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ORIGINAL PAPER

Reproductive parameters and factors influencing calf survival of bottlenose dolphins that engage in a unique foraging cooperation with fishermen

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Abstract

A subset of the bottlenose dolphin *Tursiops truncatus gephyreus* population in Laguna, southern Brazil, specialize in foraging cooperatively with fishermen. In this study, we describe reproductive parameters for these dolphins and investigate whether this specialized tactic generates reproductive advantages for females that frequently engage in this unusual behavior. We analyzed photo-identification data collected during 233 boat-based surveys during 2007–2009 and 2013–2017. From 27,808 high-quality photographs, we identified and tracked the fate of 24 reproductive females and 45 of their calves. Calving was found to be seasonal, with most births occurring in late spring/summer. The average crude birth rate was 0.09, and estimated fecundity was 0.17. The mean inter-birth interval was 2.09 (for all calves) or 2.43 years (for surviving calves only). Survival to 1 and 2 years estimated by the Kaplan–Meier method was 0.78 (95% CI 0.65–0.92) and 0.65 (95% CI 0.51–0.83), respectively—which represents a survival rate in the second year of 0.83. We investigated the potential influence of birth timing, resource availability, and maternal foraging tactic, home range size and frequency of interaction with fishermen on calf survival. Timing of birth was a significant predictor of calf survival. Giving birth close to the local mullet season would provide lactating females with increased seasonal prey resources, leading to increased calf survival. Due to our sample size ($n=9$ cooperative and 15 non-cooperative females), we could not conclude whether or not the cooperative foraging tactic influences calf survival and female reproductive success. We emphasize the importance of long-term monitoring of populations to understand regional life history characteristics and provide accurate information for viability analyses.

Introduction

Long-term individual-based studies provide information on multiple aspects of mammalian ecology, such as individual life history (Mann et al. 2000), social systems (Alberts 2019), population and community processes (Gough and Kerley 2006; Swanson et al. 2014), as well as ecophysiology (Schradin et al. 2015), and these have guided major conservation efforts (Mintzer et al. 2013). While essential for assessing population dynamics, status, and viability (Beissinger and McCullough 2002), long-term studies require lots of primary field data, and extensive investment in time, effort and finances (Hayes and Schradin 2017). For cetaceans, long-term studies are even more challenging since they are wide-ranging, deep-diving and fast-moving (Mann and Karniski 2017). Therefore, some demographic parameters, such as reproductive parameters, are particularly difficult to obtain, requiring extended periods of systematic field effort. As a result, it

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is common in cetacean population assessments to rely on secondary data obtained from different populations of the same species (Reed et al. 2002); however, since different populations might be exposed to different ecological conditions and pressures (Baker et al. 2018), such assessments may have limited utility. There are clear benefits to local conservation outcomes, therefore, to use regionally specific demographic parameters to produce reliable population viability analyses (Manlik et al. 2016, Arso Civil et al. 2017).

Moreover, understanding the factors influencing female reproductive success, in terms of calf survival, provides valuable insights into the causes of low population sizes, declines and even extinction risks (Craig and Ragen 1999, Baker et al. 2007). Reproductive success may be driven by ecological (Thompson et al. 2007), socio-behavioural (Cameron et al. 2009), environmental (Frick et al. 2010) or morphological factors (Blueweiss et al. 1978; Pomeroy et al. 1999). For cetaceans, in particular, calf survival seems to vary with birth timing due to the influence of environmental conditions such as water temperature and resource availability (Brough et al. 2016); in parallel, the mother's experience, age, and size are also reported as a key factor for calf survival (Elwen and Best 2004; Brough et al. 2016; Karniski et al. 2018). The influence of behavioural tactics, such as foraging specializations, or other ecological drivers, such as resource availability, on the reproductive success in cetacean populations needs further investigation.

Bottlenose dolphins (*Tursiops* spp.) show a wide distribution in temperate and tropical waters, in a variety of habitats (Wells and Scott 1999). They have been the subject of several long-term research efforts worldwide (e.g., Wells and Scott 1990; Mann et al. 2000; Fruet et al. 2015; Arso Civil et al. 2019; Cheney et al. 2019), enabling studies of many aspects of their life history and reproductive biology in the wild. Life history traits, such as female reproductive parameters, may vary considerably throughout its distribution. Births can occur year-round (Félix 1994, Urian et al. 1996) or seasonally (Thayer et al. 2003), varying geographically. Peaks in calving season have been described for several bottlenose dolphin populations, mainly those found in high latitudes (Wells et al. 1987, Bearzi et al. 1997, Mann et al. 2000, Henderson et al. 2014), but also in tropical waters (Fearnbach et al. 2012). Average inter-birth interval (IBI), fecundity and calf survival vary greatly among populations (Mann et al. 2000, Robinson et al. 2017, Baker et al. 2018), and reproductive success of individual females may vary within populations as well (Henderson et al. 2014; Fruet et al. 2015; Brough et al. 2016; Robinson et al. 2017), due to natural individual heterogeneity. Factors that may affect female reproductive success include mother's age (Karniski et al. 2018) and foraging tactic (Mann et al. 2000, 2008; Foroughirad and Mann 2013; Senigaglia et al. 2019), and her ability to give birth at an optimum time in the calving season (Brough et al. 2016).

The bottlenose dolphins in Laguna, southern Brazil, are a small, resident (Simões-Lopes and Fábian 1999; Daura-Jorge et al. 2013, Bezamat et al. 2019) and genetically discrete population (see Fruet et al. 2014). Some individuals from this population interact with artisanal fishermen in a rare cooperative foraging tactic, which seems to benefit both species (Simões-Lopes et al. 1998, 2016). Dolphins herd schools of fish, mainly mullet, towards fishermen, who stand in shallow water waiting to cast their nets in response to the dolphins' stereotyped behavioural cues (Simões-Lopes et al. 1998, Peterson et al. 2008). This specialized foraging tactic influences the social structure (Daura-Jorge et al. 2012), space use (Cantor et al. 2018) and acoustic repertoire (Romeu et al. 2017) of the dolphins. The interaction has also been shown to influence survival with slightly higher survival rates among dolphins that regularly interact with fishermen (Bezamat et al. 2019). Although in recent years, we have investigated many aspects of the dynamic behaviour and social organization of this small dolphin population, there is currently no information on reproductive parameters and their influence on population viability.

Furthermore, the Society for Marine Mammalogy's Committee on Taxonomy (2017) has recently recognized the coastal bottlenose dolphins from Southwest Atlantic (southern Brazil, Uruguay and central Argentina), which includes the bottlenose dolphin population from Laguna, as the subspecies *Tursiops truncatus gephyreus*. This subspecies is endemic to the area and is comprised by only a few small and discrete population units (at least five; see Fruet et al. 2014), probably totaling no more than a few hundred individuals. It is noteworthy that at least two of these populations specialize in foraging with fishermen (Simões-Lopes et al. 1998). There is limited information on the reproduction of this subspecies and only two of these units have reproductive parameters estimated: the community in the Patos Lagoon estuary (Fruet et al. 2015), about 520 km south of Laguna, southern Brazil; and the population in Bahía San Antonio, Argentina (Vermeulen and Bräger 2015). In the Patos Lagoon estuary, calving is seasonal, with most births occurring during late spring and summer; mean IBI was estimated to be 3 years (mode = 2), and fecundity to be 0.11; first- and second-year calf survival estimates were 0.84 and 0.86, respectively; most probable weaning age is 2 years (estimated by stable isotope analysis); females first reproduced at a minimum age of 8–10 years; and reproductive success varied considerably among individually identified females. In Bahía San Antonio, calving is also seasonal (83% of calves were born in spring or early summer); mean IBI was estimated to be 3.5 (± 1.03) years; and minimum annual birth rate to be 0.04. As a regional assessment of this subspecies is on the agenda, we should focus now on estimating such life history traits for other population units and investigating which factors may influence heterogeneity in female reproductive success, so we can examine variability of reproductive rates and calf survival among and within populations.

