. (1996) Life history of the vaquita, *Phocoena sinu* (Phocoenidae, Cetacea). *Journal of Zoology* 239: 235-251.
- Huggett, A., St. G. and Widdas, W.F. (1951) The relationship between the mammalian foetal weight and conception age. *Journal of Physiology* 114: 306-317.
- Iwasa, M. and Atkinson, S. (1996) Analysis of corpora lutea to estimate reproductive cycles of wild Hawaiian monk seals (*Monachus schauinslandi*). *Marine Mammal Science* 12 (2):182-198.
- Kasuya, T. (1977) Age determination and growth of the Baird's beaked whale with a comment on the fetal growth rate. *Scientific Report of the Whales Research Institute* 29: 1-20.
- Kasuya, T. and Brownell, R.L., Jr. (1979) Age determination, reproduction, and growth of the franciscana dolphin, *Pontoporia blainvillei*. *Scientific Report of the Whales Research Institute* 31: 45-67.
- Kasuya, T. and Marsh, H. (1984). Life history and reproductive biology of the short-finned pilot whale,

- Globicephala macrorhynchus*, off the Pacific coast of Japan. *Rep. Int Whal. Commn.* (special issue) 6: 259-310.
- Kiltie, R.A. (1982) Intraspecific variation in mammalian gestation period. *Journal of Mammalogy* 63: 646-652.
- Lockyer, C. (1984). Review of baleen whale (Mysticeti) reproduction and implications for management. *Report of the International Whaling Commission* (special issue) 6: 27-48.
- Majluf, P. (1992) Timing of births and juvenile mortality in the south American fur seal in Peru. *Journal of Zoology* 227: 367-383.
- Marsh, H. and Kasuya, T. (1984) Changes in the ovaries of the short-finned pilot whale, *Globicephala macrorhynchus*, with age and reproductive activity. *Report of the International Whaling Commission*. (special issue 12) 6: 311-335.
- Miyazaki, N. (1977) Growth and reproduction of *Stenella coeruleoalba* off the Pacific coast of Japan. *Scientific Report of the Whales Research Institute* 29: 21-48.
- Moreno, I.B., Ott, P.H. and Danilewicz, D. (1997) Análise preliminar do impacto da pesca artesanal costeira sobre *Pontoporia blainvillei* no litoral norte do Rio Grande do Sul, sul do Brasil. P. 31-41. *in*: Pinedo, M.C. and Barreto, A. (Eds) Proceedings of the Second Workshop for the Research Coordination and Conservation of the Franciscana (*Pontoporia blainvillei*) in the Southwestern Atlantic. Rio Grande. 88p.
- Ott, P.H. and Danilewicz, D. (1998) Presence of franciscana dolphins (*Pontoporia blainvillei*) in the stomach of a killer whale (*Orcinus orca*) stranded in southern Brazil. *Mammalia* 62 (4): 605-609.
- Ott, P.H. (1998) *Análise das capturas acidentais da toninha, Pontoporia blainvillei, no litoral norte do Rio Grande do Sul, sul do Brasil*. Master Dissertation, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre. 120pp.
- Ott, P.H., Secchi, E.R., Moreno, I.B., Danilewicz, D., Crespo, E.A., Bordino, P., Ramos, R., Di Benedetto, A.P., Bertozzi, C., Bastida, R., Zanelatto, R., Perez, J. and Kinan, P.G. (2002) Report of the working group of fishery interactions. *Latin American Journal of Aquatic Mammals* (special issue) 1: 55-64.
- Perrin, W.F., Coe, J.M., and Zweifel, J.R. (1976) Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fishery Bulletin* 74: 229-269.
- Perrin, W.F., Holts, D.B., and Miller, R.B. (1977) Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. *Fishery Bulletin* 75: 725-750.
- Perrin, W.F. and Donovan, G.P. (1984) Report of the workshop. *Report of the International Whaling Commission* (special issue 6): 1-24.
- Perrin, W.F. and Reilly, S.B. (1984) Reproductive parameters of dolphins and small whales of the family Delphinidae. *Report of the International Whaling Commission* (special issue 6): 97-133.
- Pinedo, M.C. (1991) Development and variation of the franciscana, *Pontoporia blainvillei*. Doctoral Thesis. Santa Cruz. University of California. 406 p.
