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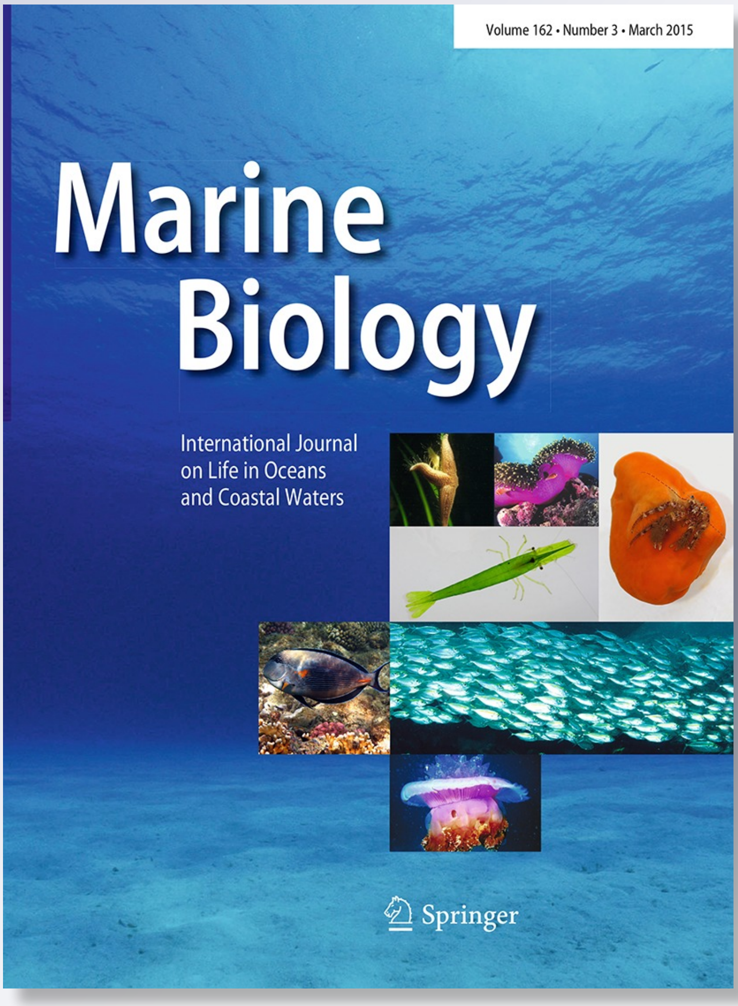

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ORIGINAL PAPER

Using mark-recapture and stranding data to estimate reproductive traits in female bottlenose dolphins (*Tursiops truncatus*) of the Southwestern Atlantic Ocean

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Abstract Despite bottlenose dolphins being well studied in several regions around the world, there is very limited information about the reproduction of these animals in the Southwestern Atlantic Ocean (SWA). In this study, data from a long-term mark-recapture and stranding monitoring program were used to estimate life history traits of female bottlenose dolphins inhabiting the Patos Lagoon estuary, a sub-tropical coastal region in the SWA. From the analysis of 32,296 high-quality dorsal fin photographs, the fate of 37 individual females and 66 of their calves was tracked. Results supported a birth pulse dolphin community, with most births occurring during late spring and summer, in association with increasing water temperature and food supply. Female bottlenose dolphins first reproduced at a minimum age of 8 years. Mean inter-birth interval was 3 years (mode = 2), and fecundity was 0.11. A clear change in the $\delta^{13}C$ and $\delta^{15}N$ profiles in teeth from stranded carcasses near age 2 indicated the most probable weaning age. First and second year annual calf survival estimates were 0.84 (95 % CI 0.72–0.90) and 0.86 (95 % CI 0.74–0.94), respectively. No evidence was found to support that timing of birth plays a role in calf survival, suggesting that variability in water temperature and food resources within the year is unlikely to impact upon survival of calves. Older females reproduced at lower rates, suggesting an age-related decrease in reproductive fitness. At an individual level, marked variation in reproductive success was observed. Our findings highlight the importance of long-term studies for long-lived mammals to yield individual- and population-level parameters for demographic and viability analyses that are useful for conservation and management.

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P. F. Fruet (✉)
Programa de Pós-Graduação em Oceanografia Biológica, Univeridade Federal do Rio Grande - FURG, Rio Grande, Brazil
e-mail: pfruet@gmail.com

P. F. Fruet · R. C. Genoves · E. R. Secchi
Museu Oceanográfico "Prof. Eliézer C. Rios", FURG, Rio Grande, Brazil

P. F. Fruet · R. C. Genoves · S. Botta · E. R. Secchi
Laboratório de Ecologia e Conservação da Megafauna Marinha (EcoMega), Instituto de Oceanografia, FURG, Rio Grande, Brazil

P. F. Fruet · L. M. Möller
Cetacean Ecology, Behaviour and Evolution Lab, School of Biological Sciences, Flinders University, Adelaide, Australia

P. F. Fruet · L. M. Möller
Molecular Ecology Laboratory, School of Biological Sciences, Flinders University, Adelaide, Australia

Introduction

The rate at which population abundance changes largely depends on individuals' ability to reproduce. In slow reproductive species, this is primarily governed by females' survival and reproductive potential, as most population dynamics models assume that some variation in male availability does not necessarily limit female reproduction in polygamous or promiscuous systems (Caswell 2001). Female reproductive potential is influenced by a series of factors such as age at first reproduction, fecundity, inter-birth interval (IBI), longevity, and senescence, which in turn underlies complex interactions between biological, ecological, and social factors (e.g., Lindström 1999; Stanton and Mann 2012). Therefore, fitness (or its associated constituents, survival, and reproduction) is expected to vary among closely related species, and between and within populations of the same species, as local populations are exposed to specific environmental conditions, social systems, and individual variation in coping with these forces.

The common bottlenose dolphin (*Tursiops truncatus*) (hereafter "bottlenose dolphin") is widely distributed and inhabits several kinds of environments such as open oceans, river mouths, estuaries, and tidal cricks (e.g., Wells and Scott 1999). As a result of such plasticity, its life history parameters and reproduction onset can vary at different scales along its distribution. For example, female bottlenose dolphins apparently start to reproduce early in life in the Sarasota Bay community, Northwest Atlantic (minimum age at first reproduction is 6 years; mean = 9; Wells and Scott 1990; Wells 2000), in contrast to individuals studied in Doubtful Sound, South Pacific (mean = 11.6 years; Henderson 2012). Generally, bottlenose dolphins inhabiting high latitudes have a well-defined birth season coincident with periods of high levels of prey density (e.g., Henderson et al. 2014) in contrast to a diffuse birth period reported for those in lower latitudes (e.g., Urian et al. 1996) where resources are less predictable in space and time. Average IBI also varies among regions, and female reproductive success (RS) can vary greatly between individuals within populations (Wells 2000; Henderson et al. 2014). Thus, estimating reproductive parameters at both populational and individual levels is important for a better understanding of the basic biology of the species, how it interacts with the environment, and how it impacts upon population dynamics.

