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Received: 3 June 2019 | Accepted: 1 June 2020

Running head: SILVA ET AL.

ARTICLE

Reproductive parameters of franciscana dolphins (*Pontoporia blainvillei*) of Southeastern Brazil

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Abstract

Reproductive parameters of 168 franciscana dolphins, *Pontoporia blainvillei* (73 females and 95 males) incidentally caught (*n* = 163) or stranded (*n* = 5) between 2005 and 2016 in southeastern Brazil are presented. Ovarian macroscopic analysis revealed 55 immature (75.3%) and 18 mature (24.7%) females. Annual pregnancy rate was estimated to be 0.36, with a calving interval of 2.8 years. Testicular histology revealed 66 immature (69.5%) and 29 mature (30.5%) males. Males with combined testis weight above 4 g were mature, and 1-year-old mature males and a 2-year-old pregnant female are reported for the first time for the species. Reproductive seasonality does not seem to occur in the study area. Mean age and length at sexual maturation were estimated to be at 2.7 years and 128.5 cm for females, and 2.7 years and 114.0 cm for males. These estimates are lower than most of the estimates for this species. These results add novel and valuable information on the reproductive patterns of this endangered species, threatened by high levels of mortality in gillnet fisheries. The information presented here represents an important effort to obtain more reliable parameter estimates for

the studied area, needed for a better assessment of its current conservation status.

KEYWORDS

age at sexual maturation, calving interval, franciscana dolphin, length at sexual maturation, ovulation asymmetry, *Pontoporia blainvillei*, pregnancy rate, reproduction

1 | INTRODUCTION

The franciscana dolphin, *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844), is endemic to the southwestern Atlantic Ocean, occurring in coastal waters from Itaúnas (18º25′S) in northern Espírito Santo State, Brazil (Siciliano, 1994), to Golfo San Matías (41º10′S) in Chubut Province, Argentina (Crespo, Harris, & González, 1998). Based on sightings and incidental catches in fishing operations, franciscana dolphins are known to inhabit a narrow strip of coastal water up to 30 m in depth (Danilewicz et al., 2009; Pinedo, Praderi, & Brownell, 1989; Praderi, Pinedo, & Crespo, 1989). This coastally oriented behavior is directly related to the considerable number of reported incidental catches by commercial fishing operations (e.g., Capozzo et al., 2007; Ott et al., 2002; Pinedo, 1994; Secchi et al., 1997; Siciliano, 1994), the main threat to *P. blainvillei* conservation (e.g., Praderi et al., 1989; Secchi, Ott, & Danilewicz, 2003). Currently, the franciscana dolphin is categorized as "vulnerable" under criterion "A3d" on the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN) (Zerbini, Secchi, Crespo, Danilewicz, & Reeves, 2017) and is considered “critically endangered” by the Brazilian Government (MMA, 2017). Although the main threat to the species is known, few effective initiatives have been implemented in Brazil to reduce or eliminate the mortality of franciscanas in fisheries (Ott et al., 2002; Rocha-Campo, Danilewicz, & Siciliano, 2010; Secchi, 2010).

Over the past 40 years, only eight studies on franciscana life history related to reproduction (hereafter life history) have been published (Danilewicz, 2003; Danilewicz, Claver, Carrera, Secchi, & Fontoura, 2004; Harrison, Bryden, McBrearty, & Brownell, 1981; Kasuya & Brownell, 1979; Panebianco et al., 2016; Panebianco, Negri, & Capozzo, 2012; Ramos, Di Beneditto, & Lima, 2000; Rosas & Monteiro-Filho, 2001), although further unpublished studies exist. This species is one of the smallest odontocetes; estimates of asymptotic length range from 129 to 158 cm for females and 113 to 136 cm for males, with long recognition that females are larger than males (Barreto & Rosas, 2006; Botta et al., 2010). Age at sexual maturation (ASM) reported in the above-mentioned studies range from 2.7 to 5 years for females at average lengths of 122–140 cm. For males, ASM estimates range from 2 to 5 years at average lengths 112–131 cm. Maximum longevity is 21 years or less (Pinedo & Hohn, 2000). Despite the limited results, it is apparent that franciscana dolphins have a life history more similar to porpoises (Phocoenidae; Read & Hohn, 1995) than to most of the dolphins (Perrin & Reilly, 1984), i.e., early maturing and short lived.

The threat to franciscana dolphins is compounded by the existence of up to four stocks rather than one panmictic population (Cunha et al., 2014; Secchi, Danilewicz, & Ott, 2003). The commonly accepted division is four stocks, referred to as Franciscana Management Areas (FMA), FMA I through FMA IV (from northernmost in central Brazil to southernmost in Argentina). The variation in estimates of life-history parameters for franciscana dolphins stems from multiple sources, including small sample sizes, differences in methodologies, and, importantly, likely differences among the stocks. In addition, because some life-history parameters may be density-dependent, e.g., age at attainment of sexual maturity (Perrin & Reilly, 1984), and stocks have been subjected to high mortality rates from incidental captures in several areas, it is necessary to update parameter estimates as samples become available. For FMA II, the source stock for the individuals analyzed in this study, the only previous investigation on life history parameters was published two decades ago, with a relatively small sample size (n = 40 individuals incidentally caught; Rosas & Monteiro-Filho, 2001).

In this study, we describe life-history parameters relative to reproduction (hereafter life history in the text) of female and male franciscana dolphins using carcasses from bycatch and strandings collected between 2005 and 2016 in FMA II. We present results of ovarian and testicular characteristics and their relation to attainment of sexual maturity, age and length at sexual maturation, annual pregnancy rate, calving interval, and reproductive seasonality. The results were then evaluated in the context of previous studies throughout the range of the species.