- Pinedo, M.C. (1994) Impact of incidental fishery mortality on the age structure of *Pontoporia blainvillei* in southern Brazil and Uruguay. *Report of the International Whaling Commission*. (special issue 15): 261-264.
- Pinedo, M.C. and Barreto, A. (eds) (1997) Proceedings of the Second Workshop for the Research Coordination and Conservation of the Franciscana (*Pontoporia blainvillei*) in the Southwestern Atlantic. Rio Grande. 88p.
- Pinedo, M.C. and Hohn, 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.
- Praderi, R. (1985) Relaciones entre *Pontoporia blainvillei* (Mammalia: Cetacea) e tiburones (Selachii) de aguas Uruguayas. *Comunicaciones Zoológicas Museu de Historia Natural de Montevideo*. 11 (151): 1-19.
- Praderi, R., Pinedo, M.C. and Crespo, E.A. (1989) Conservation and management of *Pontoporia blainvillei* in Uruguay, Brazil and Argentina. *In*: Perrin, W.F., Brownell, R.L., Zhou Kaya, Liu Jiankang (eds.). *Biology and Conservation of River Dolphins*, p. 52-56.
- Ramos, R.M.A. (1997) Determinação de idade e biologia reprodutiva de *Pontoporia blainvillei* e da forma marinha de *Sotalia fluviatilis* no litoral norte do Rio de Janeiro. Dissertação de Mestrado. Rio de Janeiro. Universidade Estadual do Norte Fluminense. 95p.
- Ramos, R.M.A., Di Benedetto, A.P.M. and Lima, N.R.W. (2000) Growth parameters of *Pontoporia blainvillei* and *Sotalia fluviatilis* (Cetacea) in northern Rio de Janeiro, Brazil. *Aquatic Mammals* 26 (1): 65-75.
- Read, A. and Hohn, A. (1995) Life in the fast lane: the life history of the harbour porpoises from the Gulf of Maine. *Marine Mammal Science* 11: 423-440.
- Rosas, F.C.W. and Monteiro-Filho, E.L.A. (2001) Reproductive parameters of *Pontoporia blainvillei* (Cetacea, Pontoporidae), on the coast of São Paulo and Paraná States, Brazil. *Mammalia* 66 (2): 231-245.
- Rutberg, A.T. (1987) Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *American Naturalist* 130: 692-710.
- Secchi, E.R. (1999) *Taxa de crescimento potencial intrínseco de um estoque de franciscanas, Pontoporia blainvillei (Gervais & D'Orbigny, 1846) (Cetacea, Pontoporiidae) sob o impacto da pesca costeira de emalhe*. Master Thesis, Fundação Universidade do Rio Grande, Rio Grande. 152pp.
- Secchi, E.R., Zerbini, A.N., Bassoi, M., Dalla Rosa, L., Moller, L.M. and Rocha-Campos, C.C. (1997) Mortality of franciscanas, *Pontoporia blainvillei*, in coastal gillnetting in southern Brazil. *Report of the International Whaling Commission* 47: 653-658.
- Secchi, E.R., Ott, P.H., and Danilewicz, D. (2002) Report of the fourth workshop for the coordinated research and conservation of the franciscana dolphin (*Pontoporia blainvillei*) in the western South Atlantic. *The Latin American Journal of Aquatic Mammals* (special issue) 1:11-20.
- Secchi, E.R., Ott, P.H. and Danilewicz, D. (2003) Effects of fishing bycatch and the conservation status of the franciscana dolphin, *Pontoporia blainvillei*. Pages 174-191 *in* Gales N., Hindell, M. and Kirkwood, R. (Eds) *Marine Mammals: Fisheries, Tourism and Management Issues*. SCIRO Publishing. Collingwood. Australia.
- Siciliano, S., Di Benedetto, A.P. and Ramos, R.M.A. (2002) A toninha, *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844) (Mammalia, Cetacea, Pontoporiidae), nos estados do Rio de Janeiro e Espírito Santo, costa

- sudeste do Brasil: caracterizações dos habitats e fatores de isolamento das populações. *Boletim do Museu Nacional, Zoologia*. 476:1-15.
- Slooten, E. (1991) Age, growth, and reproduction in Hector's dolphins. *Canadian Journal of Zoology* 69: 1689-1700.
- Walter, T. (1997) *Curvas de crescimento aplicadas a organismos aquáticos. Um estudo de caso para a toninha, Pontoporia blainvillei (Cetacea, Pontoporiidae) do extremo sul do Brasil*. Bachelor Dissertation, Fundação Universidade do Rio Grande, Rio Grande. 102pp.

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