A common approach for estimating life history parameters in cetaceans is based on age estimation and histological or gross observation of gonadal tissue from stranded or bycaught individuals (e.g., Perrin and Donavan 1984). This method has been widely used to estimate reproductive parameters of bottlenose dolphins in several regions of the world (e.g., Cockcroft and Ross 1990; Stolen and Barlow 2003). However, such cross-sectional studies often provide only a "snapshot" of some parameters at a specific point in time with no assessment of individual and temporal variability.

Alternatively, information on life history traits can be obtained through the use of mark-recapture (MR) data to track naturally marked dolphins over the time (i.e., longitudinal studies). When repeated sightings of marked females over multiple years are available, it is possible to build individual reproductive histories from which fertility, birth season, birth intervals, and age at first reproduction can be assessed (Hammond et al. 1990). This type of data allows the description of reproduction patterns over time and also provides the opportunity to investigate individual variation in reproductive rates, which is often lacking in cetacean studies.

Bottlenose dolphins are common in the coastal waters of southern Brazil. In this area, they are typically found forming small and year-round resident communities (sensu Wells et al. 1987) associated to estuaries and river mouths such as in the Patos Lagoon estuary (PLE) and the adjacent coast (Castello and Pinedo 1977), with restricted dispersal (Fruet et al. 2014).

The small and resident community of bottlenose dolphins from PLE has been studied since the mid-1970s (Castello and Pinedo 1977). Mark-recapture data collected non-systematically before 2005 and systematically since then made possible to track several individuals for many years, allowing determination of their sex, age, and some key life history parameters. Presently, approximately 70 % of the individuals, including all adult females, are recognized by natural marks in their dorsal fins (Fruet et al. in press a). In addition, the regular beach surveys conducted along the core area of the community (Fruet et al. 2012) made possible to collect stranding carcasses of some marked individuals with known reproductive histories from which relevant life history traits can be inferred (e.g., calving season, age at death, and last reproduction).

While substantial information about female bottlenose dolphin reproductive parameters has emerged in the last decades, limited information is available for bottlenose dolphins from the southwestern Atlantic Ocean (SWA) (Fruet et al. in press b). In this study, we used 8 years of data collected from a systematic MR study to estimate life history traits of female bottlenose dolphins of the PLE community, including calving seasonality, IBIs, weaning onset, and age at first reproduction. A database from a >35-year-long stranding monitoring program provided supporting evidence for some of these estimates. We also investigated temporal and individual variation in female RS and estimated calf survival rates. As life history theory predicts that births should pulse during better environmental conditions in areas subjected to substantial seasonal changes in biological conditions, such as the PLE, we hypothesized that calves born during the pulse should have greater chances of survival. The results of this study will provide crucial information for future comparative analysis aiming at understanding how this top predator interact with distinct habitat types subjected to divergent environmental conditions along its distribution.

Methods

Study area and surveys

Boat-based surveys for monitoring bottlenose dolphins were conducted regularly between December 2004 and March 2013 in the PLE and adjacent coast, encompassing

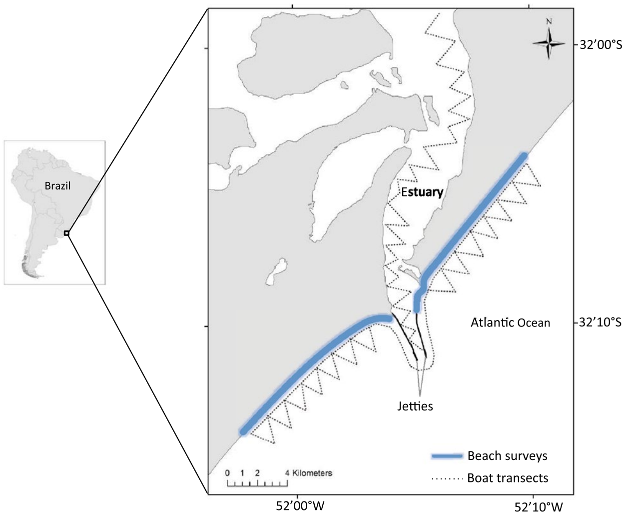

Fig. 1 Map of study area in the SWA showing transects designed for mark-recapture (MR) (*dotted lines*) and beach surveys (*blue lines*) for common bottlenose dolphins (*T. truncatus*) in the PLE and surrounding coastal areas in southern Brazil

an area of approximately 85 km^2 (Fig. 1). This is the core area of occurrence of this dolphin community (Mattos et al. 2007; Di Tullio 2009). The area is characterized by high anthropogenic influence (such as boat traffic and industrial activities) and turbid, though high productive waters, being considered one of the most productive fishing grounds in Brazil (e.g., Odebrecht et al. 2010). As typical of sub-tropical regions, this area is subject to strong seasonal variation in temporal and spatial patterns of resources, including the occurrence and abundance of fish assemblages (Garcia et al. 2012; Rodrigues and Vieira 2013).

Surveys were run throughout the year using ca. 5-m-long boats powered by 60 or 90 hp outboard engines. These were photo-identification surveys that generally followed pre-determined routes consisting of zigzag or linear transect inside the estuary and/or perpendicular transects to the adjacent coast. As a standard protocol for this boat-based monitoring program (see Fruet et al. in press a for more details), photo-identification took place for every dolphin or group of dolphins encountered using digital single lens reflex (SLR) cameras equipped with 300 mm (*f* 2.1) or 70–300 mm (*f* 4.5–5.6) lens.

Individual identification

In the laboratory, each photograph was graded relative to photographic quality (Q_1–Q_3). To be considered excellent (Q_1), the dorsal fin photograph needed to be clearly visible and large enough to allow the detection of any irregularities on either its leading or trailing edge (i.e., dorsal fin required to be well exposed, in sharp focus, with the dorsal fin orientated perpendicular to photographer). Photographs not meeting these criteria (Q_2–Q_3) were excluded from the analysis. From Q_1 photographs, individuals were identified by the presence of long-lasting marks in their dorsal fins, such as cuts, nicks, and/or deformities (Würsig and Jefferson 1990). Only well-marked dolphins that could be consistently identified in a long-term basis were considered as marked individuals. Dolphins presenting single, subtle long-lasting marks, or other short-term duration mark-types (e.g., scratches, tooth rakes) were not considered for the analysis to avoid false positive/negative errors (Würsig and Jefferson 1990), except to assist in differentiating unmarked individuals to calculate annual crude birth rate (see below).

