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ARTICLE

Age and Length at Sexual Maturity, Calving Interval, and Ovarian Activity of Female Tamanend's Bottlenose Dolphins (*Tursiops erebennus*) in South Carolina Waters

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ABSTRACT

Tamanend's bottlenose dolphins (*Tursiops erebennus*) face population and environmental stressors that influence the age and length at sexual maturity (ASM and LSM, respectively) and calving interval, which are life history traits used to assess population status and health. We provide initial estimates of the ASM, LSM, and calving interval, as well as descriptions of ovarian activity of female Tamanend's bottlenose dolphins that stranded in South Carolina waters. ASM and LSM estimates were approximately 10 years and 215 cm, respectively. Analysis of carcasses sampled over a three-decade period (1992–2022) indicated temporal variations in maturation, possibly related to unusual mortality events and/or periods of poor animal health. Stranding location did not appear to influence maturation. The calving interval estimate averaged between 2 and 4 years. Corpora counts relevant to age supported previous findings of corpora accumulation in bottlenose dolphins. In mature females, the left ovary accumulated more corpora and generally weighed more than the right ovary, suggesting asymmetric ovarian activity. To support the conservation of this newly recognized coastal and estuarine species, we suggest continued monitoring of the onset of sexual maturation and calving interval.

1 | Introduction

Marine mammals are long-lived and slow-growing and often exhibit delayed sexual maturity in which juveniles spend multiple years investing in growth and social development rather than in reproduction (Charnov 1990; Fowler 1981; Galezo et al. 2020; McFee et al. 2010). Due to the high energetic costs of gestation and lactation in females, maturation indicates when an animal can efficiently begin diverting energy toward reproduction (Gallagher et al. 2018; Reddy et al. 1994). In contrast to physical maturity, which is based on a critical mass and fusing of vertebral elements, sexual maturity is determined based on the development of reproductive organs and hormones (Mead and Potter 1990). The onset of sexual maturity is estimated as the age at sexual maturity (ASM) and length at sexual maturity (LSM). Calving intervals, the time between sequential calves, can also be estimated to assess population growth. Determining the onset of sexual maturity and calving interval for different populations and species is important to elucidate the relationships between maturation, reproduction, and environmental and animal health.

Sexual maturity and calving intervals can be estimated from stranded marine mammals. As mammals, dolphins have two ovaries with follicles containing eggs, and follicle growth is stimulated by increased estrogen and decreased progesterone levels (Boness 2009). As a follicle grows, fluid accumulates, and when a sexually mature female ovulates, the mature follicle, referred to as a Graafian follicle, bursts and releases an egg (Slijper 1962). Luteal tissue forms in the ruptured follicle and creates a corpus luteum (CL) that is composed of connective and glandular tissue and produces progesterone to maintain pregnancy (Slijper 1962; Yoshida et al. 1977). Following fertilization and pregnancy, the CL inhibits subsequent ovulation; however, after an unfertilized cycle or parturition, the CL degenerates into a corpus albicans (CA), also known as an ovarian scar (Yoshida et al. 1977). Scar regression has been observed in Franciscana dolphins (*Pontoporia blainvillei*; Harrison et al. 1981) and short-beaked common dolphins (Dabin et al. 2008; however, recent research by Palmer et al. (2022) suggests that scars may persist throughout life in this species). However, in other cetacean species, including bottlenose dolphins (*Tursiops* spp.), scars appear to accumulate throughout life (Best 1982; Harrison and Ridgway 1971; Kemper et al. 2019; Lockyer 1987; Tarpley et al. 2016). Scar retention allows the reproductive status and ovarian activity of deceased cetaceans to be evaluated based on ovarian corpora.

ASM and LSM of marine mammals are influenced by environmental conditions and prey availability (Eberhardt 1977; Kasuya 1991; Kato 1987; Laws 1956; Lydersen and Gjertz 1987), contaminant exposure, and diseases impairing growth and gonadal development (Murphy et al. 2015; Roca-Monge et al. 2022), population density (Kasuya 1991; Kjellqwist et al. 1995; Ohsumi 1986), and other factors that affect growth rates. In general, conditions favoring faster growth rates of immature animals (e.g., favorable prey availability, good health, or lower population density) may result in sexual maturation at younger ages and/or greater body lengths and vice versa. Additionally, as large mammals and K-strategists, cetaceans have reproductive rates that are characterized by slow growth, low reproductive rates, long gestation, high maternal investment, and long lifespans (Boness et al. 2002; MacArthur and Wilson 1967). Calving intervals and reproductive output in cetaceans are influenced by calf mortality, prey and nutrient availability, and maternal health. Calf mortality (Fruet et al. 2015; Haase and Schneider 2001; Henderson et al. 2014; Robinson et al. 2017) and favorable prey and nutrition availability (Kasuya 1991; Meyer-Gutbrod et al. 2015) have been associated with shorter calving intervals. In contrast, poor maternal health (Christiansen et al. 2020) and maternal senescence (Karniski et al. 2018; Robinson et al. 2017) have been associated with longer calving intervals.

ASM, LSM, and calving intervals have not previously been estimated for Tamanend's bottlenose dolphins (*Tursiops erebennus*; previously referred to as *T. truncatus*, see Costa et al. (2022); hereafter also referred to as “dolphins”) found in coastal and estuarine waters of the western North Atlantic. However, before recognition as a distinct species, Tamanend's bottlenose dolphins were likely included in common bottlenose dolphin (*T. truncatus*) studies, and as such, parameter estimates in the literature may overlap. Female common bottlenose dolphins, found worldwide and offshore in the western North Atlantic, generally reach sexual maturity between 5 and 12 years of age and at body lengths between 220 and 235 cm (e.g., Fruet et al. 2015; Harrison and Ridgway 1971; Mead and Potter 1990; Odell 1975; Robinson et al. 2017; Schwacke et al. 2022; Sergeant et al. 1973; Wells et al. 1987) and exhibit calving intervals of at least 2 years (e.g., Fruet et al. 2015; Haase and Schneider 2001; Wells et al. 1987).

In South Carolina waters, dolphins are exposed to numerous stressors (e.g., contaminants (Reif et al. 2017), low prey availability, human interaction, and infectious diseases (McFee and Lipscomb 2009) that may affect female maturation and reproductive success. The objective of this research was to provide initial (1) estimates of the ASM and LSM for the species and according to the time frame of stranding and stranding location, (2) estimates of the calving interval, and (3) descriptions of ovarian activity of females of the newly recognized species of Tamanend's bottlenose dolphins that stranded in South Carolina waters from 1992 to 2022.

2 | Methods

2.1 | Study Area and Strandings

Deceased, stranded Tamanend's bottlenose dolphins in coastal and estuarine waters of South Carolina, USA (Figure 1) were collected from 1992 to 2022. Total body length (measured from the tip of the upper jaw to the fluke notch), stranding date and location, sex, and decomposition code were collected for each stranding. Necropsies were performed opportunistically in either the field or laboratory. Carcasses were fresh and not frozen. One or both ovaries were collected during necropsy, opportunistically weighed and measured, and immediately stored in 10% buffered formalin for a minimum of 24 h. before transferring to ethanol for permanent storage.

Animals were grouped based on the time frame of stranding and geographic stranding location. The time frame of stranding was categorized according to three consecutive (~10 year) time periods: 1992–2001, 2002–2011, and 2012–2022. Stranding locations were classified as coastal (including barrier islands and coastal beachfronts) or estuarine (including bays, sounds, harbors, rivers, and tributaries).