In this study, we used 8 years of mark–recapture photo-identification data to estimate female reproductive parameters for the Laguna bottlenose dolphin population, including calving seasonality, fecundity, IBI, and calf survival rates. We investigated potential factors influencing reproductive success, in terms of calf survival, such as the mother's foraging specialization and home range, and timing of birth in relation to the mullet *Mugil liza* season, a key local prey species. We also investigated the influence of the foraging specialization on reproductive parameters, by comparing parameters for females that frequently cooperate with fishermen and those that tend to forage independently. Understanding the life-history characteristics of the Laguna bottlenose dolphin population is essential to evaluate its status and viability, improving conservation and management actions for this population and the subspecies *Tursiops truncatus gephyreus*.

Methods

Data collection

From 2007–2009 to 2013–2017, we carried out boat-based surveys of a small and resident bottlenose dolphin population in the Santo-Antônio–Imaruí–Mirim lagoon system, an area of approximately 200 km^2 in Laguna, southern Brazil (28°20′ S–48°50′ W; Fig. 1). During each survey, we followed a 30-km predefined route using a 5-m boat powered by an outboard engine aiming to cover the main area used by the dolphins (Cantor et al. 2018). A group of dolphins was defined as all individuals within a 50-m radius of each other and engaged in similar behaviour (as in Daura-Jorge et al. 2013; Bezamat et al. 2019). During encounters with dolphins, we attempted to photograph both sides of the dorsal fin of all individuals and using only high-quality pictures (on a scale of A to C in terms of angle, focus, exposure; Williams et al. 1993) identified them from the nicks and marks on their dorsal fins (Würsig and Jefferson 1990). During encounters we also recorded time, location, group size and whether or not dolphins were interacting with artisanal fishermen (see Daura-Jorge et al. 2012).

Individually identified adults seen in close association with a calf—individuals of small size, dark gray in colouration or visible fetal folds—for two or more subsequent and independent encounters were assumed to be mothers. While the mother–calf pairs were seen together, calves were typically tracked via identification of their accompanying mothers, since young calves usually do not have long lasting marks ($n=45$). Temporary marks on the dorsal fin and body (e.g., scratches) also assisted in identifying calves individually. If a mother was sighted without her calf before it turned 2 years old (minimum age at weaning cf. Fruet et al. 2015), in two or more subsequent and independent encounters, the calf was assumed to have died. From the photo-identification database, we extracted a detailed record of sightings and calving histories for all reproductively active females identified throughout the study (i.e., those known to have given birth to viable calves; $n=24$).

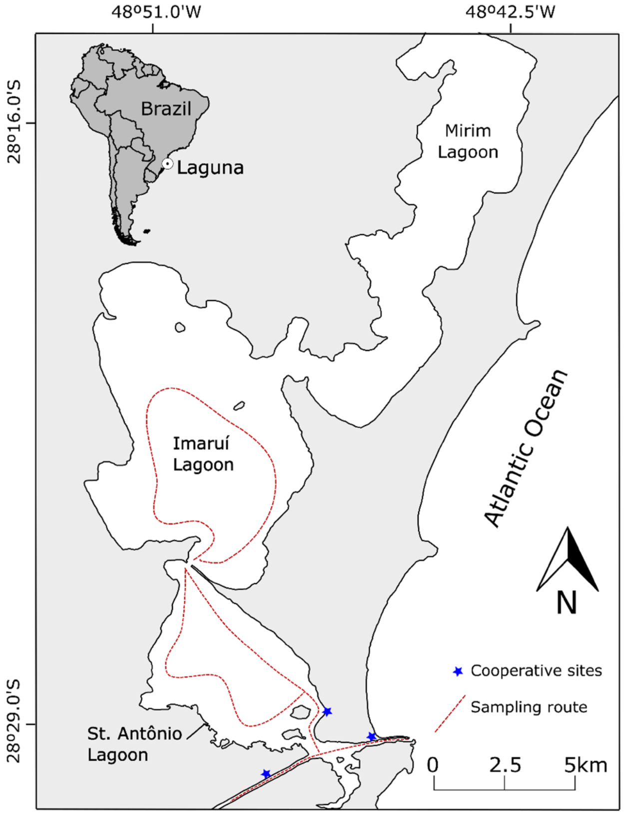

Fig. 1 The coastal lagoon system, adjacent to Laguna, southern Brazil. Red line shows the predefined sampling route and blue stars the sites where the interaction between dolphins and fishermen often occurs

Reproductive parameters

The annual number of births was obtained from counts of neonatal calves recorded each year. The annual crude birth rate was calculated as the total number of documented births divided by the total abundance of Laguna dolphins, estimated each year using mark–recapture models (see Bezamat et al. 2019; Table 2).

We assumed females become adults the year before the production of the first known calf, given that pregnancy lasts about a year for the species (e.g., Perrin and Reilly 1984). We used longitudinal photo-identification data to verify the minimum number of adult females seen each year, and then estimated fecundity as the number of female calves (assuming a calf sex ratio of 1:1 for mammals; Caughley 1977), produced by adult females in a given year (after Fruet et al. 2015):

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

where $\hat{F}_i$ is the estimated fecundity in year i; n is the total number of years; N_{ci} is the total number of calves born in year i (range 2–7); and N_{mi} is the number of adult females alive in year i (range 12–20; Table 2).

The seasonality of births and the peak birth period were examined based on the estimated calendar month of parturitions. For calves classified as newborns—with obvious fetal fold marks, floppy fins, and less than half the length of their mothers (Urian et al. 1996; Mann and Smuts 1999)—birth was assigned to the month of their first sighting. Otherwise, month of birth was estimated as the midpoint between the date of the last sighting of a mother without the calf and the date of the first sighting of the mother with the new calf (adapted from Wells et al. 1987), when this interval was ≤ 60 days. In addition to data on newborns with known mothers (Table 1), we also included data on two newborns found dead on the beach during a systematic monitoring program (personal communication from Pedro V. Castilho) in estimates of the number of calves born in 2016 and 2017, calving seasonality and fecundity (Table 2).