Identification of mothers and calves

We considered all large dolphins that have been recorded with a closely associated calf (small size, dark grey in coloration) on ≥3 independent sampling occasions (days) along the study period to be a "mother" (i.e., mature female). As calves generally do not acquire long-lasting marks in the dorsal fin in their first years of life, they were tracked by following their well-marked (supposedly) mothers until weaning. Temporary marks in the dorsal fin (e.g., scratches) were also used to assist in identifying calves without long-lasting marks.

Annual crude birth rate and fecundity

Number of births was obtained by counting individual newborns on an annual basis. The annual crude birth rate was calculated for each year as $\frac{N_b}{\hat{N}_T}$, where N_b is the total number of documented births, and $\hat{N}_T$ is the total abundance estimated for PLE dolphin community (Fruet et al. in press a).

We estimated fecundity (the number of female offspring produced by mature females in a given year, assuming the expected calf sex ratio of 1:1 for mammals; Caughley 1977) as a measure of the potential reproductive capacity of the PLE dolphin community. We used longitudinal photo-identification data to estimate the minimum number of mature females in the community in each given year. Non-systematic photo-identification data collected in the PLE between 1976 and 2004 were also used to assist our analysis. Using these data, individuals that have never been seen with a calf on ≥3 independent sampling occasions (days) during the 2005–2012 period, but that were classified as "mothers" in previous years, were also included as mature females. Thus, mean fecundity was calculated as

$$\hat{F}_i = \frac{1}{2n} \times \sum_{i=1}^{n} N_{ci}/N_{mi}$$

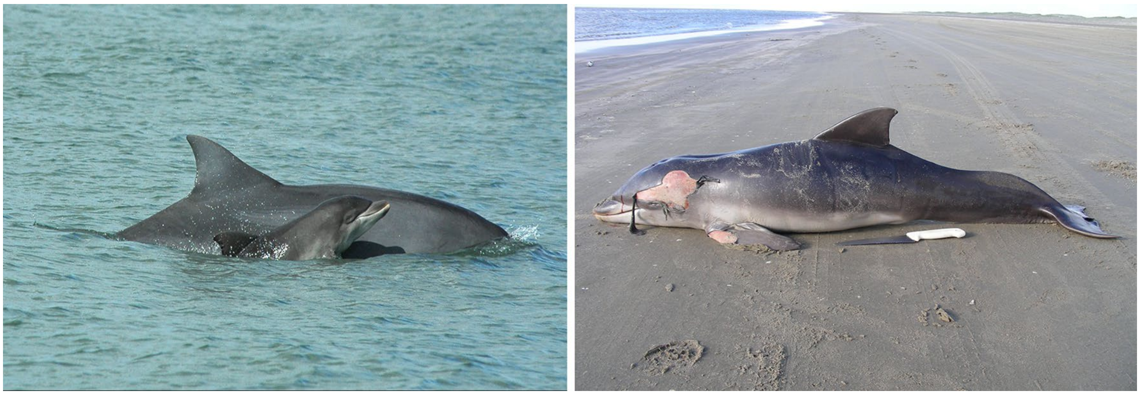

Fig. 2 Adult bottlenose dolphin accompanied by a small *dark-gray* calf was one of the typical criterions to identify mothers during mark-recapture surveys (*left*). Freshly stranded carcass found during beach surveys presenting clear characteristics of newborn such as prominent fetal folds and small size (*right*)

where $\hat{F}_i$ is the estimated fecundity in year i; n is the total number of years; N_{ci} is the number of calves born in year i; and N_{mi} is the number of mature females alive in year i.

Seasonality in reproduction

Seasonal patterns in reproduction were investigated based on the estimated month of births. The month of a calf's birth was estimated as the midpoint between the day of the last sighting of its mother without the newborn and the date of her first sighting with the calf (adapted from Wells et al. 1987). If this time exceeded 45 days, the estimated date of birth was not included in the analyses, except when calves presented clear characteristics of newborns (dark grey coloration, prominent fetal folds, floppy dorsal fin; Fig. 2), with birth assigned to the month of their first sighting. Additionally, calving seasonality was investigated by analyzing stranding data collected from the beach surveys carried out monthly by experienced personnel along the coastal beaches adjacent to the PLE between 2005 and 2012. Fresh to moderately decomposed carcasses (conditions code ≤ 3 of Geraci and Lounsbury 2005) with total length ≤ 140 cm and having any characteristic of a newborn mentioned above were assigned as neonates (Fig. 2). From these combined dataset, we constructed a frequency distribution of birth dates and defined the birth pulse (based on MR data) as the shortest period where ≥ 70 % of births had occurred. Seasons were defined as follows: spring (October–December), summer (January–March), autumn (April–June), and winter (July–September). Monthly surface water temperature data were collected in the estuary between December 2004 and March 2013. These data have been systematically collected since 1998 by *Universidade Federal do Rio Grande* (FURG) at a portion of the PLE frequently used by the dolphins as part of the Brazilian Long Term Ecological Research (BR_LTER) (Seeliger and Odebrecht 2010). Pearson's correlation coefficient was calculated to investigate the potential linear correlation between average monthly surface water temperature and calving.

Calf survival

We run Cormack–Jolly–Seber (CJS) open population models (Cormack 1964; Jolly 1965; Seber 1965; Lebreton et al. 1992) in program MARK 7.1 (White and Burnham 1999) to estimate annual calf survival rates from calves born to mothers with conspicuous dorsal fin marks that gave birth between 2004 and 2011 ($n = 30$). For each year, we collapsed sighting history data from surveys conducted within the birth pulse of the PLE dolphin community (November–March). As the minimum weaning age was estimated to be around 2 years for this dolphin community (see results), we assumed that a calf had died if it was no longer seen in association with its regularly sighted mother until the end of the calf's second year of life. In this case, we set calf's capture history to zero from the year of disappearance until the end of the study period. Otherwise, if survived, capture history was set to series of ones. We estimated age-specific survival by fitting age models to calf sighting history data, letting survival (Φ) be constant ($\cdot$) or to vary with time (t), with constant recapture probabilities for all candidate models (justified by intense field effort and high rates of encounter of adult females in this community; Fruet et al. in press a). Our models included the following age classes: 0–1, 1–2, and >2 years. The potential effect of timing of birth on calf survival until weaning was investigated by fitting models where the calf's sighting history data were split into two groups: dolphins born during the pulse birth season (December–February, $n = 34$) and born out-of-pulse birth season (March–November, $n = 10$). Dolphins born after 2011 were excluded from this analysis because not enough time has elapsed to estimate survival until weaning.