2.2 | Ovarian Analysis

Ovarian analysis was performed based on the methods of Akin et al. (1993). Each ovary was blotted dry, weighed, measured (length, width, and depth), and grossly examined for externally visible CLs and CAs. Each ovary was sliced into 1 mm thick sections to ensure that each corpus was visible in at least one slice. Slices were examined sequentially under a Nikon SMZ1500 stereomicroscope (Tokyo, Japan), and images of ovaries and ovary slices were captured using a Jenoptik ProgRes Gryphax camera (Jena, Germany). A dolphin was classified as sexually mature if at least one CL or CA was present in either ovary. CLs were distinguished externally and internally from CAs based on CLs' rounded protrusion from the ovary's surface and the presence of yellow-layered granulosa cells, connective tissue, and blood vessels (Akin et al. 1993). Yellow or orange scars with no dense connective tissue may be regressed nonovulatory follicles, also

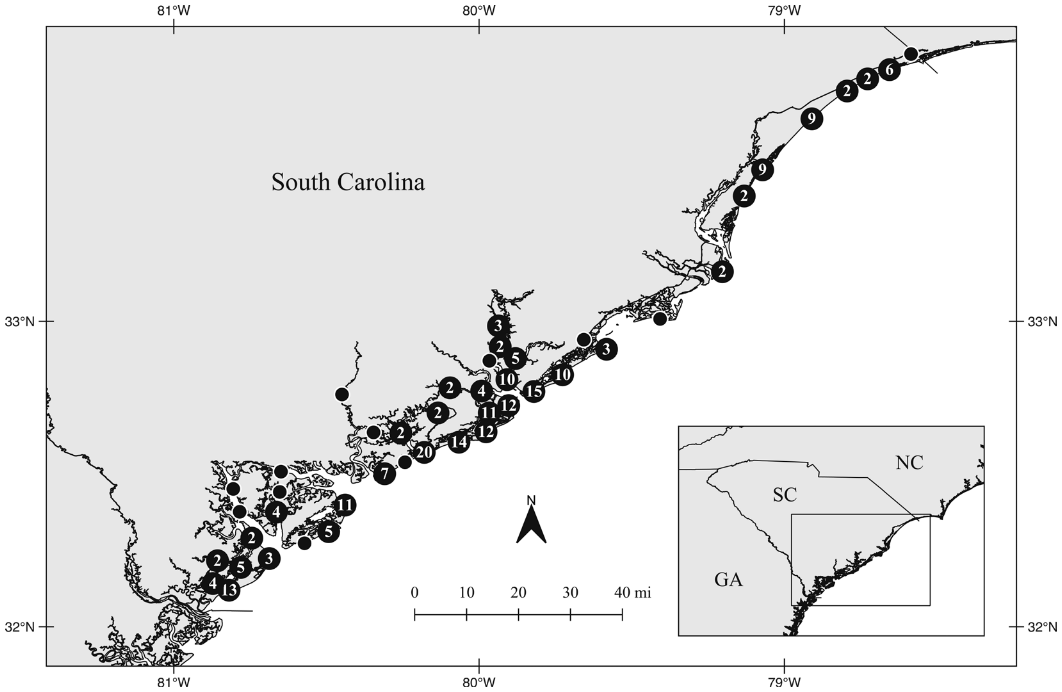

FIGURE 1 | Stranding locations of female Tamanend's bottlenose dolphins (*Tursiops erebennus*) included in this study. Multiple overlapping stranding locations along the coast of South Carolina, USA, have been clustered into a single data point labeled with the number of strandings they represent (Version 3.34.8; QGIS 2023).

known as atretic follicles (Akin et al. 1993). Although such scars should ideally not be included when determining maturity, differentiation between atretic follicles and CAs is typically not possible without histologic examination (Perrin and Donovan 1984).

2.3 | Age at Sexual Maturity (ASM) and Length at Sexual Maturity (LSM)

ASM and LSM were estimated for female dolphins at the species scale, time frame of stranding, and geographic stranding location. Tooth-based age estimates were available for a subset of individuals ($n = 160/227$) that had been aged in previous age-related studies (McFee et al. 2010; Powell et al. 2019; Schwacke et al. 2017). Briefly, teeth were sectioned and stained, and to estimate mean age, growth layer groups (GLGs) were counted three times, often by the same reader, with 1 week between each reading to prevent bias (McFee et al. 2010).

To model the growth of females, a Gompertz growth curve was created using the equation:

$$L_t = L_\infty(\exp(-b\ \exp(-kt))),$$

in which L_t is the body length at age t, L_∞ is the asymptotic body length, b is the constant of integration, and k is the growth rate constant (Fitzhugh Jr. 1976; Gompertz 1825).

ASM was estimated using the DeMaster method (DeMaster 1978), and LSM was estimated using a modified version of the DeMaster method (DeMaster 1978), in which age was replaced by body length. ASM and LSM were also estimated with logistic regression to estimate the age at which 50% of individuals were mature (Danilewicz 2003).

Based on the method of Demaster (DeMaster 1978), ASM and LSM were estimated using the equation:

$$\text{ASM} / \text{LSM} = \sum\nolimits_{t=j}^{k} t\left(f_t - f_{t-1}\right),$$

in which f_t is the proportion of mature animals of the age/body length class t, j is the age/body length class of the youngest/smallest mature animal, and k is the age/body length class of the oldest/longest animal.

The variances of ASM and LSM were estimated using the DeMaster method (DeMaster 1978) with a modification of Ferrero and Walker (1993) to account for the width of each age/body length class using the equation:

$$\text{VAR}(\text{ASM} / \text{LSM}) = w^2 \sum\nolimits_{t=j}^{k} \frac{f_t\left(1 - f_t\right)}{N_t - 1},$$

in which w is the interval width of the age/body length class, f_t is the proportion of mature animals of the age/body length class t, j is the age/body length class of the youngest/smallest mature animal, k is the age/body length class of the oldest/longest animal, and N_t is the number of individuals in the age/body length class t. Age/body length class widths varied so that each indeterminate age/body length class (comprised of immature and mature females) contained at least two animals. For ASM estimates, interval widths were as follows: species (3), years 2002–2011 (3), coastal (3), and estuarine (4). For LSM estimates, interval widths were as follows: species (5), years 1992–2001 (10), years

2002–2011 (5), years 2012–2022 (7), coastal (10), and estuarine (10). Larger age/body length class widths were a result of smaller sample sizes of indeterminate ages/body lengths.

Binary logistic regression was used to model the distribution of mature and immature individuals with the logistic regression equation:

$$Y = \frac{1}{1 + e^{(-xb+a)}},$$

in which Y is the proportion of mature individuals, x is the age/body length of the individual, b is the slope of the regression, and a is the regression intercept. The logistic regression equation was simplified to $\mathrm{ASM/LSM} = -a/b$ to estimate the age/body length at which 50% of individuals were mature.

Ovarian analysis indicated whether an animal was immature or mature at its age/body length of stranding; however, each animal's age/body length at sexual maturation is unknown. Both the DeMaster and logistic regression methods produced one ASM/LSM estimate for each group of animals rather than estimating the age/body length at sexual maturation for each animal and then producing an averaged ASM/LSM estimate. Therefore, statistical differences between multiple groups could not be tested, and confidence intervals were used to compare groups.

2.4 | Calving Interval

The calving interval was estimated using two methods.

1. A simple linear regression was used to model the relationship between the total number of corpora and the estimated age of mature females. The model's slope was reciprocated to estimate the calving interval (Kemper et al. 2019).
2. The summation method (gestation + lactation + resting phases) was calculated using the Perrin et al. (1977) equation:

$$\text{Calving Interval} = \text{Length of Gestation} + \left(\frac{L}{P}\right)G + \left(\frac{R}{P}\right)G,$$

in which the duration of gestation is in months, L is the proportion of sexually mature lactating females, P is the proportion of pregnant females, G is the duration of gestation in years, and R is the proportion of sexually mature females not lactating or pregnant.

The duration of gestation was calculated using the Huggett and Widdas (1951) equation:

$$\text{Total Gestation Period}\left(t_g\right) = t_0 + \left(t_g - t_0\right),$$

in which t_0 is the duration of the nonlinear growth phase, and t_g-t_0 is the duration of the linear growth phase.

2.5 | Ovarian Symmetry

To test for ovulatory symmetry, counts of the left and right corpora in mature females were compared using a paired *t*-test. Ovarian weights were analyzed separately for fresh (i.e., during necropsy and prior to formalin fixation) and formalin-fixed ovaries. Not all ovaries weighed when fresh were also weighed when fixed, and vice versa. To test for weight differences related to maturation, combined ovarian weights (i.e., the total weight of a left and right ovary pair) of immature and mature females were compared using a Welch's *t*-test. To test for the symmetry of ovarian growth and development in relation to maturation, the paired left and right ovarian weights of immature and mature females were tested using a paired *t*-test or a nonparametric sign test if the assumptions of the paired *t*-test were not met.

Statistical analyses were performed using *SPSS* (Version 27; IBM Corp 2020), and regressions and growth models were performed using *R* (Version 4.1.1; R Core Team 2021). *P*-values were interpreted in the evidence-based language of Muff et al. (2022). *P*-value ranges and their associated evidence-based language regarding a finding are as follows: 1–0.1 (no evidence), 0.1–0.05 (weak evidence), 0.05–0.01 (moderate evidence), 0.01–0.001 (strong evidence), and 0.001–0.0001 (very strong evidence).

3 | Results

3.1 | Age at Sexual Maturity (ASM) and Length at Sexual Maturity (LSM)

All dolphins included in this study were identified through genetic analysis as Tamanend's bottlenose dolphins (Costa et al. 2022). In total, 518 female dolphins stranded in South Carolina waters from 1992 to 2022. Of these, 238 females and 453 ovaries were analyzed for maturity. For 227 females, both ovaries were examined and were included in statistical analysis; 11 females were not included because only one ovary was available and noted as immature; thus, maturity could not be determined.