Inter-birth interval (IBI) was estimated as the time elapsed between subsequent births for individual mothers with two consecutive births where the estimated breeding season of birth was available for both calves. Since calving in Laguna is seasonal (most births occurred from December to March; see results), we opted to use the breeding season of birth here instead of month of birth (we could assign month of birth for only 26 calves) to enlarge our sample size. We used two approaches to calculate IBIs: (a) considering only the intervals in which the first calf survived to age 2 (minimum age at weaning estimated by stable isotope analysis cf. Fruet et al. 2015; $n = 7$), (b) considering all intervals ($n = 11$), including those in which the first calf died before

Table 1 Sightings of reproductive females (ID# = individual photo-ID catalogue number) and their calves from 2007 to 2009 and 2013 to 2017 in Laguna, including sightings of females without a calf (marked with a "•") and their first (1), second (2), third (3), or fourth (4) calves. Calf ages were categorized as young-of-year (< 1 year old; YC) and calves (1–3 years old; C). The number of adult females in each year (#F) and the number of calves born in each year (#YOY) are also shown. Calves included in the survival analysis are underlined

ID#	Years							
	2007	2008	2009	2013	2014	2015	2016	2017
2	•	•	•	C1	•	YC2	C2	C2
8	•	YC1	C1	C2	C2	YC3	C3	C3
9	C1	C1	C1					
10	•	•	YC1	•	YC2	•	YC3	C3
11	YC1	C1	C1	•	YC2	C2	C2	YC3
12	YC1	C1	C1	YC2	•	•	•	•
14	YC1	C1	C1					
18	YC1	C1	C1	C2	C2	•	•	•
19	C1	C1	C1					
21	•	•	•	YC1	YC2	C2	C2	C2
23	•	•	•	•	•	•	•	YC1
24	•	•	•	•	•	YC1	C1	C1
27	•	•	•	•	•	•	YC1	C1
28	•	•	•	YC1	C1	C1	YC2	
31	YC1	C1	C1	•	•	•	•	•
36	YC1	C1						
40	•	•	YC1	YC2	C2	C2	C2/YC3	C3
42	•	YC1	C1	YC2	C2	C2 + YC3	C2 + C3	•
44		•	•		•	•	•	YC1
50	YC1	C1	C1	•	YC2	YC3	C3	YC4
51	•	•	•	•	•	•	•	YC1
52	•	YC1	C1	•	YC2	C2	YC3	C3
56				•	•	YC1	C1	C1
63				•	YC1	C1	YC2	C2
#F	12	14	13	14	16	17	20	20
#YOY	7	3	2	5	6	6	6	5

Table 2 Summary of reproductive rates of bottlenose dolphins in Laguna, Southern Brazil, estimated from mark–recapture studies; Fecundity = ratio between the number of female calves (assuming a calf sex ratio of 1:1) and the number of adult females in Laguna (cf. Fruet et al. 2015)

	2007	2008	2009	2013	2014	2015	2016	2017
Photo-ID surveys	25	49	31	51	15	25	23	14
Abundance[a]	54	60	60	55	53	52	60	–
Adult females	12	14	13	14	16	17	20	20
Newborn calves	7	3	2[b]	5	6	6	7[c]	6[b,c]
Calves surviving to age 1	6	3	–	3	3	5	6	–
Calves surviving to weaning (age 2)	6	–	–	3	2	4	–	–
Reproductive success	0.86	–	–	0.60	0.17	0.67	–	–
Crude birth rate	0.13	0.05	0.03	0.09	0.11	0.12	0.12	–
Fecundity	0.29	0.11	0.08	0.18	0.19	0.18	0.175	0.15

[a] Extracted from Bezamat et al. 2019

[b] Number of births could be underestimated, since we conducted few surveys at the end of these years

[c] We included one newborn of unknown mother, found dead in the study area

1 year. A difference between these two estimates could suggest the anticipation of a new pregnancy when females lose their calves early in life.

We assumed that a female reproduced successfully if her calf survived from birth to age 2 (the minimum age at weaning *cf.* Fruet et al. 2015; Mann et al. 2000; Senigaglia et al. 2019). We then estimated female annual reproductive success as the proportion of calves born in a given year that survived to age 2 (Table 2). To validate the weaning age used as reference (Fruet et al. 2015), we estimated weaning age as the length of time a calf remains with its mother swimming in infant position, based on the estimated month of birth and the estimated date of weaning (adapted from Mann et al. 2000). Date of weaning was estimated as the mid-point between the date of the last sighting of the mother-calf pair closely associated and the first sighting of the mother without the calf (Karniski et al. 2018; Senigaglia et al. 2019). We only considered calves we could track after separating from their mothers, to make sure they survived to weaning ($n = 3$). Besides estimating reproductive parameters for the whole population, we also estimated fecundity and IBI separately for cooperative and non-cooperative females. We classified cooperative and non-cooperative dolphins according to the relative frequency with which they interact with artisanal fishermen, following procedures described in Cantor et al. 2018.

Factors influencing calf survival

We used survival analysis to estimate calf survival and investigate potential factors affecting mortality over the first 3 years of life (Kleinbaum and Klein, 2012). We included 36 calves in this analysis, those we tracked from birth. Twelve of these were tracked from birth to death. The remaining 24 were labeled as right censored, including those that were still alive at the end of the study, and those we could not keep track and therefore we do not know whether they survived or not within 3 years (the maximum time we evaluated considering the study period). We used the Kaplan–Meier nonparametric method to estimate survival probabilities over time (Kaplan and Meier 1958; Cleves et al. 2010). For each time interval, survival probability is calculated as the number of individuals surviving divided by the number of individuals at risk (i.e., alive and not censured).

We then investigated the potential influence of several factors on calf survival using Cox proportion hazard models, which describe how the instantaneous risk of death occurring at a given time is affected by covariates (Cox 1972). The following predictive variables were considered: (1) Mother$_{fi}$—mother frequency of interaction with fishermen estimated as the number of independent events each female was observed foraging with artisanal fishermen divided by the total number of observed foraging events (see Bezamat et al. 2019); (2) Mother$_{HR}$—mother home range size estimated from location data using the adaptive local convex hull method (a-LoCoH; Getz et al. 2007) minimizing spatial autocorrelation bias by randomly selecting a single location point per female per sampling day, excluding land, and selecting the a parameter as the average maximum distance between any two location points for each female following the heuristic rule proposed by Getz et al. (2007) in R (R Core Team 2017) using the adehabitatHR package (Calenge 2006); (3) Mother$_{\text{Coop}}$—mother foraging tactic—females that were seen interacting with fishermen in more than 31.6% of their observed foraging events were classified as cooperative, and the others were classified as non-cooperative (this cut-off was defined following Cantor et al. 2018); (4) T_{mullet}—the time (in months) between birth and the peak of the following mullet season (June; Lemos et al. 2014); (5) N_{mullet}—the fishery yield off southern and southeastern Brazil of the mullet season following the birth (Sant'ana and Kinas 2016; Sant'ana et al. 2017). Covariates 1–3 investigate whether mothers participation in the cooperative tactic with fishermen influences calf survival; covariates 4 and 5 are proxies for prey availability for lactating females—in Laguna, there is a marked seasonality in prey availability related to a peak in the abundance of mullet from May to July, when mullet migrate from Argentina to southern Brazil to spawn (Lemos et al. 2014).

To model calf survival as a function of these 5 covariates, we constructed a set of univariate Cox models. All models were fitted adding mother ID as a random effect using the function *coxme*, from R package *coxme* (Therneau 2018). For each Cox PH model, we report the estimated hazard ratio and p value. A hazard ratio of 1 indicates that the predictive variable has no effect on survival; a hazard ratio of less than 1, indicates a reduction in the mortality risk with a higher value of the variable; and a hazard ratio of more than 1, indicates an increase in the mortality risk. We used Akaike's Information Criterion and Akaike weight to rank and found the most parsimonious model by favoring the model with lowest AIC. For calculations of AIC and Akaike weight (see Burnham and Anderson 2002), we used the R package 'MuMIn' (Barton 2009).