2 | MATERIALS AND METHODS

2.1 | Sample collection and processing

A total of 168 carcasses (163 incidentally captured and 5 stranded) was collected on the southern coast of São Paulo State (25°00′S, 47°55′W), southeastern Brazil. The Cananeia gill net fleet was monitored from 2004 to 2007 and from 2011 to 2016 to document cetacean incidental captures. When fishing boats had room in their hulls, carcasses of franciscanas were frozen for later study. Beach surveys for franciscanas carcasses were opportunistically conducted from 1996 to 2015 covering from 75 to 115 km. All specimens were included in the Projeto Atlantis (PA) collection and received a specimen identification number (e.g., PA-246), which was associated with morphometric data, recovered stomach contents, gonads, teeth, and samples for contamination and genetic analyses for each individual.

Body measurements and weight were recorded following Norris (1961) prior to all necropsies. Gonads and teeth were collected for reproductive and age analyses, respectively. Weight, length, and width of gonads (testes with epididymis and ovaries) were measured during necropsy. Ovaries and testes were weighed to the nearest 0.1 g. Length and width were measured to the nearest 0.1 mm. Gonads weighing less than 0.1 g were listed as <0.1 g. Afterwards, gonads were stored in 10% formalin for at least 24 hr, most for more than one week, and then transferred to a 70% ethanol solution. A few small incisions were made in the testes to allow better formalin penetration. Shorter fixation times still resulted in adequate histological results for these small gonads. Uteri were cut opened and scanned for the presence of a fetus and mammary slits were examined for the presence of milk. Females were considered pregnant when a fetus was present and as lactating when milk was detected in the mammary slits. When fetuses were found, sex, total length, and weight were recorded.

2.2 | Age estimation

Teeth were stored dry. The straightest and least-worn tooth from each specimen was collected whole and prepared for age estimation following Hohn, Scott, Wells, Sweeney, and Irvine (1989) and Pinedo and Hohn (2000). For processing, the whole tooth was fixed in 10% formalin for at least 12 hr, rinsed in tap water and decalcified in RDO decalcifying solution (Apex Engineering Products Corporation, Aurora, IL). The time interval required for decalcification varied in relation to tooth size, thickness, and the age of the specimen, ranged from 1 to 16 hr, with shorter times for younger specimens and longer for older ones. When a tooth was flexible and translucent, it was rinsed in tap water and thin-sectioned at 25 μm in an anteriorposterior orientation on a freezing stage attached to a sliding microtome. Sections were stained in Mayer’s hematoxylin for 40 to 50 min, rinsed in tap water, and washed with diluted ammonia solution (1 ml of 10% ammonia solution in 150 ml of water) for 15 s. After rinsing in tap water, the sections were soaked sequentially in 50% glycerin for 30 min and then in 100% glycerin until mounting on slides. Age was estimated by counting growth layer groups (GLGs; Perrin & Myrick, 1980) present in dentine and cement of the teeth, as described by Pinedo and Hohn (2000), at 40× and 100× magnifications. One reading was carried out by each of three readers, independently, with no reference to biological data or other details about the specimen. When differences in readings occurred, an additional reading was made collaboratively by all readers to reach the best estimate. Ages were assigned considering only completed GLGs, each corresponding to one year, which is the suggested deposition rate for franciscana dolphins (Pinedo & Hohn, 2000).

2.3 | Female reproduction

The reproductive status of females was determined according to the terminology recommended by Perrin and Donovan (1984).

Females with no ovarian corpora were considered sexually immature. Females exhibiting at least one corpus luteum (CL) or corpus albicans (CA) in one of the ovaries were classified as sexually mature.

For each female, both ovaries were measured, weighed, and examined for corpora. Since corpora can occupy a large portion of the ovary and consequently affect their size and weight, analyses were done separately for immature and mature females, and excluded pregnant and lactating females due to the large size of the CL or recent CA. For each female, the mean ovarian weight, length, and width was calculated from measurements from the two ovaries taken during necropsies. Similarly, combined ovary weight and combined ovary length were calculated as the sum of the weights and lengths of both ovaries, respectively. Relative ovarian weight was determined as the ratio of the combined ovary weight to the female's body weight. An ovarian maturity index was calculated following Danilewicz et al. (2004), using the combined ovary weight divided by the combined ovary length.

Corpora (CL and CA) were identified and counted grossly in both ovaries from each female, first from an external examination and then from cross-sections of approximately 1–2 mm thick made by hand, following the method of Harrison et al. (1981). The total number of corpora in left and right ovaries was recorded separately and tested for asymmetry to compare to prior studies. Whenever possible, all corpora were measured in three orthogonal dimensions and the mean of these measurements was used as the mean diameter of the corpus (Harrison et al., 1981).

The month of occurrence of a CL in nonpregnant and nonlactating females was used to determine the timing of ovulation or seasonality (Harrison et al., 1981). Although it is possible that an apparently nonpregnant female with a CL could be preimplantation or early post implantation (Harrison et al., 1981), this effect on determining the timing of ovulation should be small.

The annual pregnancy rate (APR) and calving interval (CI) were estimated following Perrin and Reilly (1984). The APR value was calculated as the percentage of sexually mature females that were pregnant divided by the gestation period in years (e.g., 9 months = 0.75 year). Because the small sample size of fetuses precluded estimation of the gestation period in the present study, the gestation period estimated by Danilewicz (2003) for samples from FMA III was used. This is feasible because gestation period is a conserved trait that should not vary between populations of the same species (Kiltie, 1982). The CI was calculated as the reciprocal of the APR value (i.e., CI = 1/APR).

2.4 | Male reproduction

For each male, both testes with epididymides were weighed and measured. Epididymides were disregarded when measuring the length and width of the testes. Weight, length, and width of right and left testes were compared to test for symmetry. For each male, the mean testicular weight, length, and width of the left and right testes was calculated from measurements taken during necropsies. Combined testis weight and combined testis length were the sum of weights and lengths, respectively, from both testes. Percentage of relative testicular weight was determined as the ratio of the combined testis weight to the specimen weight. A testicular maturity index was calculated following Danilewicz et al. (2004) as the ratio of the combined testis weight to the combined testis length to evaluate the feasibility of using testis metrics as an alternative to histology to determine sexual maturity.

