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ARTICLE

Age, Growth, and Reproduction of the Striped Dolphin, *Stenella coeruleoalba*, Off the South-East Coast of South Africa

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ABSTRACT

The striped dolphin, *Stenella coeruleoalba*, is an oceanic species found worldwide in tropical to warm-temperate waters. Globally, populations are threatened through direct fishing, bycatch, and pollution. Little is known about the life history of this species in South African waters, and an understanding of basic life history parameters is critical for conservation and management. Age and growth were determined for 61 animals stranded along the southeast coast of South Africa between 1972 and 2012 by counting the number of growth layer groups (GLGs) in longitudinal tooth sections. A von Bertalanffy growth curve was fitted to the data, indicating that physical maturity was reached around 231 cm and 21 years in males and 224 cm and 18 years in females. Analyses of the gonads of 48 individuals showed that males reached sexual maturity between 8 and 12 years of age and between 209 and 224 cm total body length, while females reached sexual maturity between 7 and 8 years and between 213 and 216 cm total body length. Maximum age estimates were 21 years for males and 20.2 years for females. Overall, the life history of the species off southeastern South Africa is similar to that reported for populations elsewhere, with minor geographic variations.

1 | Introduction

The striped dolphin, *Stenella coeruleoalba*, is an oceanic species that prefers deep waters beyond the continental shelf (Archer II 2009; Perrin et al. 1994) and occurs in tropical to warm-temperate waters of the Atlantic, Pacific, and Indian Oceans and in the Mediterranean Sea (Best 2007; Dizon et al. 1994; Kroese 1993; Perrin et al. 1994; Ross 1984; Wilson et al. 1987). The species is currently listed as "Least Concern" by both the International Union for the Conservation of Nature (IUCN; Braulik 2019) and the local South African Red List Assessment (Plön and da Silva 2025). However, the latter assessment has suggested that net fisheries in the western Indian Ocean, including those utilizing drift nets south of Madagascar, could potentially emerge as a significant unrecorded risk to this species, particularly in the context of pelagic trawls or purse-seine fisheries (Plön and da Silva 2025). In addition, ship strikes have been shown to have a locally detectable impact on the species (Schoeman et al. 2020). Furthermore, there is a rising concern about detrimental organochlorine contamination in cetaceans, including the striped dolphin off the coast of southern Africa (Cockcroft 1999; Cockcroft et al. 1991; Gui et al. 2016). In response to these potential threats, the latest South African Red List Assessment has identified several research priorities for the striped dolphin off South Africa, one of which includes the assessment of population size, composition, trends, and updated basic life history parameters (Plön and da Silva 2025).

While several studies have been conducted in Japanese (Kasuya 1976; Kasuya and Miyazaki 1976; Miyazaki 1977a,

1984) and Mediterranean (Aguilar 2000; Calzada et al. 1996; Di-Meglio et al. 1996; Guarino et al. 2021) waters, few studies have investigated various aspects of the general biology of the striped dolphin in southern African waters (Best 2007; Ross 1984), with only one study, considered to be gray literature, focusing on life history aspects of striped dolphins (Kroese 1993). While Kroese (1993) examined striped dolphin specimens from both the west coast and east coast of South Africa combined, assuming a single population, a more recent study suggested the differentiation of the South African population of *S. coeruleoalba* into a west and east coast population, on either side of Cape Agulhas, based on a significant difference in dorsal and ventral cranial shape (Conry et al. 2016). In this respect, original life history parameters may also need to be revised.