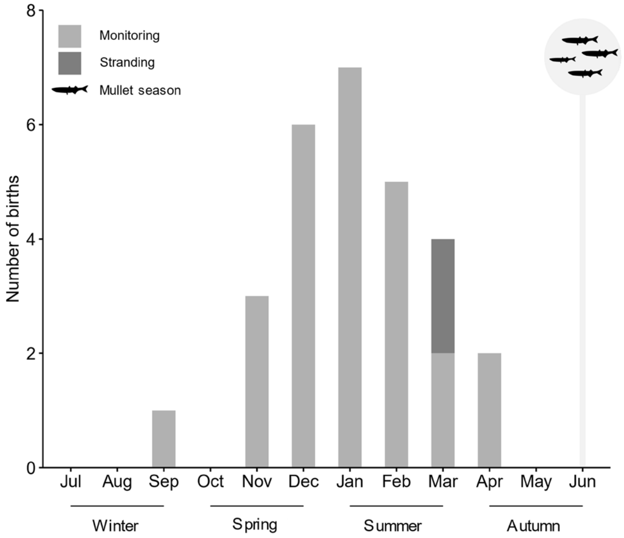

Fig. 2 Birth seasonality for bottlenose dolphins in Laguna based on a long-term monitoring study (2007–2009 and 2013–2017) in relation to the peak of the mullet season in June. Light gray bars express the number of births estimated from mark–recapture surveys conducted in the lagoon system, while the dark gray bar expresses the number of neonates found stranded during beach surveys

Results

Reproductive parameters

We analyzed photo-identification data collected systematically during 233 boat-based surveys in 2007–2009 and 2013–2017. From 27,808 high-quality photographs, we identified and tracked the reproductive history of 24 females (Table 1). The maximum number of documented calves per female was four (mode = 1). During the study, we documented 40 births and five one-year-old calves first sighted in 2007 and 2013, as well as two dead neonates stranded on the beach. The annual number of reproductive females (range 12–20) and births (range 2–7) varied throughout the study (Table 2). The average crude birth rate was 0.09 (SD = 0.04) and estimated fecundity was 0.17 (SD = 0.06). We successfully assigned the month of birth for 26 newborns of 17 known females, and both dead neonates. Births occurred from September to April, but the majority (79%) from December to March (late spring and summer months; Fig. 2).

Inter-birth interval for females with surviving calves was either 2 or 3 years, and the mean IBI was 2.43 years ($n = 7$ IBIs for six individual females). Including intervals in which the first calf died before one year of age, mean IBI was 2.09 years ($n = 11$ IBIs for nine individual females; mode = 2). Two females had a 1-year calving interval; they have lost their calves within the first weeks of life, making them receptive for another pregnancy.

Weaning age was documented for only three calves. Separation of the mother and calf occurred after 2 ($n = 1$) or 3 years ($n = 2$). They left their mothers probably few weeks (1–3 months) before a new calf was born. In one case, the older sibling, after nursing for 2 years, continued to associate with its mother ID#42 and her new calf eventually for at least another year. We managed to track only one female ID#51 from birth until her first calving. She gave birth for the first time in 2017 at age 10, and her calf survived to age 2.

Factors influencing calf survival

Survival to 1 and 2 years estimated by the Kaplan–Meier method were 0.78 (95% CI 0.65–0.92) and 0.65 (95% CI 0.51–0.83), respectively—which represents a survival rate in the second year of 0.83. Results from the best fitting Cox model showed that birth timing influences calf survival (Table 3). Calves born closer to the mullet season have a significantly lower mortality risk than calves born earlier in the calving season ($\text{Calf}_{\text{hazard}} \sim 0.82.T_{\text{mullet}}$; hazard ratio = 2.29; SE = 0.36; $z = 2.28$; $p = 0.02$; Table 3). Calf survival is not significantly related to the other four predictive variables.

Out of the 24 individually identified females, we classified nine as cooperatives and 15 as non-cooperatives. Mean annual fecundity was 0.18 (SD = 0.14) for cooperatives and 0.15 (SD = 0.05) for non-cooperatives. Mean IBI (including intervals in which the first calf died before 1 year of age) was 2 years for cooperative females ($n = 4$) and 2.14 years for non-cooperative females ($n = 7$).

Table 3 Summary of the Cox proportional hazard models for factors influencing calf survival. Fixed input parameters include mother frequency of interaction with fishermen (Mother_{fi}), mother home range size ($\text{Mother}_{\text{HR}}$), mother foraging tactic classification ($\text{Mother}_{\text{Coop}}$), time between birth and the peak of the following mullet season (T_{mullet}) and fishery yield of the mullet season following the birth (N_{mullet}). All models contain the random effect of mother ID. Models are ranked according to the lowest Akaike information criterion corrected for small sample size (AICc). Notation: delta AICc (ΔAICc), log-likelihood (logLik), degrees of freedom (*df*) and AICc model weight (weight). For each model we reported the estimated hazard ratio (Haz) and *p* value (*p*)

Cox models	Haz	*p*	AICc	ΔAICc	logLik	*df*	Weight
$\text{Calf}_{\text{hazard}} \sim T_{\text{mullet}}$	2.29	0.02	48.6	0.00	− 17.20	4	0.968
$\text{Calf}_{\text{hazard}} \sim 1$	–	–	57.3	8.73	− 19.21	5	0.012
$\text{Calf}_{\text{hazard}} \sim N_{\text{mullet}}$	4.26	0.24	58.1	9.48	− 18.79	6	0.008
$\text{Calf}_{\text{hazard}} \sim \text{Mother}_{fi}$	1.00	0.95	59.5	10.92	− 19.19	6	0.004
$\text{Calf}_{\text{hazard}} \sim \text{Mother}_{\text{Coop}}$	0.70	0.75	59.8	11.19	− 19.04	6	0.004
$\text{Calf}_{\text{hazard}} \sim \text{Mother}_{\text{HR}}$	0.97	0.52	59.8	11.25	− 18.54	6	0.003

Because our sample size is small, we cannot tell whether this slight difference between groups is statistically significant or not.

Discussion

This study extends our knowledge on bottlenose dolphin reproduction, especially on a small and resident population, representative of the recently recognized subspecies *Tursiops truncatus gephyreus* endemic to the Southwest Atlantic, and with a very specialized and unusual forage behavior. Using longitudinal sighting data from dedicated boat surveys in Laguna, southern Brazil, we established long-term reproductive histories of known females and investigated calf production, IBIs and calf survival. We also evaluated the potential factors influencing calf survival, including mothers' features, such as the frequency with which they interact with fishermen, and the timing of birth in relation to prey availability. Moreover, we estimated fecundity and IBI separately for females that often cooperate with fishermen, and for females that tend not to cooperate.

Calving season in Laguna was the same as in the Patos Lagoon estuary (Fruet et al. 2015), as expected due to the proximity of the two populations (520 km). Crude birth rate, mean IBI, fecundity and calf survival were also similar. Although the Laguna population is apparently genetically isolated from other population units (Fruet et al. 2014), they share similar reproductive traits, suggesting consistence among populations of the subspecies. Differences in life history parameters may reflect the different ecological and environmental conditions and pressures to which each population or community is subject. Anthropogenic threats faced by dolphins in both places include habitat degradation and entanglement in fishing gear (Fruet et al. 2012; Daura-Jorge et al. 2013; Bezamat et al. 2019; Righetti et al. 2019), which will be discussed later.