Of the 227 female dolphins for which maturity could be estimated, 102 were immature, and 125 were mature (Table 1). The body lengths of sexually immature and mature females ranged from 85–233 cm and 205–260 cm, respectively. Tooth GLG age estimates were determined for 160 animals (74 immature and 86 mature). The ages of sexually immature and mature females ranged from 0–15 years and 4.5–42 years, respectively (for the animal aged 4.5 years, the growth layer after the fourth year was approximately half the width of the fourth-year layer, thus indicating an extra 0.5 years). The smallest, and also the youngest, sexually mature female had a body length of 205 cm and an estimated age of 4.5 years. The largest sexually immature female had a body length of 233 cm, and the oldest sexually immature female had an estimated age of 15 years.

A Gompertz growth curve modeled the estimated growth of female dolphins (Figure 2). Parameter estimates (± SE) were as follows: $L_\infty = 238.04\ (\pm 1.49)$, $b = 0.81\ (\pm 0.02)$, and $k = 0.41\ (\pm 0.03)$.

Due to small sample sizes of animals with ages within the range of sexual maturation, ASM could not be estimated using the DeMaster equation for the years 1992–2001 and 2012–2022. ASM could also not be estimated using logistic regression for the years 2012–2022. For groups in which both ASM and LSM were estimated, the DeMaster equation and logistic regression methods produced similar estimates based on confidence intervals. Between the two methods, mean ASM estimates for each group of animals (i.e., species, time frame of stranding, and stranding location) differed between 0.1 and 0.7 years, and mean LSM estimates differed between 0.3 and 1.8 cm. For all dolphins stranded in South Carolina, using the DeMaster equation, the mean (± SD) ASM estimate was 9.9 (±0.5) years (95% CI: 8.9–10.9 years), and the LSM estimate was 215.2 (±2.2) cm (95% CI: 210.8–219.6 cm). Using logistic regression, the ASM estimate was 9.8 years (95% CI: 8.0–11.5 years), and the LSM estimate was 215.7 cm (95% CI: 211.5–219.8 cm; Table 2).

Temporally, average ASM estimates were higher in 2002–2011 (11–12 years) compared to 1992–2001 (7 years). Average LSM estimates were higher from 2002–2011 (223 cm) than from 1992–2001 (211–212 cm) and 2012–2022 (211–212 cm); however, overlapping confidence intervals resulted in ambiguity (Table 2). Based on stranding location, coastal and estuarine dolphins had similar average ASM (11 and 9–10 years, respectively) and LSM (215 and 216–217 cm, respectively) estimates (Table 2).

TABLE 1 | Sample sizes of various analyzed characteristics of female Tamanend's bottlenose dolphins (*Tursiops erebennus*).

Characteristics analyzed	*n*		
	Immature	Mature	Total
Maturity	102	125	227
Age	74	86	160
Ovary pairs	102	113	215
Corpora	N/A	98	98
Fresh weights	14	18	32
Formalin-fixed weights	27	54	81
Pairs of differentiated left and right ovaries	25	43	68
Pairs of undifferentiated left and right ovaries	2	11	13

3.2 | Calving Interval

Based on linear regression, there was very strong evidence of a positive linear relationship between age and total corpora count ($F_{[1,79]} = 32.53$, $R^2 = 0.2917$, $p < 0.0001$; Figure 3). Based on the regression slope of 0.449, the calving interval estimate was 2.23 years.

The second calving interval estimate used the summation method. Based on data from 319 fetuses and neonates, the sum of the duration of the nonlinear phase of growth (62.4 days) and the duration of the linear phase of growth (312.1 days) resulted in a total gestation period of 374.5 days (12.31 months, 1.03 years). Of the 105 mature females to which pregnancy and lactation status could be attributed, 9 were pregnant, 20 were lactating, and none were simultaneously pregnant and lactating. The proportions of lactating, pregnant, and resting females were 0.19 (20/105), 0.09 (9/105), and 0.72 (76/105), respectively. The durations of gestation (12.31 months), lactation (2.28 months), and resting (8.66 months) phases yielded a calving interval estimate of 23.25 months (1.94 years).

3.3 | Ovarian Symmetry

Among 125 mature females, both the left and right ovaries of 98 females were analyzed. Twenty-three females presented corpora in the left but not the right ovary, and 6 females presented corpora in the right but not the left ovary. There was very strong evidence that the mean number of corpora in the

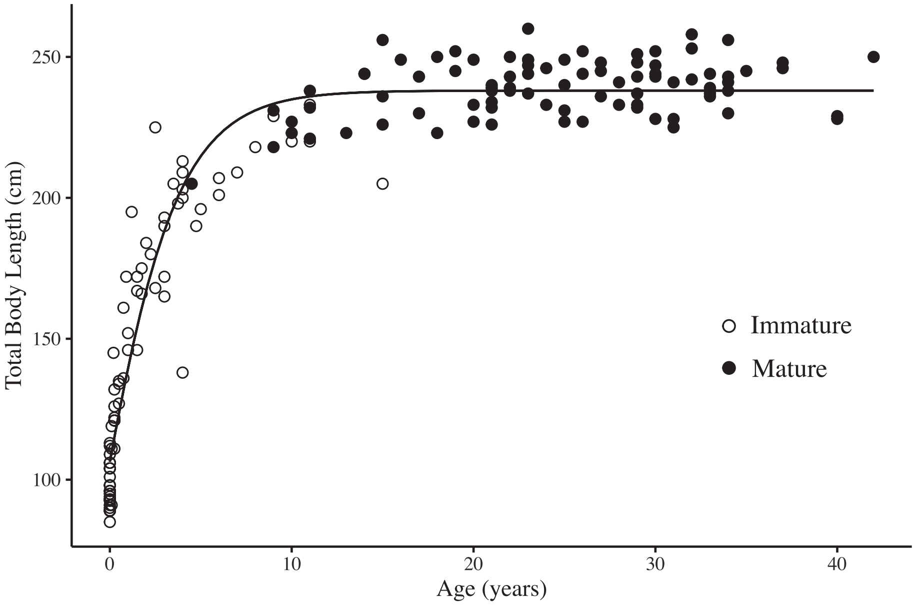

FIGURE 2 | Gompertz growth model of female Tamanend's bottlenose dolphins (*Tursiops erebennus*) in the current study.

TABLE 2 | Estimates of mean age (years) and body length (cm) at sexual maturity (ASM and LSM, respectively) for female Tamanend's bottlenose dolphins (*Tursiops erebennus*) stranded in South Carolina waters.

	ASM			LSM		
	n	**DeMaster equation**	**Logistic regression**	***n***	**DeMaster equation**	**Logistic regression**
All females	160	9.9[a] ± 0.5	9.8	227	215.2 ± 2.2	215.7
		(8.9–10.9)[b]	(8.1–11.5)		(210.8–219.6)	(211.5–219.8)
Time frame of stranding						
1992–2001	77	N/A[c]	6.9	77	211.3 ± 5.1	212.0
			(4.3–9.5)		(201.2–221.4)	(203.1–221.0)
2002–2011	68	11.7 ± 1.1	11.1	79	222.6 ± 1.6	223.0*
		(9.5–13.9)	(9.0–13.3)		(219.4–225.8)	(218.2–227.9)
2012–2022	15	N/A	N/A	71	212.5 ± 1.0	210.7
					(210.4–214.5)	(202.5–218.8)
Stranding Location						
Coastal	78	11.3 ± 0.8	10.9	110	215.2 ± 2.9	214.9
		(9.8–12.7)	(8.6–13.2)		(209.6–220.8)	(208.6–221.0)
Estuarine	82	9.8 ± 1.6	9.0	117	216.8 ± 3.5	216.4
		(6.6–12.9)	(6.7–11.3)		(210.9–223.5)	(210.8–221.9)

[a] Average ASM or LSM estimate ± SD.
[b] 95% confidence interval.
[c] Estimates could not be calculated due to the small sample size of animals with ages in the range of sexual maturation.
*Logistic regression model produced fitted probabilities indistinguishable from 0 or 1. This was likely due to a small sample size and may indicate an unreliable model fit.