Assessing the life history of a species assists in understanding its basic biology and ecology (Danil and Chivers 2006) as well as its stock structure, mating system, and possible anthropogenic impacts (Chivers and Myrick 1993; Dizon et al. 1994; Murphy et al. 2005). Population dynamics cannot be understood without knowledge of age composition, age at sexual maturity, age at first reproduction, and longevity (Myrick et al. 1983). Thus, data on the life history of a species are needed for robust conservation plans (Cockcroft and Ross 1990). Age determination and the assessment of reproductive parameters are important for the determination of life history parameters (Myrick et al. 1983; Scheffer and Myrick 1980), which, in turn, are required to assess the impact of fisheries and habitat degradation (Perrin and Henderson 1984; Read and Gaskin 1990). Information on attainment of sexual maturity (ASM; both age and length) can be used in comparative biological studies at both the interspecific and intraspecific levels and in the management of anthropogenic activities impacting populations (Hohn et al. 1985). A number of factors can influence age and length at ASM, including environmental conditions, level of exploitation, diet, and body weight (Bryden and Harrison 1986; Wootton 1987). Therefore, information on age and length at ASM can play an important role in stock assessment or in determining the degree of exploitation of a population (Perrin and Henderson 1984; Read and Gaskin 1990). Monitoring information on age and length at ASM is vital for determining if the population density of a species is changing.

Our study aimed to provide a better understanding of the life history of the striped dolphin off the southeast coast of southern Africa. A number of growth and reproductive parameters were determined, including age, length, and weight at birth and at sexual maturity and at physical maturity, and determining ovulation rate, pregnancy rate, calving interval (CI), and reproductive seasonality.

2 | Materials and Methods

2.1 | Study Area and Sample

For the present study, data and samples from 130 animals stranded along the South African coastline between Table Bay (33°52′1.95″ S; 18°26′14.24″ E) and Sodwana Bay (27°33′23.25″ S; 32°40′02.29″ E) between 1969 and 2012 were analyzed (Figure 1). All carcasses underwent routine necropsies during which basic biological and morphological data, such as body length (cm) and mass (kg), were recorded in accordance with Norris (1961). Additionally, when available, standard biological samples—teeth, gonads, and stomach contents—were collected. Samples for analysis were available for 72 specimens: teeth from 61 specimens (32 males and 29 females) were available for age determination, while reproductive organs were available for 48 specimens (21 males and 27 females). The samples available for analysis spanned the period from April 1972 to February 2012.