To identify the reproductive status of males, a subsample of approximately 5 mm^3 of the testes was prepared using standard histological techniques. The testes from franciscana dolphins are small, with the width ranging from 6 to 22 mm across all specimens in the present study. So, most subsamples included an entire cross-section from the middle of the testes that was 5 mm thick. Each subsample was dehydrated gradually in ethanol solutions (70%, 80%, 90%, 96%, and 100%) and immersed in two baths of pure xylene. The subsample was then embedded in two baths of high-purity paraffin at 60°C and, after hardening at room temperature, was thin-sectioned on a rotary microtome into 6 μm sections. These sections were put on slides and stained with hematoxylin-eosin and permanently mounted with synthetic Canada balsam. The sexual maturity status was determined following the criteria suggested by Hohn, Chivers, and Barlow (1985) with a few modifications, described as follows. Immature specimens were defined as having abundant interstitial tissue surrounding the seminiferous tubules; the seminiferous tubules were generally circular or slightly elongated in cross-section; the lumen of the tubules was totally or partially closed; the seminiferous tubules primarily contained spermatogonia and, in some cases, spermatocytes. Mature individuals had seminiferous tubules surrounded by little interstitial tissue; the tubules were elongated and convoluted resulting in large diameters in cross sections and an extended oval appearance when sectioned obliquely; the lumen of the tubules was usually open; the seminiferous tubules often contained all cells of the spermatogenic lineage: spermatogonia, spermatocytes, spermatids and spermatozoa. Although the presence of spermatozoa clearly indicates sexual maturity, specimens that do not contain these cells could also be considered mature based on the other criteria mentioned above. To evaluate reproductive seasonality in males, the values of combined testis weight were compared across months for incidentally caught specimens.

2.5 | Statistical analysis

The mean age at attainment of sexual maturity (ASM) for females and males was calculated using two different methods for comparison to previous studies: (1) the method by DeMaster (1978) modified by Dabin, Cossais, Pierce, and Ridoux (2008) and (2) the logistic regression. For the first method, females aged 4–7 and 11–16 years old, and males aged 4–7, 8–11, and 14–20 years were combined because the sample size must be >1 for each age group. For the logistic regression, ASM was estimated as the age when 50% of the individuals were predicted to be sexually mature.

The mean length at attainment of sexual maturity (LSM) for females and males was estimated using a logistic regression. Samples were pooled into 5 cm body length intervals and the mean length of individuals within each interval was used in the regression.

Statistical tests were performed in SigmaPlot 14.0 (Systat Software Inc, San Jose, CA). The logistic regression for ASM and LSM was performed using SAS Version 9.4 (SAS Institute Inc, Cary, NC). Data were tested for normality using the Shapiro-Wilk test and for homogeneity of variance using Levene’s test. When data violated normality and/or homogeneity assumptions, nonparametric tests were used (Wilcoxon signed rank test for paired samples and Mann-Whitney rank sum test for independent samples). Independent *t* tests or paired *t* tests were used when data were normally distributed with equal variances. As sample size of mature females was small, the Fisher's exact test was used to test if females in this sample exhibited ovulation asymmetry. The level of statistical significance was $p \leq .05$ for all tests.

3 | RESULTS

A total of 168 franciscana dolphins (73 females and 95 males) was analyzed. Total length was not taken from three individuals (one female and two males) because their rostra were broken/damaged with the net winch. Teeth from 162 specimens (90 males, 72 females) were collected; for the remaining specimens, the teeth fell out and were lost or mixed with teeth from other specimens and could not be used.

3.1 | Females

Ovaries were examined from 73 females (69 incidentally captured and 4 stranded). Corpora were found in 18 (24.7% mature) and absent in 55 (75.3% immature). Among mature females, six were pregnant and two were lactating. The ovarian morphometric parameters were significantly larger in mature than immature females (Table 1). The increase in ovarian mass is apparent when specimen total length exceeded 125 cm and, except for two immature females, all individuals with combined ovary weight above 1.1 g were mature (Figure 1). The two immature exceptions were females that had ovaries with well-developed follicles and ovary weights that overlapped that of mature ovaries. Both females were near the length and age at maturation. These 2 females are PA-357 (130 cm, 2 years old, combined ovary weight 2.5 g) and PA-363 (127.5 cm, 1 year old, combined ovary weight 1.8 g).

The distribution of corpora between left and right ovaries varied among the 17 mature individuals with corpora counts. One mature female had dry ovaries that could not be sectioned to count ovarian corpora. Of females with >1 corpus (n = 14), there was significant asymmetry of ovulation (Fisher's exact test, p = 0.006). Five (35.7%) had corpora only or predominantly in the left ovary and two (14.3%) had corpora only or predominantly in the right ovary. For all three females with only one corpus, the corpus occurred in the left ovary. The maximum number of corpora in a single female was 16 (n = 2). For mature females, data on corpora counts, ovarian dimensions, and fetus information are presented in Table 2. The combined ovary weight increased as the number of corpora increased (Figure 2). Despite the relatively small sample size, there was correlation between age and number of corpora (r Spearman = 0.76, p < 0.01, n = 17; Figure 3). An outlier female (PA-332) presented 16 ovarian corpora despite being only 6 years old. Reexamination of the corpora and the age estimate gave the same results.