Reproductive parameters

Calving in Laguna was highly seasonal, with most births occurring in late spring and summer. Bottlenose dolphins show a great variability in the seasonality of their reproduction in different areas (Urian et al. 1996). Birth seasonality may be influenced by seasonal changes in the environment, including water temperature (Wells et al. 1987; Henderson et al. 2014), food availability (Urian et al. 1996; Mann et al. 2000) and predation pressure (Mann and Watson-Capps 2005; Fearnbach et al. 2012). Females tend to give birth when the water is warm, which is thermally efficient for small calves, increasing calf survival. A high abundance of food is also important to support the costs of lactation, the most energetic demanding time of reproduction (Kastelein et al. 2002; Rechsteiner et al. 2013).

Forty-two calves were born to resident females between 2007–2009 and 2013–2017, and the average crude birth rate was 0.09, which is similar to that found for other bottlenose dolphin populations, such as Patos Lagoon Estuary, Brazil (0.09; Fruet et al. 2015), Shannon Estuary, Ireland (0.07; Baker et al. 2018) and Mikura Island, Japan (0.07; Kogi et al. 2004). As reported by other studies (e.g., Steiner and Bossley 2008; Kogi et al. 2004; Cheney et al. 2019), some births may have gone unnoticed, particularly for females that have lost their calves very soon after birth, before we were able to observe them. As a result, the number of calves born each year may be biased low, especially in 2009 and 2017, when we conducted fewer surveys during the calving season. To minimize this bias, we included the two newborns we found dead on the beach in the estimates, even though we could not tell from which females they were born. Nevertheless, the mean annual crude birth rate for Laguna dolphins of 0.09 fall within the range reported for other bottlenose dolphins populations, from 0.04 in Doubtful Sound, New Zealand (Henderson et al. 2014) and Baía San Antonio, Argentina (Vermeulen and Bräger 2015) and 0.12 in the North Sea, Scotland (Robinson et al. 2017).

Although our sample size is small, the mean IBI of 2.0 and 2.4 years estimated here is similar to those reported for the Shannon Estuary, Ireland (Baker et al. 2018) and the Adriatic Sea, Croatia (Bearzi et al. 1997), but at the lower range reported from elsewhere (see Baker et al. 2018). However, we probably missed longer IBIs since the study period was relatively short when compared to dolphins' life span, and we had a gap in data collection from 2010 to 2012. For example, female ID#31 had a calf in 2007, which stayed with her until the beginning of 2010 at least, from 2013 to 2017 she was never seen with a calf, and in 2018 (data not shown) she gave birth again.

The first-year survival rate estimated here (0.78) is similar to that reported for the Adriatic Sea (0.77; Fortuna 2007) and Sarasota Bay, USA (0.71; Mann et al. 2000). Elsewhere, rates of between 0.89 (Shannon Estuary, Ireland; Baker et al. 2018) and 0.37 (Doubtful Sound, New Zealand; Currey et al. 2009) have been reported. The cumulative impacts on individuals < 3 years old in Doubtful Sound resulted in a reduced recruitment, which is probably the cause of population decline (Currey et al. 2011). First-year survival rate is likely to have been slightly overestimated here, given that some calves probably died before being sighted (as in Mann et al. 2000; Kogi et al. 2004). Second-year calf survival rate (0.83) is comparable to the estimate obtained for bottlenose dolphins in Shark Bay, Australia (0.82; Mann et al. 2000).

Factors influencing calf survival

The causes of calf mortality in Laguna are uncertain. One of the main causes is the bycatch in illegal trammel netting in the dolphins' core area (Peterson et al. 2008, Laguna municipal law number 1.998/2018). The necropsy of dolphin carcasses recovered by a systematic monitoring program revealed several deaths caused by entanglements or injuries from fishing gear in the last few years, of both adults and calves (Bezamat et al. 2019). From December 2017 to October 2019 at least, a live calf was seen entangled in marine debris wrapped tightly around its head. Boat collision is another direct impact that threatens calf survival. In January 2019, a 1-month-old calf was found dead and the necropsy revealed a blunt trauma injury on its cervical spine, suggesting the calf was hit by a boat. Predation pressure in Laguna is very low, since predators of bottlenose dolphins (i.e., large sharks and killer whales, *Orcinus orca*) were never seen in the estuary and rarely seen in the surroundings, and we have never observed shark scars or wounds on the dolphins.

Less obvious human impacts could also be affecting calf survival, such as PCB contamination. Blubber PCB concentrations in some biopsied dolphins in Laguna exceeded the PCB toxicity threshold for the species (Schwacke et al. 2002; Righetti et al. 2019). PCBs are known to bioaccumulate in dolphins and are passed on to calves via the female, through gestation and lactation, increasing the chances of fetal and calf mortality, particularly for first-born calves (Reddy et al. 2001, Wells et al. 2005). About 80% of the mother's body burden of PCBs and t-DDT is transferred to the calf through lactation within 7 weeks post-partum, with the first-born offspring receiving the majority of the mother's body burden (Cockcroft et al. 1989). Some small or declining populations of bottlenose dolphins and killer whales in the NE Atlantic were associated with low recruitment, consistent with PCB-induced reproductive toxicity (Jepson et al. 2016). Other potential human impact is the acoustic disturbance from daily boat traffic and the construction of a 2.8 km bridge, from late 2012 to early 2015, in a core area for the dolphins at that time. Disturbance during the bridge construction included dredging (see Pirotta et al. 2013; Todd et al. 2014), pile-driving (see Bailey et al. 2010) and increased boat traffic (see Bejder et al. 2006; Pérez-Jorge et al. 2016). Since acoustic communication between mothers and calves is essential to their associations, if anthropogenic noise disrupts this communication it could lead to the severe debilitation and even death of a dependent calf (Parsons and Dolman 2004).

Calf survival was influenced by timing of birth. Calves born closer to the peak of the following mullet season had a higher chance of survival relative to calves born in other periods. As aforementioned, when giving birth close to the mullet season, lactating females can take advantage of seasonally abundant resources for raising offspring. Synchronizing time of birth with high food abundance has been correlated with reproductive success in other bottlenose dolphin populations (Urian et al. 1996; Fruet et al. 2015).

Regarding different foraging tactics within the population, our small sample size prevents us to draw conclusions on the influence of the cooperative tactic on female reproductive success. A longer time series is required to state whether or not this forage specialization increases individual fitness. Whereas even a small difference in survival, over multiple generations, could represent a selective advantage and contribute to the evolution and maintenance of the cooperative fishing specialization. In Western Australia, food-provisioning negatively affects calf survival and female reproductive success in bottlenose dolphins; calves of provisioned females had a lower survival rate to weaning age (Mann et al. 2000; Senigaglia et al. 2019). In Shark Bay, there was a decline in bottlenose dolphin survival and reproductive rates after the 2011 marine heatwave (Wild et al. 2019); interestingly, dolphins that use tools to forage—known as spongers—were less affected, suggesting that this specialized tactic plays an ecological role that reduces the negative effects of the heatwave. However, calving success of sponger females was not significantly different from non-spongers (Mann et al. 2008). Differences in calving rate within populations of killer whales due to different foraging specializations have also been described (Tixier et al. 2015; Esteban et al. 2016).