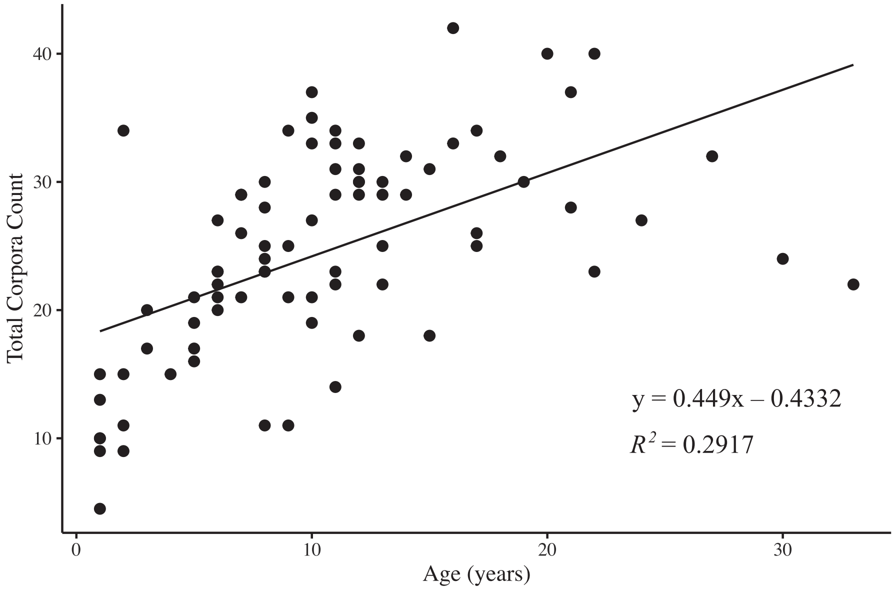

FIGURE 3 | The positive linear relationship between total corpora count and animal age (years; estimated from tooth growth layers; $R^2 = 0.2917$, $p < 0.0001$) of female Tamanend's bottlenose dolphins (*Tursiops erebennus*) in the current study.

left ($M = 6.67$, $SD = 4.88$) and right ($M = 4.44$, $SD = 4.33$) ovaries was different (Paired *t*-test, $t[97] = 3.649$, $p < 0.001$). On average, the left ovary contained 2.24 more corpora than the right ovary.

Thirty-two ovary pairs (14 immature, 18 mature) were weighed fresh, and 81 ovary pairs (27 immature, 54 mature) were weighed after fixation (Table 1; 13 pairs of fixed ovaries had nondifferentiated left and right ovaries and were, therefore, only included in the combined ovarian weight analysis and not the comparisons between left and right ovaries). For fresh weights, there was very strong evidence that the combined ovarian weight of mature females ($M = 15.51$ g, SD = 6.98 g) was greater than that of immature females ($M = 3.02$ g, SD = 1.77 g; Welch's t-test, $t[19.758] = -7.299$, $p < 0.001$). Similarly, for fixed weights, there was very strong evidence that the combined ovarian weight of mature females ($M = 12.99$ g, SD = 4.69 g) was greater than that of immature females ($M = 3.77$ g, SD = 2.45 g; Welch's t-test; $t[78.793] = 11.605$, $p < 0.001$).

For immature females, 14 ovary pairs were weighed fresh, and 25 ovary pairs were weighed after fixation (Table 1). For fresh weights, there was no evidence that the left ($M = 1.50$ g, SD = 0.86 g) and right ($M = 1.52$ g, SD = 0.93 g) ovaries weighed differently (Sign test [left ovary weight—right ovary weight: $n_{\text{positive}} = 10$, $n_{\text{ties}} = 0$, $n_{\text{negative}} = 4$, $p = 0.180$]). Similarly, for fixed weights, there was no evidence that the left ($M = 1.86$ g, SD = 1.29 g) and right ($M = 1.86$ g, SD = 1.19 g) ovaries weighed differently (Paired t-test; $t[24] = 0.018$, $p = 0.985$).

For mature females, 18 ovary pairs were weighed fresh, and 43 ovary pairs were weighed after fixation (Table 1). For fresh weights, the left ovaries ($M = 8.96$ g, SD = 6.08 g), on average, weighed more than their paired right ovaries ($M = 6.55$ g, SD = 3.78 g); however, there was weak evidence that paired left and right ovarian weights were different (Sign test [left ovary weight—right ovary weight: $n_{\text{positive}} = 13$, $n_{\text{ties}} = 0$, $n_{\text{negative}} = 5$, $p = 0.096$]). In contrast, for fixed weights, there was strong evidence that the left ovaries ($M = 7.71$ g, SD = 4.48 g) weighed more than their paired right ovaries ($M = 5.37$ g, SD = 2.67 g; Paired t-test, $t[42] = 2.889$, $p < 0.01$).

4 | Discussion

We have provided initial estimates of the age and body length at sexual maturity (ASM, LSM respectively) and calving interval, and initial descriptions of the ovarian characteristics of female Tamanend's bottlenose dolphins that stranded in South Carolina, USA, from 1992 to 2022. The ASM, LSM, and calving interval were similar to those of common bottlenose dolphins, although the ASM was on the higher end, and the LSM and calving interval were on the lower end of the typical ranges. Ovarian characteristics, including immature and mature ovarian weight, scar accumulation, and ovulatory symmetry, were also similar to those previously described in common bottlenose dolphins.

The ASM estimate for Tamanend's bottlenose dolphins was approximately 10 years of age, which is within the upper range of ages at maturation (5 to 12 years of age) typical of female common bottlenose dolphins (e.g., Robinson et al. 2017; Schwacke et al. 2022; Sergeant et al. 1973). Such overlap of ASM estimates could reflect the potential misidentification and inclusion of Tamanend's bottlenose dolphins in previous common bottlenose dolphin studies on Florida's east coast. The LSM estimate of 215 cm in this study is lower than for common bottlenose dolphins, typically recorded as between 220 and 235 cm (e.g., Harrison and Ridgway 1971; Mead and Potter 1990; Sergeant et al. 1973). Tamanend's bottlenose dolphins were likely also included in the studies of Mead and Potter (1990) and Sergeant et al. (1973), who examined dolphins from the eastern coast of the United States and northeast Florida, respectively. However, the relative contributions of coastal and estuarine Tamanend's bottlenose dolphins and offshore common bottlenose dolphins to these studies are unknown. Tamanend's bottlenose dolphins are described as being notably smaller than common bottlenose dolphins, including those offshore in the western North Atlantic, possibly related to ecological differences (Costa et al. 2022). Based on the growth curve for animals in the current study, females reach an estimated mean asymptotic body length of 238 cm, which is comparable to the estimates of 241.6 cm (McFee et al. 2010) and 240.4 cm (McFee et al. 2012) in other studies of female bottlenose dolphins in South Carolina (likely including Tamanend's bottlenose dolphins). The LSM estimates for Tamanend's bottlenose dolphins in this study are generally smaller than those for bottlenose dolphin populations in other regions (Kasuya et al. 1986; McFee et al. 2010; Mead and Potter 1990; Sergeant et al. 1973; Stolen et al. 2002). Further research will help elucidate whether smaller asymptotic body lengths and potentially slower growth rates of Tamanend's bottlenose dolphins contribute to sexual maturation at similar ages and smaller body lengths compared to common bottlenose dolphins.

LSM estimates varied temporally such that maturation occurred at smaller body lengths during the years 1992–2001 and 2012–2022 compared to 2002–2011. ASM estimates also indicated temporal variation, with earlier maturation during the years 1992–2001 compared to 2002–2011. ASM and LSM sample sizes were similar across each decadal period and did not indicate a skew toward certain years, so these observed variations are not likely due to uneven sample sizes. While yearly sample sizes were small (~7–8 animals each year), observable changes in ASM and LSM are expected to occur over a period of years, so larger sample sizes (68–79) resulting from grouping years into decadal periods likely minimize the potential effects of small sample sizes during each individual year. High neonate mortality, likely a consequence of brucellosis, was observed in 2009 (W. McFee, unpublished data) and 2012 (McFee et al. 2020). Brucellosis is an infectious disease caused by the bacterial pathogen *Brucella ceti* and is associated with spontaneous abortions and neonatal mortality (Colegrove et al. 2016; Ewalt et al. 1994; Mackie et al. 2020; Miller et al. 1999). From 2012 to 2022, maturation at smaller body lengths may represent a means of increasing reproductive output to counteract reproductive failure. Additionally, two unusual mortality events (UMEs) along the western North Atlantic coast during the years 1987–1988 and 2013–2015 were linked to morbillivirus (Lipscomb et al. 1994; NOAA Fisheries 2021). Offshore common bottlenose dolphins, the main reservoir of morbillivirus, infect spatially overlapping coastal and estuarine bottlenose dolphins, with higher exposure in coastal bottlenose dolphins (Balmer et al. 2018; Cloyed et al. 2021; Rowles et al. 2011). Exposure of Tamanend's bottlenose dolphins to morbillivirus could have resulted in poor animal health and altered maturation. A UME in South Carolina was also declared in 2011, and although no cause was officially determined, unusually cold temperatures and reduced prey availability were likely factors (Krzewinski et al. 2024) that may have affected the health, energetics, and growth of immature females. Although the compromised health of prepubescent females may have initially favored slower growth rates and maturation at longer body lengths (Craig and Ragen 1999), our findings suggest that during periods of lower population density following each UME, females may have matured at shorter body lengths and potentially earlier ages. This indicates that following periods of increased mortality, population reproductive output may have increased. Additional research about temporal variation in ASM will provide insight into if and how the onset of maturation may have been affected by UMEs.