As the CJS goodness-of-fit (GOF) test neglects age effect, model fit was assessed by estimating the median variance inflation factor ($\hat{c}$). Estimated value of $\hat{c}$ was then used to adjust for overdispersion in the data (if $\hat{c} > 1$). In this case, the most parsimonious model was selected through an information-theoretic approach using the Quasi-Akaike Information Criterion adjusted for small sample size (QAICc) (Burnham and Anderson 2002). The model with the smallest QAICc is the best approximating model for the data. Evidence ratio (the ratio of weights between two models) was used to assess the likelihood of the biological hypothesis (Burnham and Anderson 2002). Survival estimates were averaged according to weights of candidate models to account for model selection uncertainty (Burnham and Anderson 2002).

Inter-birth interval

The IBI was estimated using two approaches (adapted from Mann et al. 2000). Firstly, we used the dataset available on reproductive history which included 37 well-marked mature females in the PLE community followed from 2004 to 2013. This approach included IBI of females with large gaps between weaning of one calf and the birth of the next, therefore potentially biasing IBI upwards by failing to detect births that might have occurred in between. In the second approach, females with larger IBI (>2 years) were considered only if they remained in close association with the surviving calf until the known subsequent birth ($n = 30$). In this case, downward bias in IBI estimates may occur.

Age at weaning

The weaning age was estimated by stable isotope analysis (e.g., Newsome et al. 2006, 2009). Carbon and nitrogen isotopes in teeth from stranded carcasses were used to investigate the age at weaning. The rational for this approach is based on the fact that offspring still nursing on their mother's milk, which is produced by catabolism of her own tissues, will present higher δ^{15}N relative to the mother's signal. Likewise, they should also present lower δ^{13}C values due to the influence of high lipid content and thus ^{13}C depleted milk (Hobson and Sease 1998; Newsome et al. 2009). In this context, time of weaning was defined as the age when a change in trend of δ^{13}C (i.e., a marked increase followed by a stabilizing or reduction phase) and δ^{15}N (i.e., a marked decrease followed by a stabilizing or increasing phase) was detected (Newsome et al. 2009).

Reported weaning ages for bottlenose dolphins vary between 1.5 to 2 years of age (Wells and Scott 2009). In our study, we selected only individuals from 0 to 5 years ($n = 49$) to include the most probable weaning age classes. Dolphins aging <1 year found stranded during the birth pulse period that presented a considerable amount of postnatal dentine deposition (dentine deposited after birth) were considered as 0.5 years as they were probably almost 1 year old (Hohn et al. 1989). Teeth of each age group were processed for stable isotopes analysis following Botta et al. (2012). Isotopic results are expressed in delta notation (δ^{13}C or δ^{15}N) in parts per thousand (‰). Repeated analysis of an internal standard yielded a within run standard deviation of 0.2 % for both δ^{13}C and δ^{15}N values.

Differences in dentine δ^{13}C and δ^{15}N values among ages were assessed using a one-way analysis of variance (ANOVA). When significant differences were detected, this was followed by a post hoc Tukey's honest significant difference pairwise comparison (Zar 2010). Generalized additive models (GAMs) were used to describe the age-related changes in isotopic composition. Models were performed using R 2.15.1 program (R Development Core Team 2012), and GAMs were fitted with the mgcv package in R (Wood 2006).

Reproductive success (RS)

We assumed that a female reproduced successfully if her calf survived from birth to the minimum age at weaning estimated for PLE bottlenose dolphins (i.e., 2 years—see results). Otherwise, we considered that she had failed that reproductive attempt. We estimated average female RS of the PLE bottlenose dolphin community and also explored the potential effects of time (cohort) and individual differences in RS frequencies using the reproductive data systematically collected between 2004 and 2013. Cohort effect was assessed by building CJS models and letting survival (from birth to weaning) to vary with time (t = cohort) or to be constant ($\cdot$) (see details above for survival modelling). Individual analysis was restricted to females with $\geq$3 documented births to reduce the influence of small sample sizes of reproductive outputs. Females that gave birth during the end of the sampling period (2011–2012) were not included, as their offspring would not have completed the minimum estimated age of weaning.

Minimum age at first reproduction and reproductive senescence

Information regarding minimum age at first reproduction was documented from females born during the study period (2004–2013), and two others that had the year of their birth back calculated from their first sighting in 2005 when they were between 1 and 2 years of age. Reproductive senescence was attributed to a few females that did not give birth

Table 1 Summary of reproductive rates of common bottlenose dolphins (*T. truncatus*) from the PLE community estimated from the long-term mark-recapture program; values in parentheses for births denotes the number of birth for well-marked females per year; Fecundity = ratio between the number of females calves (assuming a calf sex ratio of 1:1) and the number of mature females in the PLE community

	2004	2005	2006	2007	2008	2009	2010	2011	2012	Average (SD)
Abundance[a]	–	81	81	82	84	87	86	88	78	83 (3)
Photo-id surveys	23	30	45	38	49	39	34	19	7	31 (13)
Adult females	–	33	35	34	35	37	37	35	31	35 (2)
Births	7 (7)	7 (7)	5 (5)	6 (5)	9 (9)	8 (7)	8 (8)	8 (7)	8 (8)	7.3 (1.2)
Survivors to age 1	7	6	5	5	7	7	6	5	–	6 (1)
Crude birth rate	–	0.09	0.06	0.07	0.11	0.09	0.09	0.09	0.10	0.09 (0.01)
Fecundity	–	0.11	0.07	0.09	0.13	0.11	0.11	0.11	0.13	0.11 (0.02)

[a] Extracted from Fruet et al. (in press a)

for several years (i.e., much longer than the mean IBI) until their death.

Results

Between December 2004 and March 2013, we spent 284 days (1,890 h) collecting data from bottlenose dolphins in the PLE and surrounding areas. Boat-based survey effort varied slightly along the year, peaking in fall (28.5 % of sampling days; $n = 81$) and being lowest during the winter months (21.5 % of sampling days; $n = 61$) (Table 1). Bottlenose dolphins were found in all surveys. From the analysis of 32,296 high-quality dorsal fin photographs, we could recognize and track the reproductive history of 37 well-marked females. Maximum number of documented births per female was four (median = 2). Nine (25 %) reproduced only once, from which four were primiparous and five multiparous mothers aging more than 20 years based on long-term observations.

Annual crude birth rate and fecundity

Fifty-nine births were documented along the study period. Seven 1-year-old calves first sighted in 2005 were also documented. The annual number of documented births varied from five in 2006 up to nine in 2008 and 2011 (mean ± SD = 7.4 ± 1.6), with slight variations in the number of mature females among years. These correspond to an average crude birth rate of 0.09 (SD = ±0.02) and an estimated fecundity of 0.11 (SD = ±0.02) (Table 1).