A total of 72 females had data on age and sexual maturity (Figure 4). Estimated ages ranged from 0 to 16 years. The oldest immature (n = 2) and the youngest mature female (n = 1, pregnant with 37 cm fetus) were both 2 years old. All females older than 3 years were classified as mature. Using the method described by Dabin et al. (2008), the estimated ASM for females was 2.72 ± 0.11 years (95% CI = 2.51–2.94 years). Using the logistic regression method, the estimated ASM for females was 2.4 years (95% CI = 2.2–2.9 years). The mean age of three females collected when they attained sexual maturity (i.e., with only one CL) was 2.66 years, close to the estimated ASM. Pregnant (*n* = 6) and lactating (*n* = 2) females had estimated ages ranging from 2 to 9 years and 10 to 15 years, respectively. No female was pregnant and lactating simultaneously. Data on length and sexual maturity were available for 70 females. The length of sexually immature and mature females ranged from 65.5 to 136.0 cm and from 125.0 to 146.0 cm, respectively. Using the logistic regression, the estimated LSM for females was 128.5 cm (95% CI = 124.5–132 cm).

Among the 18 mature females, seven nonpregnant and nonlactating females had a CL on their ovaries. Another three females had only small CAs so they were not considered for analysis of timing of ovulation. The seven females were collected in December (*n* = 1), January (*n* = 2), February (*n* = 1), and July (*n* = 1), with precise collection month not recorded for the remaining two specimens. The mean diameter of CL from these seven females was 11.6 mm (range: 8.7–14.1 mm). The APR was estimated as 0.36 ± 0.11 pregnant females/year using the gestation period of 0.93 years, i.e., 11.2 months (Danilewicz, 2003). The CI was estimated as 2.8 ± 0.89 years.

3.2 | Males

Testes were examined from 95 males (94 incidentally captured and 1 stranded). Testicular histological results from these males revealed 66 immature (69.5%) and 29 mature (30.5%) individuals. The testicular morphometric parameters were significantly larger in mature males than in immature males (Table 3). Testicular mass increased rapidly after a specimen total length over 100 cm and all individuals with combined testis weight above 4 g were mature (Figure 5).

Age and data on sexual maturity were available for 90 males (Figure 4). The estimated ages ranged from 0 to 20 years. The proportion of immature to mature males was 68.9% (n = 62) to 31.1% (n = 28). The oldest immature male was 3 years old and the youngest mature male was 1 year old (n = 3). All mature testes had a greater mass than immature testes regardless of age (Figure 6). Based on the method described by Dabin et al. (2008), the estimated ASM for males was 2.67 ± 0.36 years (95% CI = 1.97–3.37 years). Using the logistic regression method, the estimated ASM for males was 2.0 years (95% CI = 1.7–2.5 years). Length and data on sexual maturity were available for 92 males.

The length of sexually immature and mature males ranged from 59.0 to 117.0 cm and from 104.0 to 125.0 cm, respectively. Using the logistic regression method, the estimated LSM for males was 114 cm (95% CI = 112–116.5 cm).

Data on combined testis weight were available for 21 mature males. The combined testis weight did not vary throughout the year (Figure 7).

4 | DISCUSSION

This relatively recent and large sample from fransciscana carcasses revealed some novel findings for the species and potentially for odontocetes. The current sample included males that were sexually mature at 1 year of age; the prior minimum estimate was 2 years (Danilewicz et al., 2004; Kasuya & Brownell, 1979; Panebianco et al., 2012). The sample also included a 2-year-old pregnant female; the youngest previously reported pregnant female was 3 years old (Danilewicz, 2003). The 2-year-old female had substantial dentinal deposition in the second GLG, potentially approaching age 3, which suggests pregnancy occurred at 2 rather than 1 year of age. The early ages at maturity for males and pregnancy for females in the current study present new records for cetaceans. Odontocetes with the most similar life histories are the phocoenids, and the youngest ages at maturation are at least 3 years for males and females across a range of studies (e.g., harbor porpoise, *Phocoena phocoena*: Read & Hohn 1995; Lockyer 2003; Lockyer & Kinze, 2003; Learmonth et al., 2014; vaquita, *Phocoena sinus*: Hohn, Read, Fernandez, Vidal, & Findley, 1996; finless porpoise, *Neophocaena asiaeorientalis*: Lee et al., 2013; Dalls porpoise, *Phocoenoides dalli*: Ferrero & Walker, 1999). The current sample also increased the maximum age of males. For the franciscana, while the oldest female previously reported was 21 years old (Pinedo & Hohn, 2000), the record for a male was 17 years (Botta et al., 2010). The current sample included a 20-year-old male. This specimen (PA-246) exhibited all stages of spermatogenesis, including a few spermatozoids, so this male was sexually active.

Among life-history studies of the franciscana, many results are similar while some differences seem likely. The estimated ASM of 2.4–2.7 years for females and 2.0–2.7 years for males in the present study are the lowest estimates for the species throughout its distribution (Tables 4 and 5), but are close to results presented by Kasuya and Brownell (1979) for FMA III. The only other published estimate of ASM for FMA II was 4–5 years (Rosas & Monteiro-Filho, 2001), from a sample of six mature females and eight mature males and with no methodology or raw data provided. From studies in which sufficient detail was presented, it appears that age classes which contain immature and mature specimens (i.e., indeterminate age classes) encompass ages 2–4 years, excluding the three mature 1-year-old males in the current study. So, the ASM for franciscana dolphins is expected to be encompassed by these values. The estimated LSM for females and males in the present study was similar to prior estimates for the adjacent FMA I (Ramos et al., 2000) and FMA II (Rosas & Monteiro-Filho, 2001) but smaller than those for the other FMAs, despite the different methodologies used (Tables 4 and 5). Prior published evidence supports that the total length of stocks from FMA I and II are smaller than the other FMAs (Barbato et al., 2012), which is consistent with a smaller LSM for the northern two stocks.