Dolphins stranded in coastal and estuarine waters had similar ASM and LSM estimates. The stranding location of a dolphin does not necessarily represent the habitat the dolphin occupied but is used as a proxy to attempt to distinguish between coastal and estuarine dolphins. Previous research identified spatial overlap and interaction between coastal and estuarine dolphins in Charleston, South Carolina (Laska et al. 2011), so both groups may encounter similar temperature regimes, prey availability, energy requirements and expenditures, and/or other environmental factors affecting growth rates that favor similar ASMs and LSMs. Previous diet analyses of coastal and estuarine bottlenose dolphins stranded in South Carolina noted that coastal dolphins consumed a greater variety of prey and had higher stomach content weights than estuarine dolphins (Pate and McFee 2012). Despite this, it seems unlikely that energy requirements or caloric consumption vary enough regionally to differentially affect the onset of female maturation between these two groups.

The calving interval of Tamanend's bottlenose dolphins was estimated to be 2.23 years using the reciprocal of the slope of corpora counts and mature female age and 1.94 years (this is likely an underestimate due to a small sample of pregnant females) using the summation method. The reciprocal of the annual pregnancy rate (Perrin and Reilly 1984) was also investigated. However, this method produced inconclusive results due to a low proportion of pregnant females, likely reflecting that the health of stranded animals may not have been able to support pregnancy and that pregnancy data acquired from stranded animals may not reflect the general population. However, the two available estimates suggest that mature female Tamanend's bottlenose dolphins reproduce every 2 to 4 years and are consistent with common bottlenose dolphin calving intervals that typically range from 2 to 6 years, as observed in populations in waters near the west coast of Florida (Wells and Scott 1990), Argentina (Vermeulen and Bräger 2015), Brazil (Fruet et al. 2015), Ireland (Baker et al. 2018), New Zealand (Haase and Schneider 2001), and Italy (Blasi et al. 2020). Unpublished photo-identification research studying wild coastal and estuarine bottlenose dolphins (likely Tamanend's bottlenose dolphins) in North Carolina estimated a mean calving interval of 2.9 years (Thayer 2008), similar to our estimates. Because the calving interval in the current study was not estimated based on observed births and calf survival during longitudinal studies of wild dolphins, it remains unknown how various factors, including reproductive failure (such as from brucellosis) or prey availability, impact calving intervals of Tamanend's bottlenose dolphins in South Carolina waters. Estimating the calving interval using corpora accumulation was limited by multiple assumptions, including that the presence of an ovarian scar is indicative of previous ovulation and that CAs persist throughout a female's life without absorption. If scars regress with time, the calving interval may have been overestimated, and if nonovulatory scars were interpreted as CAs, the calving interval may have been underestimated. Potential biases could also arise from multiple ovulations during a single year (Kirby and Ridgway 1984), inhibited ovulation during the first few years after parturition while lactating (West et al. 2007), and reduced ovulatory activity during reproductive senescence (Ellis et al. 2018). These, therefore, serve as initial calving interval estimates for this species and geographic area. Given that stranded animals may not be of good health or representative of the population, continued monitoring is recommended by incorporating data from both strandings and photo-identification surveys.

Both the left and right ovaries were observed to be capable of accumulating ovarian scars. Ovarian scars have previously been described as remnants of ovulation that persist throughout a cetacean's life (Best 1982; Harrison and Ridgway 1971; Kemper et al. 2019; Lockyer 1987; Tarpley et al. 2016). However, scar accumulation is not comparable across all species (Inbaraj et al. 2021). For example, ovarian scars of Franciscana dolphins (*Pontoporia blainvillei*) were predicted to completely regress four years after ovulation (Harrison et al. 1981). Similarly, there was no evident relationship between age and scars of short-beaked common dolphins (*Delphinus delphis*; Dabin et al. 2008); however, recent research suggests that scars may persist throughout life in this species (Palmer et al. 2022). The observed increase of corpora with age in the current study provides initial evidence of corpora accumulation in Tamanend's bottlenose dolphins and supports previous findings of corpora accumulation in bottlenose dolphins (Cockcroft and Ross 1990; Harrison and Ridgway 1971; Kemper et al. 2019) despite variability in Cetacea.

Ovarian weights varied between maturity stages. Ovaries of mature females weighed more than those of immature females, which reflects weight changes due to corpora formation after maturation. However, sexual maturity occurs prior to physical maturity, and standard body length and ovarian weight are positively correlated in common bottlenose dolphins in the northwestern Gulf of Mexico (Turner et al. 2006). Assuming a similar relationship in Tamanend's bottlenose dolphins (bottlenose dolphins in the Gulf of Mexico are not within the geographic distribution of Tamanend's bottlenose dolphins; Costa et al. 2022), ovarian growth in females not yet at their asymptotic body length may contribute to the greater ovarian weight of mature females.

Left and right ovarian weights differed based on maturity stage. Before maturity, paired left and right ovary weights did not differ, suggesting that growth and development occur symmetrically in both ovaries. After maturation, the left ovary appeared more reproductively active based on scar accumulation and weight. The left ovary contained more scars than the right ovary, with more females having evidence of ovulation in the left ovary only compared to the right ovary, suggesting that in most females either the left ovary matured prior to the right ovary or both ovaries matured at the same time, but ovulatory activity favored the left ovary. Following maturation, there was weak evidence that fresh weights of paired left and right ovaries differed, although the left ovaries weighed more on average. However, after fixation, there was strong evidence that the left ovaries weighed more than their paired right ovaries. Formalin fixation may impact ovary weight. However, in Pacific walruses (*Odobenus rosmarus divergens*), ovary volume, but not weight, differed between fresh/frozen ovaries and formalin-fixed/ethanol-preserved ovaries (Larsen Tempel and Atkinson 2020). Ovary weights in rabbits initially increased after fixation but decreased over time to a similar weight as when fresh (Fraser 1985). In addition, ovary weights in Sprague–Dawley rats changed in the same direction and magnitude as other organs during fixation (Kanerva et al. 1983), suggesting that fixed weights could be an alternative to fresh weights. Assuming that weight changes were consistent in direction and magnitude, comparisons of fixed-ovary weights should theoretically produce valid results even if ovaries in the current study weighed more or less than when fresh. Therefore, based on the observed scar accumulation and ovarian weight asymmetry, our findings corroborate previous observations of asymmetric ovulation favoring the left ovary in bottlenose dolphins (Harrison and Ridgway 1971; Kemper et al. 2019; Orbach et al. 2016).

This research provided initial estimates of the onset of sexual maturation and calving interval of female Tamanend's bottlenose dolphins that stranded in South Carolina. The results suggest that females of this species reach sexual maturity at similar ages and somewhat smaller body lengths than common bottlenose dolphins. Temporal variations in the onset of sexual maturity highlight a possible connection between sexual maturation and animal health. Coastal bottlenose dolphins tend to have less genetic diversity and are more susceptible to anthropogenic threats than offshore bottlenose dolphins (Lowther-Thieleking et al. 2015; Natoli et al. 2004). Further monitoring is, therefore, essential to detect temporal variations of ASM, LSM, and calving interval and understand the effects of various stressors on the reproductive development and success of this newly recognized coastal and estuarine species.

Author Contributions

Jori E. Graeff: conceptualization, formal analysis, investigation, writing – original draft, writing – review and editing. **Megan M. Krzewinski:** conceptualization, resources, writing – review and editing. **Wayne E. McFee:** conceptualization, funding acquisition, resources, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

References

Akin, P. A., K. M. Peltier, and R. B. Miller. 1993. "*Techniques for the Preparation and Examination of Reproductive Samples Collected From Dolphins in the Eastern Tropical Pacific*," (NOAA Technical Report NMFS- SWFSC-192), U.S. Department of Commerce.

Baker, I., J. O'Brien, K. McHugh, and S. Berrow. 2018. "Female Reproductive Parameters and Population Demographics of Bottlenose Dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland." *Marine Biology* 165, no. 15: 1–19. https://doi.org/10.1007/s00227-017-3265-z.