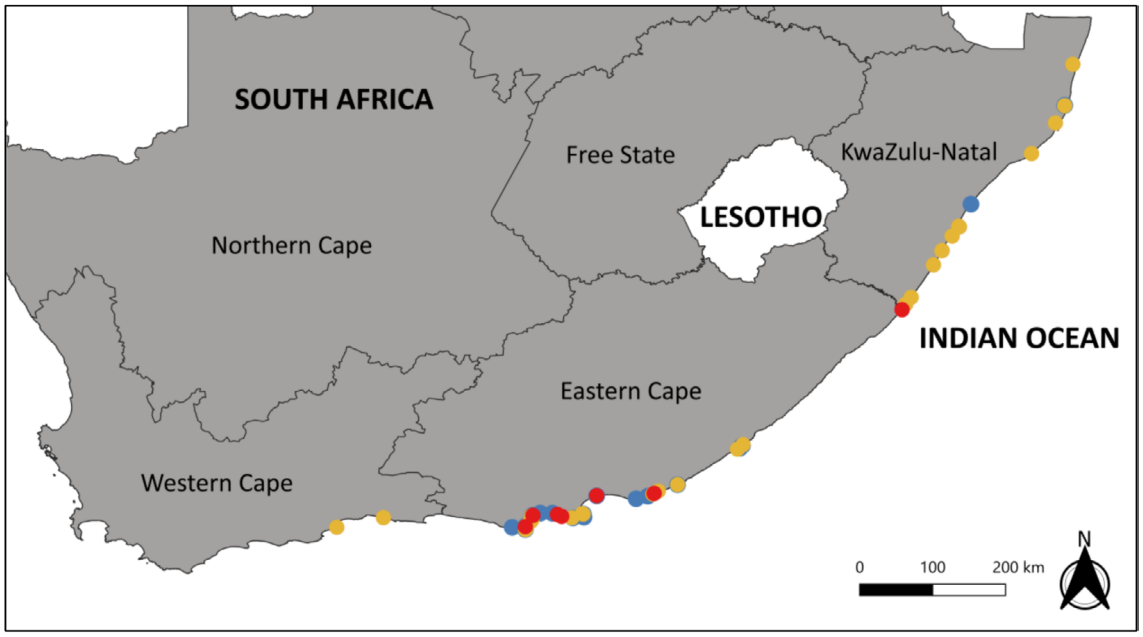

FIGURE 1 | Stranding locations of specimens stranded between 1972 and 2012 and examined in this study. Blue dots: Teeth only available for analysis ($n = 24$; 18 plotted, 6 had no location); red dots: Reproductive organs only available for analysis ($n = 11$; 8 plotted, 3 had no location); yellow dots: Both teeth and reproductive organs available for analysis ($n = 37$; 32 plotted, 5 had no location).

Given the long timespan over which the samples were obtained, examinations of possible changes in some biological parameters over time were not possible or meaningful. All subsequent statistical analyses were performed using Microsoft Excel 2019 (Microsoft Office 365).

2.2 | Age Determination

As individual teeth of striped dolphins are often curved and twisted in different planes, making a central section difficult. Hence, care was taken to choose a tooth with the least curving and with little or no abrasion and wear from each specimen for age determination. To obtain longitudinal sections of teeth for age determination, the methods of Myrick et al. (1983) were followed. Teeth were decalcified using RDO (Apex Engineering Products Corporation), sectioned into 25–40 μm thick sections on a cryomicrotome, stained with Mayer's hematoxylin, and mounted on glass slides. Only sections that were mid-longitudinal with a sharply pointed apex were selected for age determination.

Age was estimated by counting growth layer groups (GLGs) in the dentin under an Olympus SZ dissecting microscope with transmitted light at 10× and 15× magnification. One opaque and one translucent band make up a GLG, which is defined as "a repeating or semi-repeating pattern of adjacent groups of incremental growth layers within the dentin, cementum, or bone, which is defined as a countable unit" (Perrin and Myrick 1980). A number of studies concluded that the deposition of GLGs was annual in the striped dolphin, with one GLG representing 1 year of growth (Kasuya 1976; Kroese 1993; Miyazaki 1977a; Ross 1984).

Age estimates were carried out "blind" with no reference to biological data, such as body length and sex, to avoid any biases. The teeth were read by three independent observers experienced with age estimation in delphinids and *Kogia*. When the differences in readings among observers were within 15% of each other, the age was estimated as the average of all readings. However, for estimates with more than a 15% difference between observers, teeth were reread and estimates discussed until a consensus could be reached.

The completion of the last layer was estimated to the nearest 0.5 GLG; that is, if it was > 50% completed, it was considered a fully formed layer (100%) and the age estimate rounded up, but if it was < 50% formed, it was not considered a new layer (0%) and the age estimate rounded down. If the pulp cavity was fully occluded, dentinal as well as cemental growth layers were counted. Cemental layers were examined under an Olympus BX50 compound microscope at 200× magnification. To examine whether cemental growth layers could provide a good estimate of age once the pulp cavity was occluded (Kasuya 1976), a scatterplot of dentinal and cemental GLG counts was generated, and a line of linear regression was fitted to the data.

Additionally, Ross (1984) previously aged 14 striped dolphin specimens off the coast of South Africa using dentinal counts, five of which were reexamined during this study. The age estimates were similar between the two studies, with one exception, where Ross (1984) used dentinal GLGs and in the present study, cemental GLGs were used due to an occluded pulp cavity (N264; Table S1).

2.3 | Growth Models

The relationships of both body length and weight to age were fitted to both a von Bertalanffy and a Gompertz growth curve. The logarithmic growth pattern characteristic of marine mammals is represented mathematically by these growth curves, which can accurately depict the initial rapid growth period of young cetaceans, which is followed by a slowdown as they approach physical maturity and asymptotic adult size (Adamczak et al. 2023).