Gonadal characteristics are also similar among fransciscana studies. Ovulation asymmetry, primarily with left ovary preference, occurred in some females in the present study. The same was previously reported for specimens from FMA III (Danilewicz, 2003; Harrison et al., 1981). Panebianco et al. (2016) reported no ovulation asymmetry overall in a sample of 11 females with corpora counts; ovulations were reported in both ovaries, although some females had corpora on both ovaries while others had corpora on only one ovary, not consistently left or right. Thus, the findings seem similar to the current study in which individual variation is apparent and that includes some females with asymmetric ovulation. Ovulation seems to occur throughout the year. However, most females with recent ovulations were observed mainly in the austral summer (December to February) (Danilewicz, 2003; Harrison et al., 1981; Rosas & Monteiro-Filho, 2001; current study). There does not seem to be reproductive seasonality for male franciscana dolphins (Danilewicz et al., 2004; Kasuya & Brownell, 1979; current study). Testes weight seems to accurately identify mature males without the need for histological examination, as has been found in studies of other franciscana stocks (Danilewicz et al., 2004; Panebianco et al., 2012) and other species (e.g., Collet &

Saint-Girons, 1984; Hohn et al., 1985; Kasuya & Marsh, 1984; Kemper, Trentin, & Tomo, 2014; Murphy, Collet, & Rogan, 2005; Neimanis, Read, Foster, & Gaskin, 2000).

Reported estimates of APR are variable among the FMAs. The estimated APR for FMA II (0.36 ± 0.11) observed in the present study was similar to the estimated values reported for FMA IV (0.36 ± 0.02; Panebianco et al., 2016) but much lower than for FMA III (0.66 ± 0.09; Danilewicz, 2003). The corresponding calving interval for the present study was 2.8 years, almost double that of FMA III, 1.5 years (Danilewicz, 2003). APR and CI are valid only when the analyzed sample represents all the age classes in the population (Kasuya, 2017). As most samples for franciscana dolphin reproductive studies come from incidental catches, the low pregnancy rate may be due to a bias in the bycatch towards young individuals as occurs in many gill net fisheries and has been reported for the franciscana (Negri et al., 2016; Ott et al., 2002). Samples from FMA III, which showed a higher pregnancy rate, included both stranded and incidentally captured individuals, but the exact number of samples from each source of sampling was not reported (Danilewicz, 2003).

Given the limited number of franciscana studies, most of which have quite small sample sizes especially for mature animals, it seems useful to compare the life history of the franciscana with that of a species with a similar life history. Harbor porpoises, as a model, are small odontocetes (generally with asymptotic lengths of 150–160 cm for females and 140–145 cm for males) that can be generalized as having maximum ages of about 20 years but with an average life span of close to half that, a gestation period of <1 year (10–11 months), and most populations having an annual or biannual calving with females not uncommonly simultaneously pregnant and lactating (Learmonth et al., 2014; Lockyer, 2003; Lockyer & Kinze, 2003; Lockyer, Heide-Jørgensen, Jensen, Kinze, & Sørensen, 2001; Read & Hohn 1995). The estimated intrinsic rate of population growth is 5%–10% (Barlow & Boveng, 1991; Caswell, Brault, Read, & Smith, 1998; Woodley & Read, 1991). Some population variation occurs, for example, in Scotland porpoises' pregnancy rate is 0.34–0.40 (CI 2.5–3 years), likely due to a prevalence of females with a poor health status, and ASM is high (4.4 years for females and 5.0 years for males; Learmonth et al., 2014). Franciscana dolphins are smaller than the harbor porpoise, with maximum ages of about 20 years but with an average life span of close to half that, and a gestation period of <1 year (9–11 months) (Danilewicz, 2003; Harrison et al., 1981; Kasuya & Brownell, 1979; Ramos et al., 2000; Rosas & Monteiro-Filho, 2001). ASM ranges from about 2–4 years, so similar to or a little lower than most porpoise populations. While samples sizes have been small, results suggest that the calving interval for franciscana dolphins may be higher than that of harbor porpoises, closer to 2–3 years, which is supported by few reports of simultaneous pregnant and lactating females (Danilewicz, 2003; Panebianco et al., 2016). A model to estimate intrinsic growth rates for the franciscana maybe also be useful for comparison of the effects of high levels of bycatch similar to that done for harbor porpoise (sensu Caswell et al., 1998); that model is beyond the scope of the current study.

There are some important caveats when comparing this study to some of the earlier works. First, samples from franciscana dolphins are difficult to obtain. As a result, most of the studies are done with small samples, especially of mature individuals. Because it appears that there are stock differences in some life-history traits, combining samples to increase sample size is not recommended unless it can be shown that the differences are stochastic. Second, many, but not all earlier studies on franciscana provided insufficient information on methodologies for estimating parameters so the validity of the methods or lack of variance estimates constrain valid comparisons of parameters among studies.

We were able to update reproductive parameters for female and male franciscanas with a much larger sample size than previously available for FMA II. The young age at maturation reported here seems to be the common pattern in this species. However, despite this low ASM, the large calving interval presented by this franciscana stock combined with the current levels of bycatch (Secchi, 2010) have the potential to reduce population growth rates to a level that is insufficient to compensate for this mortality. The most important application of these reproductive parameters is to subsidize population viability analysis used to guide conservation action. Therefore, although uncertainty exists due to low sample sizes, the information presented here represents a valuable effort to obtain more reliable parameter estimates for the FMA II, needed for a better assessment of its current conservation status.

ACKNOWLEDGMENTS

The following institutions provided financial support to this study: Cetacean Society International (1995 to 2018), WWF - Fundo Mundial para a Natureza (CSR-050/96; 1996 to 1997), Earthwatch Institute (2003 to 2007), Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira (PROBIO) - Ministério do Meio Ambiente (BIRD/GEF/CNPq/ 2004 to 2005), and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP process number 2010/51323-6; 2011 to 2015). DFS had a 2-year Masters fellowship (FAPESP process 2008/56541-1) and MCOS had a 30-month fellowship (CNPq Produtividade em Pesquisa process number 308331/2010-9), both related to the results presented in this study. The authors thank all fishermen who helped in collecting data. Ednilson da Silva was the key community member in the field, handling and receiving logbooks and present at all necropsies. José Silvio Govone provided assistance with statistics, Renato Zacarias Silva provided assistance on gonads histological techniques, and Daniel Danilewicz and María Victoria Panebianco helped both with statistics and sexual maturity analyses. Samples were collected under permits SISBIO #15572-2 and #35635.