Calving seasonality

Through MR analysis, we assigned the month of birth for 57 neonates of 32 females. Calving was clearly seasonal, with births occurring mainly in late spring and summer months (Fig. 3). Most births ($n = 45$, 78.9 %, December–February) coincided with months of higher surface water temperatures in the estuary (range 21.7–25.3 °C), with a sudden drop in recorded births when the water temperature started to decrease (Pearson correlation coefficient, $r^2 = 0.35$, $n = 57$, $p = 0.04$). Stranding records ($n = 16$) mirrored this pattern, with higher number of dead neonates occurring between December–January ($n = 10$; 62.5 %).

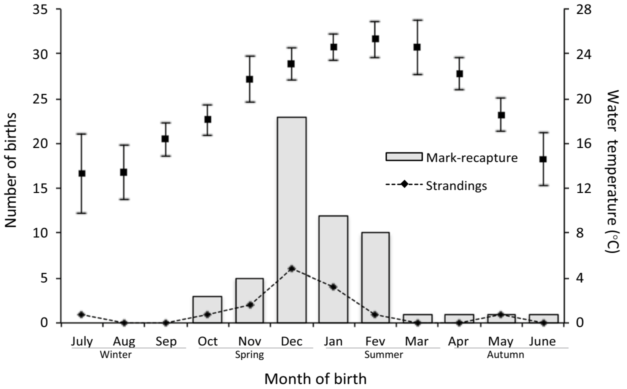

Fig. 3 Birth seasonality for common bottlenose dolphins (*T. truncatus*) of the PLE community based on a long-term monitoring study (2005–2013). *Gray bars* express the number of births estimated from mark-recapture surveys conducted in the estuary and adjacent coastal waters, while *dashed line* shows the number of neonates found stranded during beach surveys. *Black squares* and *error bars* are the averaged monthly water temperature and its associated standard error

Calf survival

Mark-recapture parameter saturated model, which incorporates time variation in survival and constant recapture probabilities for all age classes (model 5), resulted in an estimated median $\hat{c} = 1.21$ (SE = 0.03). Therefore, this value was used to adjust for overdispersion in the data. The most parsimonious model (model 1; Table 2) had constant survival and recapture probabilities and disregarded

Table 2 Summary of age-structured modification of CJS models for survival (Φ) and recapture (p) probabilities of calves (c) from common bottlenose dolphins (*T. truncatus*) of the PLE community based on a long-term mark–recapture study (2005–2013)

	Model	AICc	ΔQAIC	AICc weight	Model likelihood	No. parameters
1.	$\{\Phi(c_{0\text{–}2\text{year}(\cdot)}/c_{>2\text{year}(\cdot)})\, p_{(\cdot)}\}$	173.471	0.00	0.55	1	3
2.	$\{\Phi(c_{0\text{–}2\text{year}(\cdot)} \times g/c_{>2\text{year}(\cdot)})\, p_{(\cdot)}\}$	175.001	1.54	0.25	0.46	4
3.	$\{\Phi(c_{0\text{–}1\text{year}(\cdot)}/c_{1\text{–}2\text{year}(\cdot)}/c_{>2\text{year}(\cdot)})\, p(\cdot)\}$	175.550	2.1	0.20	0.35	4
4.	$\{\Phi(c_{0\text{–}2\text{year}\,(t)}/c_{>2\text{year}(\cdot)})\, p_{(\cdot)}\}$	186.701	13.2	0.00	0.00	10
5.	$\{\Phi(c_{0\text{–}1\text{year}\,(t)}/c_{1\text{–}2\text{year}\,(t)}/c_{>2\text{year}(\cdot)})\, p_{(\cdot)}\}$	198.660	25.2	0.00	0.00	17

Models are ranked according to the lowest AIC. Notation: (·) constant, (t) time-dependence, (g) group effect (dolphins born during the pulse birth season and born out-of-pulse birth season). Slash distinguishes age classes

age effect. Based on the information-theoretic evidence ratio, this model was 2.2 and 2.6 times more likely than the two next models with good fit (model 2 and 3, respectively). The preferred model estimated an apparent overall survival of 0.86 (95 % CI 0.75–0.92) from birth to weaning. Model accounting for timing of birth estimated survival probabilities of 0.86 (95 % CI 0.74–0.93) and 0.82 (95 % CI 0.58–0.94) from birth to weaning for dolphins born within and outside the birth pulse season, respectively. Overlapping confidence intervals and the information-theoretic evidence ratio, however, suggested that timing of birth was not significantly affecting calf survival probabilities. The stratified age class model (model 3) gave similar first and second year calf survival estimates of 0.84 (95 % CI 0.72–0.90) and 0.86 (95 % CI 0.74–0.94), respectively. For all candidate models, capture probability was estimated to be 1.

Inter-birth interval (IBI)

Thirty-seven IBIs were documented for 24 individual females. Two females had a 1-year calving interval, possibly induced by conception after losing their calves within the first weeks of life. IBI for females with surviving calves ranged from 2 to 6 years (mean ± SD = 3.3 ± 1.2; mode = 2) (Fig. 4). Similar results were obtained by excluding possible gaps between successive births of females with prolonged IBIs (>3 years) (see methods for details) (mean ± SD = 3 ± 1.2; mode = 2).

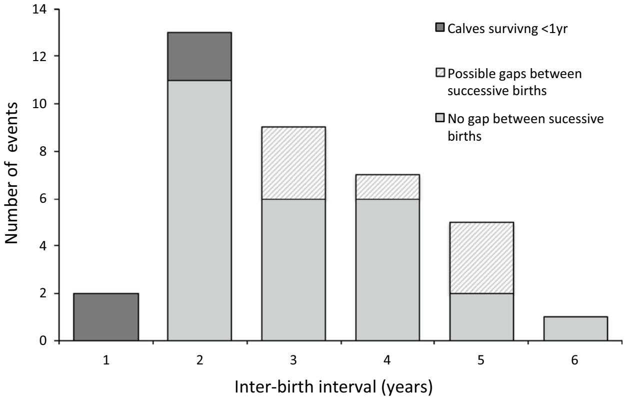

Fig. 4 Estimated IBIs for common bottlenose dolphins (*T. truncatus*) of the PLE community. "Possible gaps" included IBIs with large gaps between weaning of the first calf and the birth of the second calf, with chances of undetecting a birth in between ($n = 37$). "No gaps" included larger IBIs (>2 years) only for females that remained in close association with a surviving calf until a known subsequent birth ($n = 30$). *Dark-gray boxes* show the IBI for females that have lost their calf during the calf's first year of life