The von Bertalanffy growth model had the best fit to the overall male and female data (von Bertalanffy—males $r^2 = 0.84$; females $r^2 = 0.96$; combined sexes $r^2 = 0.90$ vs. Gompertz—males $r^2 = 0.83$; females $r^2 = 0.95$; combined sexes $r^2 = 0.89$).

Based on these r^2 values, the von Bertalanffy growth curve was used to display the data using the following equation:

$$L^t = L\infty\left(1 - e^{-k\,(t-to)}\right).$$

where L is length, k is growth rate constant, $L\infty$ is asymptotic length, to is length at birth, e is exponential, and t is estimated age.

Growth curves were plotted, and the Solver function add-in was used. By substituting a theoretical age at birth (to), growth rate constant (k), asymptotic length ($L\infty$), and the actual estimated age (obtained from counting GLGs) into the Von Bertalanffy growth equation, an expected length at each individual age estimate was generated. The difference between each individual's actual and expected lengths was calculated to determine residual errors. Depending on whether the observations lie above or below the line of best fit, the residual error values may be positive or negative. The residual error values were then squared, and the sum of the total squared residual errors (SQ) between all actual data and expected values was computed. The Solver function was then used to minimize the squared residual errors (SQ) to produce the following parameter values for the growth model that best fit the data: age at birth (to), growth rate constant (k), and asymptotic length ($L\infty$). Thus, the age, length, and weight at birth and at physical maturity can be calculated.

2.4 | Male Reproductive Biology

Testes were examined histologically to determine the state of maturity. Standard histological processing techniques were used, and the tissue was subsequently sectioned with a Leica microtome into 5–7 μm thick sections, mounted, and stained with hematoxylin and eosin. The sections were examined under an Olympus BX50 compound microscope at 200× and 400× magnification to determine sexual maturity.

Hohn et al. (1985) defined three stages of maturity, namely immature, pubertal (early spermatogenesis), and mature (late

spermatogenesis). Since tissue preservation was poor in most cases, most likely due to the material originating from stranded animals (Plön et al. 2015), individuals were classified as either mature (in late spermatogenesis) or immature (which included pubertal animals) based on the presence or absence of spermatids and spermatozoa, respectively.

The structure of the seminiferous tubules in cetaceans exhibits significant seasonal variations linked to spermatogenesis. During the peak of the breeding season, the tubules undergo a transformation in both size and complexity of cellular organization, going from a dormant, regressed state to a highly active, detailed state (Plön and Bernard 2007). Therefore, an open lumen, complex epithelium structure, high Sertoli and Leydig cell activity, and an increase in seminiferous tubule diameter are all linked to active breeding (Plön and Bernard 2007). The seasonality of spermatogenesis was determined by measuring the diameters of 20 seminiferous tubules in each testis using photographs taken with an Olympus BX50 microscope fitted with a camera at a magnification of 10×, using the image analysis software *Olympus Analysis docu*. Subsequently, the tubule diameter was plotted against the month of the individual's stranding to investigate seasonality.

2.5 | Female Reproductive Biology

Whether females were lactating and/or pregnant was established at necropsy and recorded: uteri were opened and examined for the presence of a fetus; simultaneously, ovaries were cross-checked for the presence of a *corpus luteum* (CL); mammary glands were examined for the presence of milk. If pregnant, the length, weight, and sex of the fetus were also recorded. Ovaries were weighed to the nearest gram, and the number of ovulation scars (*corpora*) was recorded. The ovaries were examined macroscopically for the presence of a CL, *corpus albicans* (CA), or *corpus atreticum* by sectioning them at intervals of approximately 1 mm in thickness. The number of *corpora* per ovary was recorded, and their dimensions (length, width, and height) were measured using vernier calipers. Females were considered sexually mature if the ovaries contained at least one CL. Females were classified into the following four reproductive states: (i) immature, (ii) resting mature (not pregnant or lactating), (iii) mature and pregnant, and (iv) mature and lactating. Since *corpora atretica* result from a non-ovulatory event (Perrin and Donovan 1984), they were not included in the *corpora* count. However, it is important to note their presence and appearance in different species, as they play an important role in the ovarian cycle by producing hormones (Perrin and Donovan 1984).