Besides estimating reproductive parameters crucial for a population assessment, our findings reveal that timing of birth in relation to resource availability may influence reproduction success of bottlenose dolphins in Laguna. Due to our small sample size, we could not conclude whether or not the cooperative foraging tactic influences calf survival and female reproductive success. Moreover, this study emphasizes the importance of long-term, individual-based monitoring of populations to understand regional life history characteristics and provide accurate information towards effective conservation and management. This is especially critical for this dolphin population in Laguna that retains the tactic of cooperating with fishermen, but also faces several human threats that put them at local and regional risk of extinction.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This study was approved by the Brazilian Ministry of the Environment (permits: SISBIO 649561 and SISBIO 478761). In addition, we tried to minimize disturbance by approaching and following dolphins slowly, from the side, always keeping a safe distance.

References

Alberts SC (2019) Social influences on survival and reproduction: insights from a long-term study of wild baboons. J Anim Ecol 88:47–66. https://doi.org/10.1111/1365-2656.12887

Arso Civil M, Cheney B, Quick NJ, Thompson PM, Hammond PS (2017) A new approach to estimate fecundity rate from inter-birth intervals. Ecosphere. https://doi.org/10.1002/ecs2.1796

Arso Civil M, Cheney B, Quick NJ, Islas-Villanueva V, Graves JA, Janik VM, Thompson PM, Hammond PS (2019) Variations in age- and sex-specific survival rates help explain population trend in a discrete marine mammal population. Ecol Evol 9:533–544. https://doi.org/10.1002/ece3.4772

Bailey H, Senior B, Simmons D, Rusin J, Picken G, Thompson PM (2010) Assessing underwater noise levels during pile-driving at an offshore windfarm and its potential effects on marine mammals. Mar Pollut Bull 60:888–897. https://doi.org/10.1016/j.marpolbul.2010.01.003

Baker JD, Polovina JJ, Howell EA (2007) Effect of variable oceanic productivity on the survival of an upper trophic predator, the Hawaiian monk seal *Monachus schauinslandi*. Mar Ecol Prog Ser 346:277–283. https://doi.org/10.3354/meps06968

Baker I, O'Brien J, McHugh K, Berrow S (2018) Female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. Mar Biol 165:15. https://doi.org/10.1007/s00227-017-3265-z

Barton K (2009) MuMIn: R functions for model selection and model averaging. R package version 0.12. 0

Bearzi G, Notarbartolo-Di-Sciara G, Politi E (1997) Social ecology of bottlenose dolphins in the Kvarnerić (Northern Adriatic Sea). Mar Mammal Sci 13:650–668. https://doi.org/10.1111/j.1748-7692.1997.tb00089.x

Beissinger SR, McCullough DR (eds) (2002) Population viability analysis. The University of Chicago Press, Chicago

Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor R, Heithaus M, Watson-Capps J, Flaherty C, Krützen M (2006) Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conserv Biol 20:1791–1798. https://doi.org/10.1111/j.1523-1739.2006.00540.x

Bezamat C, Simões-Lopes PC, Castilho PV, Daura-Jorge FG (2019) The influence of cooperative foraging with fishermen on the dynamics of a bottlenose dolphin population. Mar Mammal Sci 35:825–842. https://doi.org/10.1111/mms.12565

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. Oecologia 37:257–272. https://doi.org/10.1007/BF00344996

Brough T, Henderson S, Guerra M, Dawson S (2016) Factors influencing heterogeneity in female reproductive success in a Critically Endangered population of bottlenose dolphins. Endanger Species Res 29:255–270. https://doi.org/10.3354/esr00715

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Cameron E, Setsaas T, Linklater L (2009) Social bonds between unrelated female increase reproductive success in feral horses. Proc Natl Acad Sci USA 106:13850–13853. https://doi.org/10.3390/rs10030479

Cantor M, Simões-Lopes PC, Daura-Jorge FG (2018) Spatial consequences for dolphins specialized in foraging with fishermen. Anim Behav 139:19–27. https://doi.org/10.1016/j.anbehav.2018.03.002

Caughley G (1977) Analysis of vertebrate populations. Wiley, New York

Cheney BJ, Thompson PM, Cordes LS (2019) Increasing trends in fecundity and calf survival of bottlenose dolphins in a marine protected area. Sci Rep 9:1767. https://doi.org/10.1038/s41598-018-38278-9

Cleves M, Gould W, Gutierrez RG, Marchenko Y (2010) The Cox model: diagnostics. An introduction to survival analysis using stata, pp 203–228

Cockcroft VG, De Kock AC, Lord DA, Ross GJB (1989) Organochlorines in bottlenose dolphins *Tursiops truncatus* from the east coast of South Africa. S Afr J Mar Sci 8:207–217. https://doi.org/10.2989/02577618909504562

Cox DR (1972) Regression models and life-tables. J R Stat Soc Ser B 34:187–220

Craig MP, Ragen TJ (1999) Body size, survival, and decline of juvenile Hawaiian monk seals, *Monachus schauinslandi*. Mar Mammal Sci 15:786–809. https://doi.org/10.1111/j.1748-7692.1999.tb00843.x

Currey R, Dawson S, Slooten E, Schneider K, Lusseau D, Boisseau O, Haase P, Williams J (2009) Survival rates for a declining population of bottlenose dolphins in Doubtful Sound, New Zealand: an information theoretic approach to assessing the role of human impacts. Aquat Conserv Mar Freshw Ecosyst 19:658–670. https://doi.org/10.1002/aqc

Currey R, Dawson S, Schneider K, Lusseau D, Boisseau O, Haase P, Slooten E (2011) Inferring causal factors for a declining population of bottlenose dolphins via temporal symmetry capture—recapture modeling. Mar Mammal Sci 27:554–566. https://doi.org/10.1111/j.1748-7692.2010.00417.x

Daura-Jorge FG, Cantor M, Ingram SN, Lusseau D, Simões-Lopes PC (2012) The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biol Lett 8:702–705. https://doi.org/10.1098/rsbl.2012.0174

Daura-Jorge FG, Ingram SN, Simões-Lopes PC (2013) Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. Mar Mammal Sci 29:293–311. https://doi.org/10.1111/j.1748-7692.2012.00571.x

Elwen SH, Best PB (2004) Female southern right whales *Eubalaena australis*: are there reproductive benefits associated with their coastal distribution off South Africa? Mar Ecol Prog Ser 269:289–295. https://doi.org/10.3354/meps269289

Esteban R, Verborgh P, Gauffier P, Giménez J, Guinet C, de Stephanis R (2016) Dynamics of killer whale, bluefin tuna and human fisheries in the Strait of Gibraltar. Biol Conserv 194:31–38. https://doi.org/10.1016/j.biocon.2015.11.031

Fearnbach H, Durban J, Parsons K, Claridge D (2012) Seasonality of calving and predation risk in bottlenose dolphins on Little Bahama Bank. Mar Mammal Sci 28:402–411. https://doi.org/10.1111/j.1748-7692.2011.00481.x

Félix F (1994) Ecology of the coastal bottlenose dolphin *Tursiops truncatus* in the Gulf of Guayaquil, Ecuador. Investig Cetacea 25:235–256

Foroughirad V, Mann J (2013) Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. Biol Conserv 160:242–249. https://doi.org/10.1016/j.biocon.2013.01.001

Fortuna CM (2007) Ecology and conservation of bottlenose dolphins (*Tursiops truncatus*) in the North-Eastern Adriatic Sea. Thesis, PhD Doctor of Philosophy, University of St Andrews