Balmer, B., E. Zolman, T. Rowles, et al. 2018. "Ranging Patterns, Spatial Overlap, and Association With Dolphin Morbillivirus Exposure in Common Bottlenose Dolphins (*Tursiops truncatus*) Along the Georgia, USA Coast." *Ecology and Evolution* 8, no. 24: 12890–12904. https://doi.org/10.1002/ece3.4727.

Best, P. B. 1982. "Seasonal Abundance, Feeding, Reproduction, Age and Growth in Minke Whales Off Durban (With Incidental Observations From the Antarctic)." *Reports of the International Whaling Commission* 32: 759–786.

Blasi, M. F., C. Bruno, and L. Boitani. 2020. "Female Reproductive Output in a Mediterranean Bottlenose Dolphin *Tursiops truncatus* Population." *Aquatic Biology* 29: 123–136. https://doi.org/10.3354/ab00732.

Boness, D., P. J. Clapham, and S. L. Mesnick. 2002. "Life History and Reproductive Strategies." In *Marine Mammal Biology: An Evolutionary Approach*, edited by A. R. Hoelzel, 278–324. Blackwell Science Ltd.

Boness, D. J. 2009. "Estrus and Estrous Behavior." In *Encyclopedia of Marine Mammals*, edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen, 2nd ed., 392–396. Academic Press.

Charnov, E. L. 1990. "On Evolution of Age of Maturity and the Adult Lifespan." *Journal of Evolutionary Biology* 3, no. 1–2: 139–144. https://doi.org/10.1046/j.1420-9101.1990.3010139.x.

Christiansen, F., S. M. Dawson, J. W. Durban, et al. 2020. "Population Comparison of Right Whale Body Condition Reveals Poor State of the North Atlantic Right Whale." *Marine Ecology Progress Series* 640: 1–16. https://doi.org/10.3354/meps13299.

Cloyed, C. S., B. C. Balmer, L. H. Schwacke, et al. 2021. "Linking Morbillivirus Exposure to Individual Habitat Use of Common Bottlenose Dolphins (*Tursiops truncatus*) Between Geographically Different Sites." *Journal of Animal Ecology* 90, no. 5: 1191–1204. https://doi.org/10.1111/1365-2656.13446.

Cockcroft, V. G., and G. J. B. Ross. 1990. "Age, Growth and Reproduction in Bottlenose Dolphins From the East Coast of Southern Africa." *Fishery Bulletin* 88, no. 2: 289–302.

Colegrove, K. M., S. Venn-Watson, J. Litz, et al. 2016. "Fetal Distress and In Utero Pneumonia in Perinatal Dolphins During the Northern Gulf of Mexico Unusual Mortality Event." *Diseases of Aquatic Organisms* 119, no. 1: 1–16. https://doi.org/10.3354/dao02969.

Costa, A. P., W. McFee, L. A. Wilcox, F. I. Archer, and P. E. Rosel. 2022. "The Common Bottlenose Dolphin (*Tursiops truncatus*) Ecotypes of the Western North Atlantic Revisited: An Integrative Taxonomic Investigation Supports the Presence of Distinct Species." *Zoological Journal of the Linnean Society* 196, no. 4: 1608–1636. https://doi.org/10.1093/zoolinnean/zlac025.

Craig, M. P., and T. J. Ragen. 1999. "Body Size, Survival, and Decline of Juvenile Hawaiian Monk Seals, *Monachus schauinslandi*." *Marine Mammal Science* 15, no. 3: 786–809. https://doi.org/10.1111/j.1748-7692.1999.tb00843.x.

Dabin, W., F. Cossais, G. J. Pierce, and V. Ridoux. 2008. "Do Ovarian Scars Persist With Age in All Cetaceans: New Insight From the Short-Beaked

Common Dolphin (*Delphinus delphis* Linnaeus, 1758).” *Marine Biology* 156, no. 2: 127–139. https://doi.org/10.1007/s00227-008-1070-4.

Danilewicz, D. 2003. “Reproduction of Female Franciscana (*Pontoporia blainvillei*) in Rio Grande Do Sul, Southern Brazil.” *Latin American Journal of Aquatic Mammals* 2, no. 2: 67–78. https://doi.org/10.5597/lajam00034.

DeMaster, D. P. 1978. “Calculation of the Average Age of Sexual Maturity in Marine Mammals.” *Journal of the Fisheries Board of Canada* 35, no. 6: 912–915. https://doi.org/10.1139/f78-148.

Eberhardt, L. L. 1977. “Optimal Policies for Conservation of Large Mammals, With Special Reference to Marine Ecosystems.” *Environmental Conservation* 4, no. 3: 205–212. https://doi.org/10.1017/S0376892900025819.

Ellis, S., D. W. Franks, S. Nattrass, et al. 2018. “Analyses of Ovarian Activity Reveal Repeated Evolution of Post-Reproductive Lifespans in Toothed Whales.” *Scientific Reports* 8, no. 1: 12833. https://doi.org/10.1038/s41598-018-31047-8.

Ewalt, D. R., J. B. Payeur, B. M. Martin, D. R. Cummins, and W. G. Miller. 1994. “Characteristics of a Brucella Species From a Bottlenose Dolphin (*Tursiops truncatus*).” *Journal of Veterinary Diagnostic Investigation* 6, no. 4: 448–452. https://doi.org/10.1177/104063879400600408.

Ferrero, R. C., and W. A. Walker. 1993. “Growth and Reproduction of the Northern Right Whale Dolphin, *Lissodelphis borealis*, in the Offshore Waters of the North Pacific Ocean.” *Canadian Journal of Zoology* 71, no. 12: 2335–2344. https://doi.org/10.1139/z93-328.

Fitzhugh, H. A., Jr. 1976. “Analysis of Growth Curves and Strategies for Altering Their Shape.” *Journal of Animal Science* 42, no. 4: 1036–1051. https://doi.org/10.2527/jas1976.4241036x.

Fowler, C. W. 1981. “Density Dependence as Related to Life History Strategy.” *Ecology* 62, no. 3: 602–610. https://doi.org/10.2307/1937727.

Fraser, K. W. 1985. “Effect of Storage in Formalin on Organ Weights of Rabbits.” *New Zealand Journal of Zoology* 12, no. 2: 169–174. https://doi.org/10.1080/03014223.1985.10428276.

Fruet, P. F., R. C. Genoves, L. M. Möller, S. Botta, and E. R. Secchi. 2015. “Using Mark-Recapture and Stranding Data to Estimate Reproductive Traits in Female Bottlenose Dolphins (*Tursiops truncatus*) of the Southwestern Atlantic Ocean.” *Marine Biology* 162, no. 3: 661–673. https://doi.org/10.1007/s00227-015-2613-0.

Galezo, A. A., V. Foroughirad, E. Krzyszczyk, C. H. Frère, and J. Mann. 2020. “Juvenile Social Dynamics Reflect Adult Reproductive Strategies in Bottlenose Dolphins.” *Behavioral Ecology* 31, no. 5: 1159–1171. https://doi.org/10.1093/beheco/araa068.

Gallagher, C. A., S. J. Stern, and E. Hines. 2018. “The Metabolic Cost of Swimming and Reproduction in Harbor Porpoises (*Phocoena phocoena*) as Predicted by a Bioenergetic Model.” *Marine Mammal Science* 34, no. 4: 875–900. https://doi.org/10.1111/mms.12487.

Gompertz, B. 1825. “On the Nature of the Function Expressive of the Law of Human Mortality, and on a New Mode of Determining the Value of Life Contingencies.” *Philosophical Transactions of the Royal Society of London* 115: 513–583.

Haase, P. A., and K. Schneider. 2001. “Birth Demographics of Bottlenose Dolphins, *Tursiops truncatus*, in Doubtful Sound, Fiordland, New Zealand—Preliminary Findings.” *New Zealand Journal of Marine and Freshwater Research* 35, no. 4: 675–680. https://doi.org/10.1080/00288330.2001.9517034.

Harrison, R. J., M. M. Bryden, D. A. McBrearty, and R. L. Brownell Jr. 1981. “The Ovaries and Reproduction in *Pontoporia blainvillei* (Cetacea: Platanistidae).” *Journal of Zoology* 193, no. 4: 563–580. https://doi.org/10.1111/j.1469-7998.1981.tb01504.x.

Harrison, R. J., and S. H. Ridgway. 1971. “Gonadal Activity in Some Bottlenose Dolphins (*Tursiops truncatus*).” *Journal of Zoology* 165, no. 3: 355–366. https://doi.org/10.1111/j.1469-7998.1971.tb02193.x.

Henderson, S. D., S. M. Dawson, R. J. Currey, D. Lusseau, and K. Schneider. 2014. “Reproduction, Birth Seasonality, and Calf Survival of Bottlenose Dolphins in Doubtful Sound, New Zealand.” *Marine Mammal Science* 30, no. 3: 1067–1080. https://doi.org/10.1111/mms.12109.