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TABLE 1 Summary of ovarian morphometric parameters of female franciscana dolphins (*Pontoporia blainvillei*) from southeastern Brazil between 2005 and 2016, excluding pregnant and lactating females. The statistical test is for differences between immature and mature gonads.

Parameter	Mat	Minimum–maximum	Mean	95% CI	Median	*SD*	*n*	Statistical test and results
MOW (g)	I	0.10–1.25	0.20	0.13–0.26	0.10	0.22	46	Mann-Whitney rank sum test,
	M	0.55–2.20	1.34	0.96–1.72	1.35	0.53	10	*U* = 6.00, *p* < .001
MOL (mm)	I	6.20–19.30	11.39	10.58–12.21	11.50	2.90	51	*t* = −4.767, 59 *df*, *p* < .001
	M	6.75–21.20	16.63	13.47–19.80	18.43	4.42	10	
MOWi (mm)	I	2.85–10.45	5.08	4.65–5.52	4.55	1.55	51	Mann-Whitney rank sum test,
	M	2.70–14.26	10.54	7.99–13.09	11.13	3.56	10	*U* = 62.00, *p* < .001
OMI (g/mm)	I	0.007–0.071	0.016	0.013–0.020	0.012	0.012	45	Mann-Whitney rank sum test,
	M	0.043–0.111	0.081	0.065–0.097	0.082	0.023	10	*U* = 5.00, *p* < .001
%ROW (%)	I	0.001–0.013	0.003	0.003–0.004	0.003	0.002	45	Mann-Whitney rank sum test,
	M	0.007–0.020	0.013	0.010–0.016	0.013	0.005	10	*U* = 9.00, *p* < .001

Note. Mat: maturity status; I: immature individuals; M: mature individuals; MOW: mean ovarian weight; MOL: mean ovarian length; MOWi: mean ovarian width; OMI: ovarian maturity index; %ROW: percentage of relative ovarian weight.

TABLE 2 Ovarian dimensions, corpora counts, age, and fetuses information of mature female franciscana dolphins (*Pontoporia blainvillei*) from southeastern Brazil between 2005 and 2016.

Female #	Weight (g)		Lenth (mm)		Width (mm)		*n* corpora		*n* total corpora	Age (years)	Fetus information (if pregnant)			
	Left	Right	Left	Right	Left	Right	Left	Right			Weight (g)	Lenth (cm)	Sex	Month collected
PA-241	3.3	0.6	25	15	16.9	9.2	2	0	2	2	—	—	—	Jan
PA-247 (L)[a]	1.3	3	15.8	22.6	9.3	12.1	8	8	16	15	—	—	—	Mar
PA-252	0.6	2.1	15.3	21.4	7.7	11.9	1	3	4	2	—	—	—	Feb
PA-256 (L)	1.7	0.4	20	11.9	14.1	7.4	—	—	—	10	—	—	—	Mar
PA-277	0.8	1.1	16.5	20.5	10.6	9.9	2	2	4	8	—	—	—	May
PA-278 (P)[b]	4	0.5	24.4	11.3	15.3	7.2	6	1	7	9	6.7	6.75	—	Aug
PA-304 (P)	4.2	1.2	27.3	18.2	16.1	14.3	3	5	8	8	752	39.5	F	Jul
PA-316	1.8	0.4	15.7	13.7	11.9	8.8	1	0	1	3	—	—	—	Dec
PA-325	0.5	0.6	12.6	13.3	6.5	6.7	0	2	2	2	—	—	—	Jun
PA-331 (P)	5.6	0.5	12.6	5.1	8.6	3.2	10	0	10	9	2,600	59	F	Sep
PA-332 (P)	5	0.8	28	16.3	18	1	10	6	16	6	916	43	M	Sep
PA-369 (P)	3.1	0.3	23.5	13.5	15.6	6.1	1	0	1	2	551	37	M	—
PA-378	3.9	0.5	27.8	14.6	14.6	9.2	5	0	5	7	—	—	—	—
PA-380	1.1	0.4	—	13.5	—	5.4	1	0	1	3	—	—	—	—
PA-387	0.8	2	12.1	17.1	12.4	14.1	2	2	4	2	—	—	—	Jan

PA-398 (P)	2.5	0.5	22.5	13.7	16.2	7.5	2	0	2	3	306	28.1	M	Jun
PA-416	1.5	1.2	23.2	15.4	14.9	13.66	6	6	12	16	—	—	—	Feb
PA-421	2.6	1	24.1	15.9	15.8	10.65	6	4	10	10	—	—	—	Jul

[a]Lactating. [b]Pregnant.

TABLE 3. Summary of testicular morphometric parameters of male franciscana dolphins (*Pontoporia blainvillei*) from southeastern Brazil between 2005 and 2016. The statistical test is for differences between immature and mature gonads.