Frick WF, Reynolds DS, Kunz TH (2010) Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. J Anim Ecol 79:128–136. https://doi.org/10.1111/j.1365-2656.2009.01615.x

Fruet PF, Kinas PG, da Silva KG, Di Tullio JC, Monteiro DS, Rosa LD, Estima SC, Secchi ER (2012) Temporal trends in mortality and effects of by-catch on common bottlenose dolphins, *Tursiops truncatus*, in southern Brazil. J Mar Biol Assoc 92:1865–1876. https://doi.org/10.1017/S0025315410001888

Fruet PF, Secchi ER, Daura-Jorge F, Vermeulen E, Flores PAC, Simões-Lopes PC, Genoves RC, Laporta P, Di Tullio JC, Freitas TRO, Dalla Rosa L, Valiati VH, Beheregaray LB, Moller LM (2014) Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conserv Genet 15:879–895. https://doi.org/10.1007/s10592-014-0586-z

Fruet PF, Genoves RC, Möller LM, Botta S, Secchi ER (2015) Using mark-recapture and stranding data to estimate reproductive traits in female bottlenose dolphins (*Tursiops truncatus*) of the Southwestern Atlantic Ocean. Mar Biol 162:661–673. https://doi.org/10.1007/s00227-015-2613-0

Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC (2007) LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS One 2:e207. https://doi.org/10.1371/journal.pone.0000207

Gough KF, Kerley GIH (2006) Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: is there evidence of density dependent regulation? Oryx 40:434–441. https://doi.org/10.1017/S0030605306001189

Hayes LD, Schradin C (2017) Long-term field studies of mammals: what the short-term study cannot tell us. J Mammal 98:600–602. https://doi.org/10.1093/jmammal/gyx027

Henderson SD, Dawson SM, Currey RJC, Lusseau D, Schneider K (2014) Reproduction, birth seasonality, and calf survival of bottlenose dolphins in Doubtful Sound, New Zealand. Mar Mammal Sci 30:1067–1080. https://doi.org/10.1111/mms.12109

Jepson PD, Deaville R, Barber JL, Aguilar À, Borrell A, Murphy S, Barry J, Brownlow A, Barnett J, Berrow S, Cunningham AA, Davison NJ, Ten Doeschate M, Esteban R, Ferreira M, Foote AD, Genov T, Giménez J, Loveridge J, Llavona Á, Martin V, Maxwell DL, Papachlimitzou A, Penrose R, Perkins MW, Smith B, De Stephanis R, Tregenza N, Verborgh P, Fernandez A, Law RJ (2016) PCB pollution continues to impact populations of orcas and other dolphins in European waters. Sci Rep 6:1–17. https://doi.org/10.1038/srep18573

Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. J Am Stat Assoc 53:457–481. https://doi.org/10.1080/01621459.1958.10501452

Karniski C, Krzyszczyk E, Mann J (2018) Senescence impacts reproduction and maternal investment in bottlenose dolphins. Proc R Soc B Biol Sci 285:20181123. https://doi.org/10.1098/rspb.2018.1123

Kastelein RA, Vaughan N, Walton S, Wiepkema PR (2002) Food intake and body measures of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. Mar Environ Res 53:199–218. https://doi.org/10.1016/S0141-1136(01)00123-4

Kleinbaum D, Klein M (2012) Survival analysis—a self-learning text, 3rd edn. Springer, New York

Lemos VM, Varela AS, Schwingel PR, Muelbert JH, Vieira JP (2014) Migration and reproductive biology of *Mugil liza* (Teleostei: Mugilidae) in south Brazil. J Fish Biol 85:671–687. https://doi.org/10.1111/jfb.12452

Manlik O, Mcdonald JA, Mann J, Raudino HC, Bejder L, Connor RC, Heithaus MR, Lacy RC, Sherwin WB (2016) The relative importance of reproduction and survival for the conservation of two dolphin populations. Ecol Evol 6:3496–3512. https://doi.org/10.1002/ece3.2130

Mann J, Karniski C (2017) Diving beneath the surface: long-term studies of dolphins and whales. J Mammal 98:621–630. https://doi.org/10.1093/jmammal/gyx036

Mann J, Smuts B (1999) Behavioural development in wild bottlenose dolphin newborns (*Tursiops* sp.). Behaviour 136:529–566. https://doi.org/10.1163/156853999501469

Mann J, Watson-Capps JJ (2005) Surviving at sea: ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins, *Tursiops* sp. Anim Behav 69:899–909. https://doi.org/10.1016/j.anbehav.2004.04.024

Mann J, Connor R, Barre L, Heithaus M (2000) Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. Behav Ecol 11:210–219. https://doi.org/10.1093/beheco/11.2.210

Mann J, Sargeant BL, Watson-Capps JJ, Gibson QA, Heithaus MR, Connor RC, Patterson E (2008) Why do dolphins carry sponges? PLoS One. https://doi.org/10.1371/journal.pone.0003868

Mintzer VJ, Martin AR, da Silva VMF, Barbour AB, Lorenzen K, Frazer TK (2013) Effect of illegal harvest on apparent survival of Amazon River dolphins (*Inia geoffrensis*). Biol Conserv 158:280–286. https://doi.org/10.1016/j.biocon.2012.10.006

Parsons C, Dolman S (2004) The use of sound by cetaceans. In: Simmonds M, Dolman S, Weilgart L (eds) Oceans of noise. WDCS, the Whale and Dolphin Conservation Society, pp 45–53

Pérez-Jorge S, Gomes I, Hayes K, Corti G, Louzao M, Genovart M, Oro D (2016) Effects of nature-based tourism and environmental drivers on the demography of a small dolphin population. Biol Conserv 197:200–208. https://doi.org/10.1016/j.biocon.2016.03.006

Peterson D, Hanazaki N, Simões-Lopes PC (2008) Natural resource appropriation in cooperative artisanal fishing between fishermen and dolphins (*Tursiops truncatus*) in Laguna, Brazil. Ocean Coast Manag 51:469–475. https://doi.org/10.1016/j.ocecoaman.2008.04.003

Pirotta E, Laesser BE, Hardaker A, Riddoch N, Marcoux M, Lusseau D (2013) Dredging displaces bottlenose dolphins from an urbanised foraging patch. Mar Pollut Bull 74:396–402. https://doi.org/10.1016/j.marpolbul.2013.06.020

Pomeroy PP, Fedak MA, Rothery P, Anderson S (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. J Anim Ecol 68:235–253. https://doi.org/10.1046/j.1365-2656.1999.00281.x

Rechsteiner EU, Rosen DAS, Trites AW (2013) Energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as predicted by a bioenergetic model. J Mammal 94:820–832. https://doi.org/10.1644/12-MAMM-A-206.1

Reddy ML, Reif JS, Bachand A, Ridgway SH (2001) Opportunities for using Navy marine mammals to explore associations between organochlorine contaminants and unfavorable effects on reproduction. Sci Total Environ 274:171–182. https://doi.org/10.1016/S0048-9697(01)00741-0

Reed J, Mills L, Dunning JB Jr, Menges E, McKelvey KS, Frye R, Beissinger SR, Anstett M-C, Miller P (2002) Emerging issues in population viability analysis. Conserv Biol 16:7–19. https://doi.org/10.1046/j.1523-1739.2002.99419.x