Huggett, A. S. G., and W. F. Widdas. 1951. “The Relationship Between Mammalian Foetal Weight and Conception Age.” *Journal of Physiology* 114, no. 3: 306–317.

IBM Corp. 2020. *IBM SPSS Statistics for Macintosh, Version 27.0*. IBM Corp.

Inbaraj, K. C., Z. Yu, S. Chai, et al. 2021. “Regression of corpus Luteum in Cetaceans: A Systematic Review.” *Zoology* 149: 125960. https://doi.org/10.1016/j.zool.2021.125960.

Kanerva, R. L., F. R. Lefever, and C. L. Alden. 1983. “Comparison of Fresh and Fixed Organ Weights of Rats.” *Toxicologic Pathology* 11, no. 2: 129–131. https://doi.org/10.1177/019262338301100204.

Karniski, C., E. Krzyszczyk, and J. Mann. 2018. “Senescence Impacts Reproduction and Maternal Investment in Bottlenose Dolphins.” *Proceedings of the Royal Society B: Biological Sciences* 285, no. 1883: 20181123. https://doi.org/10.1098/rspb.2018.1123.

Kasuya, T. 1991. “Density Dependent Growth in North Pacific Sperm Whales.” *Marine Mammal Science* 7, no. 3: 230–257. https://doi.org/10.1111/j.1748-7692.1991.tb00100.x.

Kasuya, T., T. Tobayama, T. Saiga, and T. Kataoka. 1986. “Perinatal Growth of Delphinoids: Information From Aquarium Reared Bottlenose Dolphins and Finless Porpoises.” *Scientific Reports of the Whales Research Institute* 37: 85–97.

Kato, H. 1987. “Density Dependent Changes in Growth Parameters of the Southern Minke Whale.” *Scientific Reports of the Whales Research Institute* 38: 47–73.

Kemper, C., M. Talamonti, M. Bossley, and A. Steiner. 2019. “Sexual Maturity and Estimated Fecundity in Female Indo-Pacific Bottlenose Dolphins (*Tursiops aduncus*) From South Australia: Combining Field Observations and Postmortem Results.” *Marine Mammal Science* 35, no. 1: 40–57. https://doi.org/10.1111/mms.12509.

Kirby, V. L., and S. H. Ridgway. 1984. “Hormonal Evidence of Spontaneous Ovulation in Captive Dolphins, *Tursiops truncatus* and *Delphinus delphis*.” In *Reproduction in Whales, Dolphins, and Porpoises*, edited by W. F. Perrin, R. L. Brownell Jr., and D. P. DeMaster, 459–464. International Whaling Commission.

Kjellqwist, S. A., T. Haug, and T. Øritsland. 1995. “Trends in Age-Composition, Growth and Reproductive Parameters of Barents Sea Harp Seals, *Phoca groenlandica*.” *ICES Journal of Marine Science* 52, no. 2: 197–208. https://doi.org/10.1016/1054-3139(95)80035-2.

Krzewinski, M., W. McFee, and R. Young. 2024. “Spatial and Temporal Trends of Tamanend's Bottlenose Dolphin (Tursiops Erebennus) Strandings in South Carolina, USA, 2006–2020.” *Journal of Cetacean Research and Management* 25: 31–48. https://doi.org/10.47536/jcrm.v25i1.941.

Larsen Tempel, J. T., and S. Atkinson. 2020. “Pacific Walrus (*Odobenus rosmarus divergens*) Reproductive Capacity Changes in Three Time Frames During 1975–2010.” *Polar Biology* 43: 861–875. https://doi.org/10.1007/s00300-020-02693-4.

Laska, D., T. Speakman, and P. A. Fair. 2011. “Community Overlap of Bottlenose Dolphins (*Tursiops truncatus*) Found in Coastal Waters Near Charleston, South Carolina.” *Journal of Marine Animals and Their Ecology* 4: 10–18.

Laws, R. M. 1956. “Growth and Sexual Maturity in Aquatic Mammals.” *Nature* 178: 193–194. https://doi.org/10.1038/178193a0.

Lipscomb, T. P., F. Y. Schulman, D. Moffett, and S. Kennedy. 1994. “Morbilliviral Disease in Atlantic Bottlenose Dolphins (*Tursiops truncatus*) From the 1987–1988 Epizootic.” *Journal of Wildlife Diseases* 30, no. 4: 567–571. https://doi.org/10.7589/0090-3558-30.4.567.

Lockyer, C. 1987. "Observations on the Ovary of the Southern Minke Whale." *Scientific Reports of the Whales Research Institute* 38: 75–89.

Lowther-Thieleking, J. L., F. I. Archer, A. R. Lang, and D. W. Weller. 2015. "Genetic Differentiation Among Coastal and Offshore Common Bottlenose Dolphins, *Tursiops truncatus*, in the Eastern North Pacific Ocean." *Marine Mammal Science* 31, no. 1: 1–20. https://doi.org/10.1111/mms.12135.

Lydersen, C., and I. Gjertz. 1987. "Population Parameters of Ringed Seals (*Phoca hispida* Schreber, 1775) in the Svalbard Area." *Canadian Journal of Zoology* 65, no. 4: 1021–1027. https://doi.org/10.1139/z87-162.

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press.

Mackie, J. T., D. Blyde, L. Harris, W. D. Roe, and A. L. Keyburn. 2020. "Brucellosis Associated With Stillbirth in a Bottlenose Dolphin in Australia." *Australian Veterinary Journal* 98, no. 3: 92–95. https://doi.org/10.1111/avj.12903.

McFee, W. E., J. D. Adams, P. A. Fair, and G. D. Bossart. 2012. "Age Distribution and Growth of Two Bottlenose Dolphin (*Tursiops truncatus*) Populations From Capture-Release Studies in the Southeastern United States." *Aquatic Mammals* 38, no. 1: 17–30. https://doi.org/10.1578/AM.38.1.2012.17.

McFee, W. E., and T. P. Lipscomb. 2009. "Major Pathologic Findings and Probable Causes of Mortality in Bottlenose Dolphins Stranded in South Carolina From 1993 to 2006." *Journal of Wildlife Diseases* 45, no. 3: 575–593. https://doi.org/10.7589/0090-3558-45.3.575.

McFee, W. E., J. H. Schwacke, M. K. Stolen, K. D. Mullin, and L. H. Schwacke. 2010. "Investigation of Growth Phases for Bottlenose Dolphins Using a Bayesian Modeling Approach." *Marine Mammal Science* 26, no. 1: 67–85. https://doi.org/10.1111/j.1748-7692.2009.00306.x.

McFee, W. E., D. Wu, K. Colegrove, K. Terio, L. Balthis, and R. Young. 2020. "Occurrence of *Brucella ceti* in Stranded Bottlenose Dolphins *Tursiops truncatus* Coincides With Calving Season." *Diseases of Aquatic Organisms* 141: 185–193. https://doi.org/10.3354/dao03526.

Mead, J. G., and C. W. Potter. 1990. "Natural History of Bottlenose Dolphins Along the Central Atlantic Coast of the United States." In *The Bottlenose Dolphin*, edited by S. Leatherwood and R. R. Reeves, 165–195. Academic Press.

Meyer-Gutbrod, E. L., C. H. Greene, P. J. Sullivan, and A. J. Pershing. 2015. "Climate-Associated Changes in Prey Availability Drive Reproductive Dynamics of the North Atlantic Right Whale Population." *Marine Ecology Progress Series* 535: 243–258. https://doi.org/10.3354/meps11372.

Miller, W. G., L. G. Adams, T. A. Ficht, et al. 1999. "*Brucella*-Induced Abortions and Infection in Bottlenose Dolphins (*Tursiops truncatus*)." *Journal of Zoo and Wildlife Medicine* 30, no. 1: 100–110.

Muff, S., E. B. Nilsen, R. B. O'Hara, and C. R. Nater. 2022. "Rewriting Results Sections in the Language of Evidence." *Trends in Ecology & Evolution* 37, no. 3: 203–210. https://doi.org/10.1016/j.tree.2021.10.009.

Murphy, S., J. L. Barber, J. A. Learmonth, et al. 2015. "Reproductive Failure in UK Harbour Porpoises *Phocoena phocoena*: Legacy of Pollutant Exposure?" *PLoS One* 10, no. 7: e0131085. https://doi.org/10.1371/journal.pone.0131085.