Table 3 Mean (±DP) values of δ^{13}C and δ^{15}N in teeth of common bottlenose dolphins (*T. truncatus*) of the PLE community

Age class	δ^{13}C (‰)	δ^{15}N (‰)	Number of samples
0	−13.45 (±0.98)	21.50 (±1.91)	4
0.5	−11.45 (±0.87)	19.14 (±1.49)	3
1	−11.40 (±0.58)	18.48 (±1.20)	8
2	−11.22 (±0.70)	18.30 (±0.65)	14
3	−10.99 (±0.45)	17.96 (±0.87)	6
4	−11.13 (±0.37)	18.51 (±0.57)	7
5	−11.32 (±0.33)	18.57 (±1.08)	5

Age at weaning

Carbon isotope values in 0-year-old dolphins were significantly lower than all other age classes (ANOVA, $F_{(5)} = 38$, $p < 0.0001$). In the case of δ^{15}N, significant differences were found between the 0-year-old individuals and the remaining age classes (ANOVA, $F_{(5)} = 38$, $p < 0.0001$), except between 0 and 0.5-year-old dolphins (Tukey's HSD, $p = 0.06$) (Table 3). GAM models (54.6 % δ^{13}C and 47.7 % δ^{15}N explained deviance and $p < 0.00001$ for the smoothed functions) showed different functions of age for δ^{13}C and δ^{15}N. The high δ^{15}N values of the zero year class sharply decrease during the first year, followed by a moderate declining phase up to the 2–3 year class and an increasing trend onwards. As for carbon nitrogen isotopes,

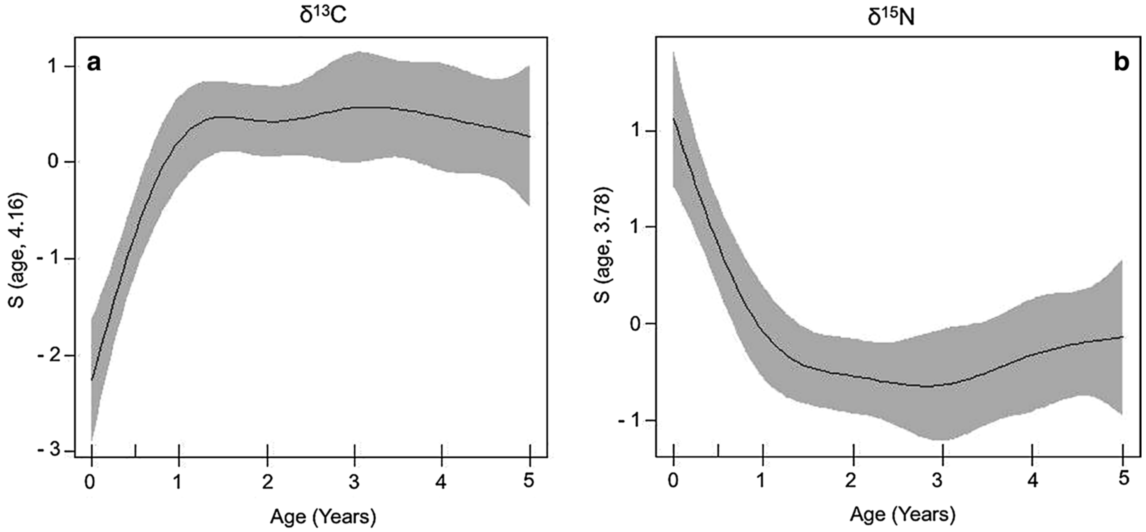

Fig. 5 Plots of GAMs of δ13C (**a**) and δ15 N (**b**) by age in teeth from common bottlenose dolphins (*T. truncatus*) of the PLE community. *X-axis* denotes age (in years) and *Y-axis* denotes relative distance from the mean. *Gray envelopes* correspond to the 95 % confidence interval

on the other hand, smoothed functions showed a markedly increase in teeth δ^{13}C during the first year of life and remaining relatively constant in older ages (Fig. 5).

Female reproductive success

Thirty-one (76 %) of 41 calves born to 27 females between 2005 and 2010 were observed to have survived until weaning. Yearly observed RS varied from 100 % for neonates born in the 2007 cohort ($n = 5$), when the number of surveys during birth season was highest, to a low of 63 % from those born in the 2010 cohort ($n = 8$), with a decline in observed RS during the last 3 years of available sample (Fig. 6). This temporal analysis resulted in a mean observed RS rate of 0.78 (SD = ±1.5). Despite this variation, cohort effect was not likely to be significant in RS, as the model with time-variant effect in survival had a poor fit (model 4, Table 2). Marked individual variation in observed RS was found. Some females had 100 % of observed RS, while others never succeeded (Fig. 7).

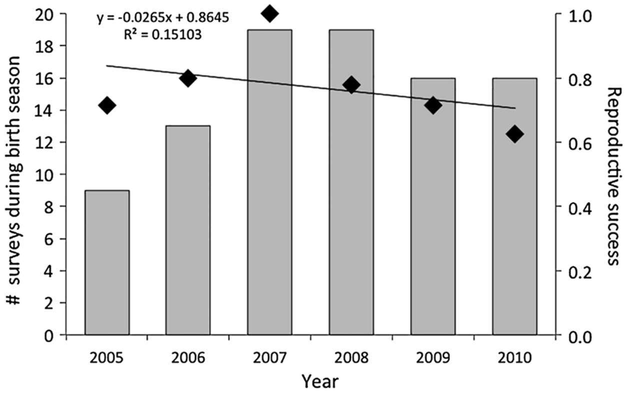

Fig. 6 Yearly changes on RS (*black diamonds*) of female common bottlenose dolphins (*T. truncatus*) of the PLE community over 6 years (2005–2010). *Gray bars* are the number of summer surveys per year. Data from calves born in the end of sampling period (2011–2012) were not included in this analysis as they did not have the minimum estimated age to be weaned (≥2 years)

Minimum age at first reproduction (AFR) and evidence of reproductive senescence

We had the opportunity to track four females since birth. Two of them (LP#091 and LP#107) gave birth for the first time at age 8. The calves of both females survived their first year of life. A 9-year-old female (LP#116) did not give birth until the end of the study. For another female (YO#021) that gave birth in the summer of 2013 AFR was estimated at 10 years, as it was aged 2 years old when first sighted in 2005.