Righetti BPH, Daura-Jorge FG, Mattos JJ, Siebert MN, Bezamat C, Fruet P, Genoves R, Taniguchi S, Da Silva J, Montone RC, Simões-Lopes PC, Bainy ACD, Lüchmann KH (2019) Biochemical and molecular biomarkers in integument biopsies of free-ranging coastal bottlenose dolphins from southern Brazil. Chemosphere 225:139–149. https://doi.org/10.1016/j.chemosphere.2019.02.179

Robinson KP, Sim TMC, Culloch RM, Bean TS, Aguilar IC, Eisfeld SM, Filan M, Haskins GN, Williams G, Pierce GJ (2017) Female reproductive success and calf survival in a North Sea coastal bottlenose dolphin (*Tursiops truncatus*) population. PLoS One 12:e0185000. https://doi.org/10.1371/journal.pone.0185000

Romeu B, Cantor M, Bezamat C, Daura-Jorge FG, Simões-Lopes PC (2017) Bottlenose dolphins that forage with artisanal fishermen whistle differently. Ethology 123:906–915. https://doi.org/10.1111/eth.12665

Rosel PE (2003) PCR-based sex determination in Odontocete cetaceans. Conserv Genet 4:647–649. https://doi.org/10.1023/A:1025666212967

Sant'ana R, Kinas PG (2016) Avaliação do Estoque de Tainha (*Mugil liza*): ampliação dos modelos Bayesianos de Dinâmica de Biomassa para múltiplas séries de CPUE, com adição de temperatura superficial do mar e capturabilidade autocorrelacionada. In: Oceana. http://brasil.oceana.org/sites/default/files/avaliacao_de_estoque_tainha_oceana_-_integra.pdf. Accessed 19 Feb 2019

Sant'Ana R, Gerhard Kinas P, Villwock de Miranda L, Schwingel PR, Castello JP, Paes Vieira J (2017) Bayesian state-space models with multiple CPUE data: the case of a mullet fishery. Sci Mar 81:361. https://doi.org/10.3989/scimar.04461.11a

Schradin C, Pillay N, Kondratyeva A, Yuen C-H, Schoepf I, Krackow S (2015) Basal blood glucose concentration in free-living striped mice is influenced by food availability, ambient temperature and social tactic. Biol Lett 11:20150208. https://doi.org/10.1098/rsbl.2015.0208

Schwacke LH, Voit EO, Hansen LJ, Wells RS, Mitchum GB, Hohn AA, Fair PA (2002) Probabilistic risk assessment of reproductive effects of polychlorinated biphenyls on bottlenose dolphins (*Tursiops truncatus*) from the southeast United States coast. Environ Toxicol Chem 21:2752–2764. https://doi.org/10.1002/etc.5620211232

Senigaglia V, Christiansen F, Sprogis KR, Symons J, Bejder L (2019) Food-provisioning negatively affects calf survival and female reproductive success in bottlenose dolphins. Sci Rep 9:8981. https://doi.org/10.1038/s41598-019-45395-6

Simões-Lopes PC, Fábian ME (1999) Residence patterns and site fidelity in bottlenose dolphins, *Tursiops truncatus* (Montagu) (Cetacea, Delphinidae) off Southern Brazil. Rev Bras Zool 16:1017–1024

Simões-Lopes PC, Fabián ME, Menegheti JO (1998) Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. Rev Bras Zool 15:709–726. https://doi.org/10.1590/S0101-81751999000400012

Simões-Lopes PC, Daura-Jorge FG, Cantor M (2016) Clues of cultural transmission in cooperative foraging between artisanal fishermen and bottlenose dolphins, *Tursiops truncatus* (Cetacea: Delphinidae). Zool 33:e20160107. https://doi.org/10.1590/s1984-4689zool-20160107

Steiner A, Bossley M (2008) Some reproductive parameters of an estuarine population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). Aquat Mamm 34:84–92. https://doi.org/10.1578/AM.34.1.2008.84

Swanson A, Caro T, Davies-Mostert H, Mills MGL, Macdonald DW, Borner M, Masenga E, Packer C (2014) Cheetahs and wild dogs show contrasting patterns of suppression by lions. J Anim Ecol 83:1418–1427. https://doi.org/10.1111/1365-2656.12231

Thayer V, Read A, Friedlaender A, Colby D, Hohn A, McLellan W, Pabst D, Dearolf J, Bowles N, Russell J, Rittmaster K (2003) Reproductive seasonality of Western Atlantic Bottlenose Dolphins off North Carolina, USA. Mar Mammal Sci 19:617–629. https://doi.org/10.1111/j.1748-7692.2003.tb01120.x

Therneau TC (2018) Mixed effects cox models. R package version 2(2-10):2018

Thompson ME, Kahlenberg SM, Gilby IC, Wrangham RW (2007) Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. Anim Behav 73:501–512. https://doi.org/10.1016/j.anbehav.2006.09.007

Tixier P, Authier M, Gasco N, Guinet C (2015) Influence of artificial food provisioning from fisheries on killer whale reproductive output. Anim Conserv 18:207–218. https://doi.org/10.1111/acv.12161

Todd VLG, Todd IB, Gardiner JC, Morrin ECN, MacPherson NA, DiMarzio NA, Thomsen F (2014) A review of impacts of marine dredging activities on marine mammals. ICES J Mar Sci 72:328–340. https://doi.org/10.1093/icesjms/fsu187

Urian KW, Duffield DA, Read AJ, Wells RS, Shell ED (1996) Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. J Mammal 77:394–403. https://doi.org/10.2307/1382814

Vermeulen E, Bräger S (2015) Demographics of the disappearing bottlenose dolphin in Argentina: a common species on its way out? PLoS One 10:e0119182. https://doi.org/10.1371/journal.pone.0119182

Wells RS, Scott MD (1990) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Reports Int Whal Comm 407–415

Wells RS, Scott MD (1999) Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In: Ridgway SH, Harrison R (eds) Handbook of marine mammals, vol 6. The second book of dolphins and the porpoises. Academic Press, San Diego, pp 137–182

Wells RS, Scott MD, Irvine AB (1987) The social structure of free-ranging bottlenose dolphins. In: Genoways HH (ed) Current mammalogy, vol 1. Plenum Press, New York, pp 247–305

Wells RS, Tornero V, Borrell A, Aguilar A, Rowles TK, Rhinehart HL, Hofmann S, Jarman WM, Hohn AA, Sweeney JC (2005) Integrating life-history and reproductive success data to examine potential relationships with organochlorine compounds for bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Sci Total Environ 349:106–119. https://doi.org/10.1016/j.scitotenv.2005.01.010

Wild S, Krützen M, Rankin RW, Hoppitt WJE, Gerber L, Allen SJ (2019) Long-term decline in survival and reproduction of dolphins following a marine heatwave. Curr Biol 29:R239–R240. https://doi.org/10.1016/j.cub.2019.02.047

Williams JA, Dawson SM, Slooten E (1993) The abundance and distribution of bottlenosed dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. Can J Zool 71:2080–2088. https://doi.org/10.1139/z93-293

Worton BJ (1989) Kernel nethods for estimating the utilization distribution in home-range studies. Ecology 70:164–168. https://doi.org/10.2307/1938423

Würsig B, Jefferson TA (1990) Methods of photo-identification for small cetaceans. Rep Int Whal Comm 43–52