Natoli, A., V. M. Peddemors, and A. Rus Hoelzel. 2004. "Population Structure and Speciation in the Genus Tursiops Based on Microsatellite and Mitochondrial DNA Analyses." *Journal of Evolutionary Biology* 17, no. 2: 363–375. https://doi.org/10.1046/j.1420-9101.2003.00672.x.

NOAA (National Oceanic and Atmospheric Association) Fisheries. 2021. "2013–2015 Bottlenose Dolphin Unusual Mortality Event in the Mid-Atlantic (Closed)," https://www.fisheries.noaa.gov/national/marine-life-distress/2013-2015-bottlenose-dolphin-unusual-mortality-event-mid-atlantic.

Odell, D. K. 1975. "Status and Aspects of the Life History of the Bottlenose Dolphin, *Tursiops truncatus*, in Florida." *Journal of the Fisheries Board of Canada* 32, no. 7: 1055–1058. https://doi.org/10.1139/f75-124.

Ohsumi, S. 1986. "Yearly Change in Age and Body Length at Sexual Maturity of a Fin Whale Stock in the Eastern North Pacific." *Scientific Reports of the Whales Research Institute* 37: 1–16.

Orbach, D. N., C. D. Marshall, B. Würsig, and S. L. Mesnick. 2016. "Variation in Female Reproductive Tract Morphology of the Common Bottlenose Dolphin (*Tursiops truncatus*)." *Anatomical Record* 299, no. 4: 520–537. https://doi.org/10.1002/ar.23318.

Palmer, E. I., E. L. Betty, S. Murphy, M. R. Perrott, A. N. Smith, and K. A. Stockin. 2022. "Reproductive Biology of Female Common Dolphins (*Delphinus delphis*) in New Zealand Waters." *Marine Biology* 169, no. 12: 1–21. https://doi.org/10.1007/s00227-022-04139-3.

Pate, S. M., and W. E. McFee. 2012. "Prey Species of Bottlenose Dolphins (*Tursiops truncatus*) From South Carolina Waters." *Southeastern Naturalist* 11, no. 1: 1–22. https://doi.org/10.1656/058.011.0101.

Perrin, W. F., and G. P. Donovan. 1984. "Report of the Workshop." In *Reproduction in Whales, Dolphins, and Porpoises*, edited by W. F. Perrin, R. L. Brownell Jr., and D. P. DeMaster, 1–24. International Whaling Commission.

Perrin, W. F., D. B. Holts, and R. B. Miller. 1977. "Growth and Reproduction of the Eastern Spinner Dolphin, a Geographical Form of *Stenella longirostris* in the Eastern Tropical Pacific." *Fishery Bulletin* 75, no. 4: 725–750.

Perrin, W. F., and S. B. Reilly. 1984. "Reproductive Parameters of Dolphins and Small Whales of the Family Delphinidae." In *Reproduction in Whales, Dolphins, and Porpoises*, edited by W. F. Perrin, R. L. Brownell Jr., and D. P. DeMaster, 97–133.International Whaling Commission.

Powell, J. W. B., D. A. Duffield, J. J. Kaufman, and W. E. McFee. 2019. "Bone Density Cannot Accurately Predict Age in the Common Bottlenose Dolphin, *Tursiops truncatus*." *Marine Mammal Science* 35, no. 4: 15997. https://doi.org/10.1111/mms.12591.

QGIS. 2023. "QGIS Geographic Information System," Open Source Geospatial Foundation Project, http://qgis.org.

R Core Team. 2021. "R: A Language and Environment for Statistical Computing," R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/.

Reddy, M., T. Kamolnick, C. Curry, D. Skaar, and S. Ridgway. 1994. "Energy Requirements for the Bottlenose Dolphin (*Tursiops truncatus*) in Relation to Sex, Age and Reproductive Status." *Marine Mammals: Public Display and Research* 1, no. 1: 26–31.

Reif, J. S., A. M. Schaefer, G. D. Bossart, and P. A. Fair. 2017. "Health and Environmental Risk Assessment Project for Bottlenose Dolphins *Tursiops truncatus* From the Southeastern USA. II. Environmental Aspects." *Diseases of Aquatic Organisms* 125, no. 2: 155–166. https://doi.org/10.3354/dao03143.

Robinson, K. P., T. M. Sim, R. M. Culloch, et al. 2017. "Female Reproductive Success and Calf Survival in a North Sea Coastal Bottlenose Dolphin (*Tursiops truncatus*) Population." *PLoS One* 12, no. 9: e0185000. https://doi.org/10.1371/journal.pone.0185000.

Roca-Monge, K., R. González-Barrientos, M. Suárez-Esquivel, et al. 2022. "Age and Sexual Maturity Estimation of Stranded Striped Dolphins, *Stenella coeruleoalba*, Infected With *Brucella ceti*." *Oceans* 3, no. 4: 494–508. https://doi.org/10.3390/oceans3040033.

Rowles, T. K., L. S. Schwacke, R. S. Wells, et al. 2011. "Evidence of Susceptibility to Morbillivirus Infection in Cetaceans From the United States." *Marine Mammal Science* 27, no. 1: 1–19. https://doi.org/10.1111/j.1748-7692.2010.00393.x.

Schwacke, L. H., T. A. Marques, L. Thomas, et al. 2022. "Modeling Population Effects of the Deepwater Horizon Oil Spill on a Long-Lived

Species." *Conservation Biology* 36, no. 4: e13878. https://doi.org/10.1111/cobi.13878.

Schwacke, L. H., L. Thomas, R. S. Wells, et al. 2017. "Quantifying Injury to Common Bottlenose Dolphins From the Deepwater Horizon Oil Spill Using an Age-, Sex- and Class-Structured Population Model." *Endangered Species Research* 33: 265–279. https://doi.org/10.3354/esr00777.

Sergeant, D. E., D. K. Caldwell, and M. C. Caldwell. 1973. "Age, Growth, and Maturity of Bottlenosed Dolphin (*Tursiops truncatus*) From Northeast Florida." *Journal of the Fisheries Board of Canada* 30, no. 7: 1009–1011. https://doi.org/10.1139/f73-165.

Slijper, E. J. 1962. *Whales* (A. J. Pomerans, Trans.). Hutchinson & Company.

Stolen, M. K., D. K. Odell, and N. B. Barros. 2002. "Growth of Bottlenose Dolphins (*Tursiops truncatus*) From the Indian River Lagoon System, Florida, USA." *Marine Mammal Science* 18, no. 2: 348–357. https://doi.org/10.1111/j.1748-7692.2002.tb01042.x.

Tarpley, R. J., D. J. Hillmann, J. C. George, J. E. Zeh, and R. S. Suydam. 2016. "Morphometric Correlates of the Ovary and Ovulatory Corpora in the Bowhead Whale, *Balaena mysticetus*." *Anatomical Record* 299, no. 6: 769–797. https://doi.org/10.1002/ar.23337.

Thayer, V. G. 2008. *Life History Parameters and Social Associations of Female Bottlenose Dolphins (Tursiops truncatus) off North Carolina, USA [Unpublished doctoral dissertation]*. Duke University.

Turner, J. P., L. S. Clark, E. M. Haubold, G. A. Worthy, and D. F. Cowan. 2006. "Organ Weights and Growth Profiles in Bottlenose Dolphins (*Tursiops truncatus*) From the Northwestern Gulf of Mexico." *Aquatic Mammals* 32, no. 1: 46–57. https://doi.org/10.1578/AM.32.1.2006.46.

Vermeulen, E., and S. Bräger. 2015. "Demographics of the Disappearing Bottlenose Dolphin in Argentina: A Common Species on Its Way Out?" *PLoS One* 10, no. 3: e0119182. https://doi.org/10.1371/journal.pone.0119182.

Wells, R. S., and M. D. Scott. 1990. "Estimating Bottlenose Dolphin Population Parameters From Individual Identification and Capture-Release Techniques." *Reports of the International Whaling Commission* 12: 407–415.

Wells, R. S., M. D. Scott, and A. B. Irvine. 1987. "The Social Structure of Free-Ranging Bottlenose Dolphins." In *Current Mammalogy*, vol. 1, 247–305. Springer. https://doi.org/10.1007/978-1-4757-9909-5_7.

West, K. L., O. T. Oftedal, J. R. Carpenter, B. J. Krames, M. Campbell, and J. C. Sweeney. 2007. "Effect of Lactation Stage and Concurrent Pregnancy on Milk Composition in the Bottlenose Dolphin." *Journal of Zoology* 273, no. 2: 148–160. https://doi.org/10.1111/j.1469-7998.2007.00309.x.

Yoshida, K., N. Baba, M. Oya, and K. Mizue. 1977. "On the Formation and Regression of corpus Luteum in the Northern fur Seal Ovaries." *Scientific Reports of the Whales Research Institute* 29: 121–128.