Parameter	Mat	Minimum–maximum	Mean	CI 95%	Median	*SD*	*n*	Statistical test and results
MTW (g)	I	0.10–2.00	0.88	0.76–1.01	0.85	0.43	48	Mann-Whitney rank sum test,
	M	2.35–5.20	3.76	3.35–4.18	3.95	0.91	21	U = 0.00, p < .001
MTL (mm)	I	10.90–45.25	28.26	26.38–30.14	28.65	6.68	51	t = −8.017, 70 df, p < .001
	M	29.55–59.30	42.59	39.23–45.95	42.9	7.38	21	
MTWi (mm)	I	2.45–9.80	6.45	6.04–6.85	6.5	1.41	50	t = −11.609, 68 df, p < .001
	M	8.95–16.60	11.31	10.40–12.23	11.03	1.96	20	
TMI (g/mm)	I	0.008–0.106	0.031	0.026–0.035	0.028	0.015	48	Mann-Whitney rank sum test,
	M	0.059–0.110	0.088	0.082–0.094	0.094	0.013	21	U = 20.00, p < .001
%RTW (%)	I	0.003–0.033	0.016	0.014–0.018	0.015	0.01	47	Mann-Whitney rank sum test,
	M	0.030–0.070	0.051	0.046–0.056	0.05	0.012	21	U = 3.00, p < .001

Note. Mat: maturity status; I: immature individuals; M: mature individuals; MTW: mean testicular weight; MTL: mean testicular length; MTWi: mean testicular width; TMI: testicular maturity index; %RTW: percentage of relative testicular weight.

TABLE 4 Estimated age and length at attainment of sexual maturity and respective methods for female franciscana dolphins (*Pontoporia blainvillei*) throughout the species distribution. Franciscana Management Areas (FMAs) are indicated. The standard deviation was included if it was available in the referenced paper. "*n*" is the total sample size for the study.

Source	FMA	Location	Age at sexual maturation (years)			Length at sexual maturation (cm)		
			Value	**Method**	***n***	**Value**	**Method**	***n***
1	I	Rio de Janeiro (21º37'S), Brazil	3	(–)	43	130	(–)	43
2	II	São Paulo (25º18'S) and Paraná (25º58'S), Brazil	4–5	(–)	18	122–126	50% mature	18
3	II	São Paulo (25º24'S) and Paraná (25º21'S), Brazil	2.72 ± 0.11 2.43	Dabin *et al.* (2008) Logistic regression	72 72	128.5	Logistic regression	70
4	III	Punta del Diablo (~34º04'S), Uruguay	2.7	Linear regression (50% mature)	86	140.3	Linear regression (50% mature)	40
5	III	Rio Grande (32º04'S) and Tramandaí (29º58'S), Brazil	3.7 ± 0.36 3.5	DeMaster (1978) Logistic regression	72 72	138.9 ± 3.14	Ferrero and Walker (1995)	94
6	IV	Necochea (~38º37'S), Bahía Blanca (38º44'S) and Él Condor (41º03'S), Argentina	3.92 ± 0.09 3.42	DeMaster (1978) Logistic regression	31 31	133.5 ± 11.11	Ferrero and Walker (1995)	31

Note. 1: Ramos *et al.* (2000); 2: Rosas & Monteiro-Filho (2001); 3: Present study; 4:

Kasuya & Brownell (1979); 5: Danilewicz, (2003); 6: Panebianco *et al*. (2016). (–): Method was not specified.

TABLE 5 Estimated age and length (in cm) at attainment of sexual maturity and respective methods for male franciscana dolphins (*Pontoporia blainvillei*) throughout the species distribution. Franciscana Management Areas (FMAs) are indicated. The standard deviation was included if it was available in the referenced paper. “*n*” is the total sample size for the study.

Source	FMA	Location	Age at sexual maturation (years)			Length at sexual maturation (cm)		
			Value	**Method**	***n***	**Value**	**Method**	***n***
1	I	Rio de Janeiro (21º35’S), Brazil	2	(–)	39	115	(–)	39
2	II	São Paulo (25º18’S) e Paraná (25º58’S), Brazil	4–5	(–)	22	112–116	50% mature	22
3	II	São Paulo (24º24’S) e Paraná (25º21’S), Brazil	2.67 ± 0.36	Dabin *et al.* (2008)	90	114	Logistic regression	90
			2	Logistic regression	90			
4	III	Punta del Diablo (~34º04'S), Uruguay	2–4	(–)	25	131.4	Linear regression (50% mature)	48
5	III	Rio Grande (32º08’S) and Tramandaí (29º58’S), Brazil	3.6 ± 0.47	DeMaster, 1978	47	128.2 ± 1.49	Ferrero and Walker (1995)	110
			3	Logistic regression	47			

6	IV	Necochea (~38º37'S) and Bahia Blanca (38º44'S), Argentina	3.54 ± 0.17	DeMaster (1978)	28	126.19 ± 0.18	Ferrero and Walker (1995)	38
			2.92 ± 0.30	Logistic regression	28	126.27 ± 3.97	Logistic regression	40

Note. 1: Ramos *et al.* (2000); 2: Rosas and Monteiro-Filho (2001); 3: Present study; 4: Kasuya and Brownell (1979); 5: Danilewicz *et al.* (2004); 6: Panebianco *et al*. (2012). (–): Method was not specified.

FIGURE 1 Combined ovary weight on standard length of female franciscana dolphins (*Pontoporia blainvillei*) collected in southeastern Brazil between 2005 and 2016.

FIGURE 2 Combined ovary weight relative to the total number of corpora of mature female franciscana dolphins (*Pontoporia blainvillei*) from southeastern Brazil between 2005 and 2016. CL: corpus luteum.

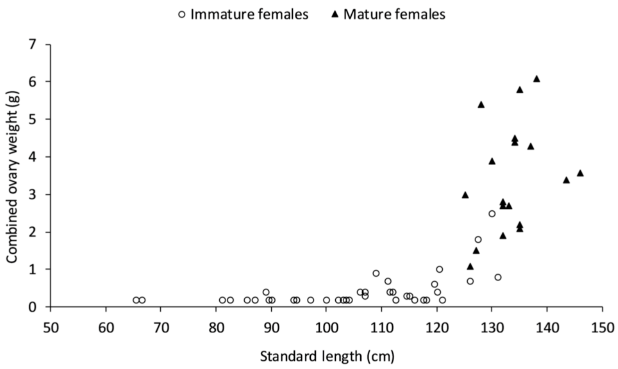
FIGURE 3 Number of ovarian corpora by age of mature females of franciscana dolphins (*Pontoporia blainvillei*) from southeastern Brazil between 2005 and 2016. The gray area represents 95% confidence intervals.