Three females (8 %) were not documented with calves between 2005 and 2013, two of them (LP#028 and LP#021) died in 2010 and had their ages estimated at 40 and 44 years old by counting growth layer groups in their teeth dentine and cement (EcoMega Research Group, unpubl. data). The third one (LP#050), frequently sighted in the studied area since 1977, suddenly disappeared and supposedly died in 2012 with a minimum age of 40 years, as it was considered adult when first sighted. Therefore, it is likely that these three females reproduced successfully for the last time in their lives when they were 32 ($n = 2$) and 36 ($n = 1$) years, respectively.

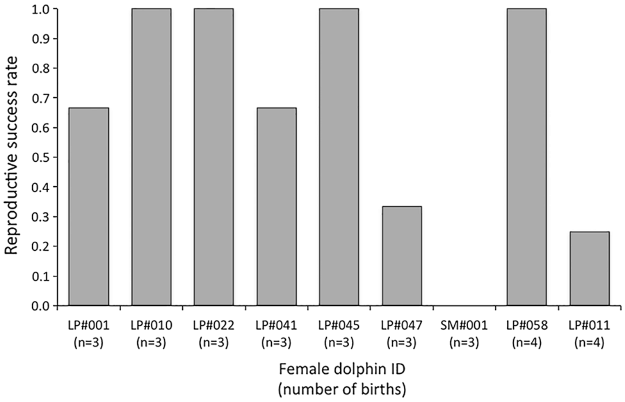

Fig. 7 Individual variation in RS for female common bottlenose dolphins (*T. truncatus*) with ≥3 documented births in the PLE community. Data from calves born at the end of the sampling period (2011–2012) were not included in this analysis as they did not have the minimum estimated age to be weaned (≥2 years)

Discussion

We described for the first time multiple reproductive parameters for female bottlenose dolphins from the SWA. The dolphin community of the PLE presents a birth pulse strategy, with calving concentrated in the warmer months. Females presented relatively shorter IBIs when compared to females from other regions around the world, with evidence of reproductive senescence. In addition, it seems that sexual maturation of females in the PLE is attained relatively early in life, though the data are limited to only a few females. At an individual level, highly variable RS was observed. These parameters can be used as a baseline for long-term monitoring of this dolphin community as well as for comparison with other communities of this widely distributed species, which is subject to distinct environmental and ecological conditions throughout its range.

Inter-birth interval, crude birth rate, and fecundity

With the exception of fecundity rate (0.11), which fall within the limits reported for bottlenose dolphins elsewhere, we found higher annual crude birth rates (0.09) and shorter (mode = 2 years) IBIs for PLE bottlenose dolphins. The mean IBI of 3 years found in this study is similar but at the lower range to what have been reported for several other regions (see Table 4 for comparisons). Wherever the reproduction of bottlenose dolphins has been studied in the wild, shorter IBI (1–2 years) was likely induced by calf loss during the first year of life. In our study, however, 2 years between successive births was common regardless of calf's fate, an unusual pattern for bottlenose dolphins. The lack of (or minimal) predatory pressure (Fruet et al. 2012) and the abundant and predictable distribution of feeding resources in our study system may provide an optimal condition for females to reduce maternal investment without adding substantial costs for young survival after weaning.

Best et al. (1984) found a shorter IBI for sperm whales in the high productive waters off the Humboldt Current than in other less productive study areas. Several other studies with aquatic mammals have found a relationship between top–down and bottom–up effects in demographic parameters after sudden changes in food availability and/or predator abundance (southern right whales, *Eubalaena australis*, Leaper et al. 2006; killer whales, Ward et al. 2009; Antarctic fur seals, *Arctocephalus gazella*, Schwarz et al. 2013). Thus, the minor year-to-year variation in fecundity and crude birth rates (and other parameters such as abundance and adult survival from this dolphin community; Fruet et al. in press a) potentially suggests a relatively

Table 4 Reproductive parameters of bottlenose dolphins (*Tursiops* spp.) estimated from long-term mark-recapture studies around the world

Species	Site	Survival to 1 year	Fecundity (SD)	Crude birth rate (SD)	IBI (years)	
					Mean	Mode
T. aduncus	Mikura island, Japan	0.86[a]	0.136 (0.04)[a]	0.071 (0.024)[a]	3.4[a]	–
T. aduncus	Shark Bay, Australia	0.71[b]	–	–	4.1[b]	4
T. aduncus	Port River, Australia	0.70[c]	–	0.064[c]	3.8[c]	–
T. truncatus	Sarasota Bay, USA	0.81[d]	0.09 (0.04)[d]	0.055 (0.009)[d]	4[e]	4–5[e]
T. truncatus	Doubtful Sound, NZ	0.86[f]	–	0.040 (0.04)[g]	5.3[h]	4–6[h]
T. truncatus	Scotland	–	0.11 (0.2)[i]	0.046[j]	3.8[i]	3–6[i]
T. truncatus	PLE, Brazil	0.84[k]	0.11 (0.2)[k]	0.090 (0.01)[k]	3[k]	2[k]

Fecundity = ratio between the number of female calves (assuming a calf sex ratio of 1:1) and the number of mature females in the PLE dolphin community. Original values of fecundity extracted from the literature were divided by 2 for adjusting the fecundity definition used in this study where only female calves were considered

[a] Kogi et al. (2004), [b] Mann et al. (2000), [c] Steiner and Bossley (2008), [d] Wells and Scott (1990), [e] Wells (2000), [f] Currey et al. (2008); [g] Haase and Schneider (2001); [h] Henderson et al. (2014); [i] Mitcheson (2008); [j] Wilson et al. (1999); [k] This study

stable environment over the course of this study period, or the ability of PLE bottlenose dolphins to respond to fluctuations in species-specific abundance of prey through feeding plasticity (Lopes 2014).

Birth seasonality

Our analysis of 8 years of MR and stranding data revealed that calving of PLE bottlenose dolphins is highly seasonal and is associated with warmer surface waters in the estuary. The PLE and adjacent coast are subjected to substantial seasonal oscillations in physical and biological processes (Möller et al. 2001; Garcia et al. 2012). Abundance of adults of several estuarine-dependent fishes that are important prey species for PLE bottlenose dolphins (e.g., *Micropogonias furnieri*; *Paralonchurus brasiliensis*; Lopes 2014) pulses during spring and summer months with a drastic reduction during winter (Garcia et al. 2012; Rodrigues and Vieira 2013). As prey abundance decrease, time and, therefore, energy spent to search for sparse food likely increases. Hence, synchronizing time of birth with high food abundance and warmer temperatures is probably favoring infant survival by minimizing thermoregulation-related stress and maximizing the opportunity of mothers to explore the optimal levels of resources during early–mid lactation, the most energetically expensive time of reproduction (e.g., Rutberg 1987; Gaillard et al. 1993; Rechsteiner et al. 2013). In addition, as lower energetic demand of thermoregulation is need for the mother in warmer waters (Williams et al. 1992), calving during this period may improve quality of maternal milk and promote a rapid calf growth, thus potentially enhancing calf survival (see Whitehead and Mann 2000 for review). Several other studies on bottlenose dolphins and other small dolphin species have reported birth pulse in areas of similar or higher latitudes (e.g., *T. truncatus*, Urian et al. 1996; Thayer et al. 2003; Henderson et al. 2014; *Pontoporia blainvillei*, Danilewicz 2003; *Delphinus delphis*, Westgate and Read 2007), where they are also subjected to intra-annual changes in prey availability and water temperature.