FIGURE 4 Age distribution of franciscana dolphins (*Pontoporia blainvillei*) (n = 162) from southeastern Brazil between 2005 and 2016.

FIGURE 5 Combined testis weight on standard length of male franciscana dolphins (*Pontoporia blainvillei*) from southeastern Brazil, between 2005 and 2016.

FIGURE 6 Combined testis weight on age of male franciscana dolphins (*Pontoporia blainvillei*) from southeastern Brazil, between 2005 and 2016. A total of 29 males were excluded because testis weight or age were not available, including one 3-year-old immature male.

FIGURE 7 Combined testis weight on month for male franciscana dolphins (*Pontoporia blainvillei*) from southeastern Brazil, between 2005 and 2016.



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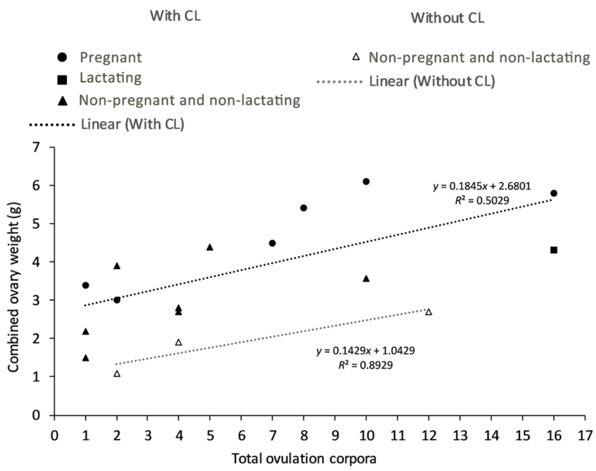

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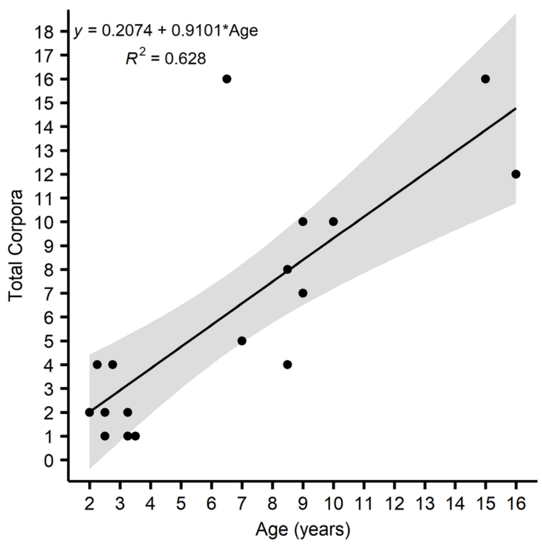

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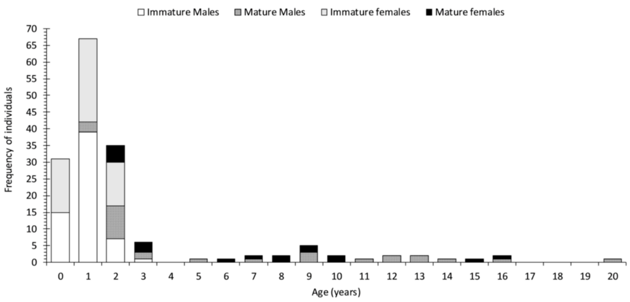

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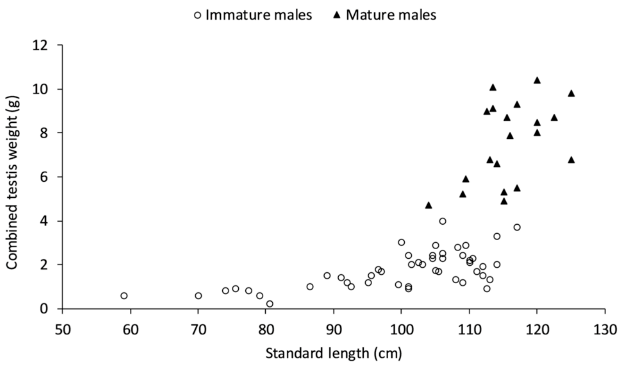

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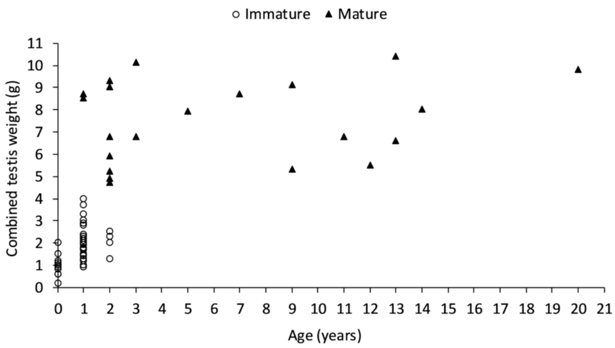

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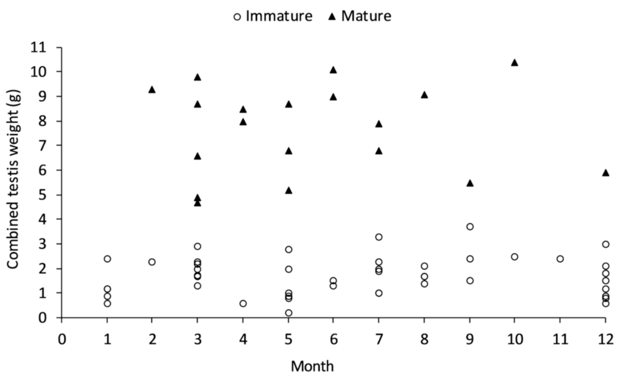

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