Calf survival

The first-year survival rate estimated here falls within the range of values obtained from long-term MR data for other bottlenose dolphin communities (Sarasota Bay, mean ± SD = 0.81 ± 0.06, Wells and Scott 1990; Doubtful Sound, mean = 0.86, 95 % CI 0.69–0.95, Currey et al. 2008). It was also similar to the first-year survival rate estimates for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) at Mikura Islands (mean = 0.86; Kogi et al. 2004) (Table 4). However, as in other MR studies, first-year survival is possibly overestimated. As most deaths probably occur during the first month of life (e.g., Henderson et al. 2014), this narrow time interval coupled with sampling limitations increase the chances of missing an early death and thus overestimating first-year survival rate. This could be the reason why we did not find significant differences in apparent survival rates between age classes of 0–1 and 1–2.

As we found that PLE bottlenose dolphins have a narrow birth pulse coinciding with optimal environmental conditions (warmer water temperature and potentially high food supply), we predicted that the timing of birth should play a critical role in calf survival, with infants born out-of-pulse birth season having lower survival rates. Nevertheless, we did not found significant evidence to support this hypothesis, but large uncertainties around survival estimates could indicate a lack of statistical power. Despite these limitations, this result suggests that variability in water temperature and food resources within the year is unlikely to impact upon survival of calves born at, or out-of-pulse, birth season.

Weaning

Findings from field studies suggest that lactation can last between 1.5 and 2 years in bottlenose dolphins (see review in Wells and Scott 2009). As separation between mother and calf tends to occur before the birth of the next calf (Wells 2000; Mann et al. 2000; this study), we deduced that the most typical IBI in this study (mode = 2) should at least roughly coincide with the time of weaning in PLE bottlenose dolphins. C and N stable isotopes analysis provided congruent results with estimated IBIs. The clear change in the δ^{13}C and δ^{15}N profiles near age 2 indicated the most probable weaning age in this bottlenose dolphin community. Low ^{13}C and high ^{15}N isotopic values were found in <1-year-old individuals, when gradually started to increase and decrease up to age 1.5–2 years. These results suggest higher nutritional investment by mothers (through lactation) during the calf's first year of life and a gradual incorporation of solids concomitant with a decreasing milk intake during the next year as part of the weaning process. This may be necessary to both promote a fast development so the calf becomes independent and to allow a recovery period for the female by the time her next calf is born.

Reproductive success

The observed RS of the PLE female bottlenose dolphins revealed a high individual and community level variation, with some multiparous females failing at all observed reproductive attempts while others successfully weaning all their observed calves. Only few cetacean studies have assessed female RS at an individual level based on a longitudinal observational sampling, but it seems that such a high individual variability may be common in wild bottlenose dolphins (Wells 2000; Mann et al. 2000; Frère et al. 2010; Henderson et al. 2014; this study) as is in other mammal and bird species (e.g., Krüger and Lindström 2001; Hamel et al. 2009). Henderson et al. (2014) found that mother identity is crucial to calf survival of the Doubtful Sound bottlenose dolphin community, and when "good mothers" has calves influence the temporal variation in abundance. Whereas the detrimental effects that demographic stochasticity plays in the dynamics of small populations are well known (Lande et al. 2003), the mechanisms influencing variations at individual level are still not well understood.

Age-dependent effects possibly affect female RS, as experienced mothers should invest more in parental care than in reproduction, which in turn is likely to play an important role icreasing survival probabilities of dependent youngs (Wells 2000). In our study, two old living females that reproduced for the last time just prior to the implementation of our systematic monitoring have carried out parental care duties for 8 years. This suggests that aging PLE bottlenose females may change their role from 'breeding' to 'nursing' individuals, compensating for their negative effect on average fecundity by increasing the RS of the community, as predicted by classical life history theories for species with low adult mortality (Clutton-Brock 1984).

Preliminary evidence of an early age at first reproduction and of reproductive senescence

Although based on limited sample size, our results showed that female PLE bottlenose dolphins may attain sexual maturation early in life. Two primiparous females were 8 and 10 years old, suggesting that sexual maturity was attained, respectively, at ages of 7 and 9, or earlier. In Sarasota Bay, Northwest Atlantic, female bottlenose dolphins as young as 6 or 7 years old have given birth, but 8 years was the most common age observed for first reproduction (Wells et al. 1987; Wells and Scott 1999; Wells 2000). Later sexual maturation was observed for bottlenose dolphins elsewhere (9–14 years: Perrin and Reilly (1984) in the Northeastern Pacific; Mead and Potter (1990) in the Northwest Atlantic; Henderson (2012) in the South Pacific). It is possible that some PLE dolphins of unknown sex that are females did not start reproducing until the end of the study, which could have led to a downward bias in the estimates. Although future studies will be necessary to estimate the mode of age at first reproduction for the PLE community, the data provide information on minimum age of sexual maturity, and first evidence of an early reproduction for these animals.

Three highly sighted old females were about 32–36 years when they had potentially given birth for the last time, suggesting an age-related decrease in individual's reproductive fitness in bottlenose dolphins from the PLE community. Although it is possible that undetected abortions or newborn deaths may have occurred, our intensive survey effort during the breeding season (2005–2012: average number of surveys during birth season was 15; SD = ±4) minimizes the risk of underdetection. In addition, the fact that two old living females have carried out parental care duties for 8 years (EcoMega Research Group, unpubl. data) suggests that aging PLE females may be compensating their negative effect on average fecundity by increasing the overall RS of the dolphin community. Evidence of reproductive senescence was reported for the Sarasota dolphin community, as older females appear to invest much less in reproduction to improve RS (Wells 2000).

This study demonstrates that the bottlenose dolphins from the PLE are seasonal breeders and that females seem to invest more in reproduction early in life while changing their role from "breeding" to "nursing" individuals at older ages. This could be a strategy to increase calf survival as an offset for senescence in order to obtain overall high RS and increase long-term viability.

Our findings highlight the importance of long-term studies of long-lived mammals to yield individual- and population-level parameters for demographic and viability analyses that are useful for conservation and management.

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