Various reproductive parameters, such as pregnancy rate, CI, resting period, and ovulation rate, were calculated, following Perrin and Reilly (1984). By dividing the percentage of pregnant females in the sample by the gestational age, expressed in years, the annual pregnancy rate (APR) was calculated (Perrin and Reilly 1984). The gestation period is the least variable component of the reproductive cycle of a species (Perrin and Reilly 1984), and due to a lack of any conclusive data, such as a seasonal trend in ovulations and/or presence of very small fetuses in the sample, it was assumed to be 1 year (12 months) in the present study according to Kasuya (1972) and Miyazaki (1977b). The CI is an estimate of the interval between parturitions in mature females. By computing the inverse of the APR estimate, this interval was ascertained (Perrin and Reilly 1984). The percentage of resting females in the sample divided by the percentage of pregnant females was used to determine the resting period (TR; Perrin and Reilly 1984). Finally, the ovulation rate was estimated, assuming that CAs persist indefinitely (Perrin and Reilly 1984). A linear regression was fitted to the number of ovarian *corpora* against age in order to calculate the ovulation rate. According to Perrin and Reilly (1984), the slope of the regression line corresponds to the rate at which *corpora* are formed.

3 | Results

3.1 | Age and Growth

In longitudinal sections of teeth, the neonatal line was clearly visible, and it was easy to distinguish between prenatal and postnatal dentin. However, accessory lines within the postnatal dentin were numerous. The first GLG was generally the widest, with the widths of the subsequent layers decreasing toward the pulp cavity. There was a good correlation between dentinal and cemental GLG counts for 44 individuals ($r^2 = 0.926$; Figure 2), indicating that cemental age estimates were reliable in individuals where the pulp cavity was occluded. Dentinal and cemental age estimates were well correlated up to an age of about 11 years (Figure 2), at which occlusion of the pulp cavity started. The smallest individual with an occluded pulp cavity measured 227 cm.

A von Bertalanffy growth curve was fitted to length-at-age and weight-at-age data for both males and females separately and for males and females combined (Figure 3, Figure S1); for individuals with occluded pulp cavities, the cemental age estimate was used. A summary of the estimated parameters is listed in Table 1. Length and weight at birth were estimated to be 116.2 cm and 19.8 kg for males and 102.7 cm and 11.1 kg for females by the von Bertalanffy growth equation, with the shortest male in the sample measuring 99 cm and weighing 8.6 kg, and the shortest female measuring 93 cm and weighing

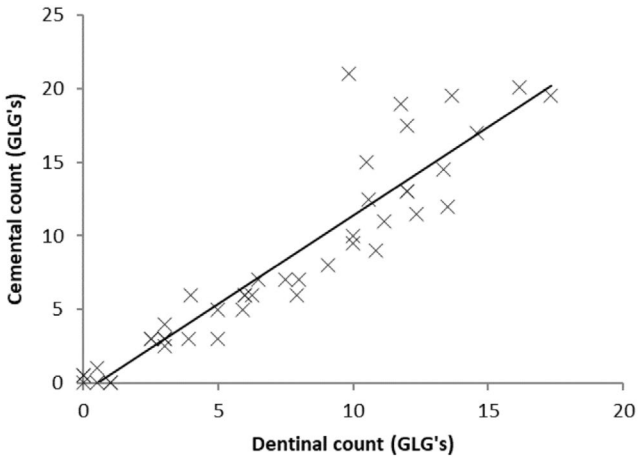

FIGURE 2 | The relationship between dentinal and cemental GLGs in the teeth of *Stenella coeruleoalba* stranded along the southeast coast of South Africa. A linear regression is fitted to the data ($r^2 = 0.926$).

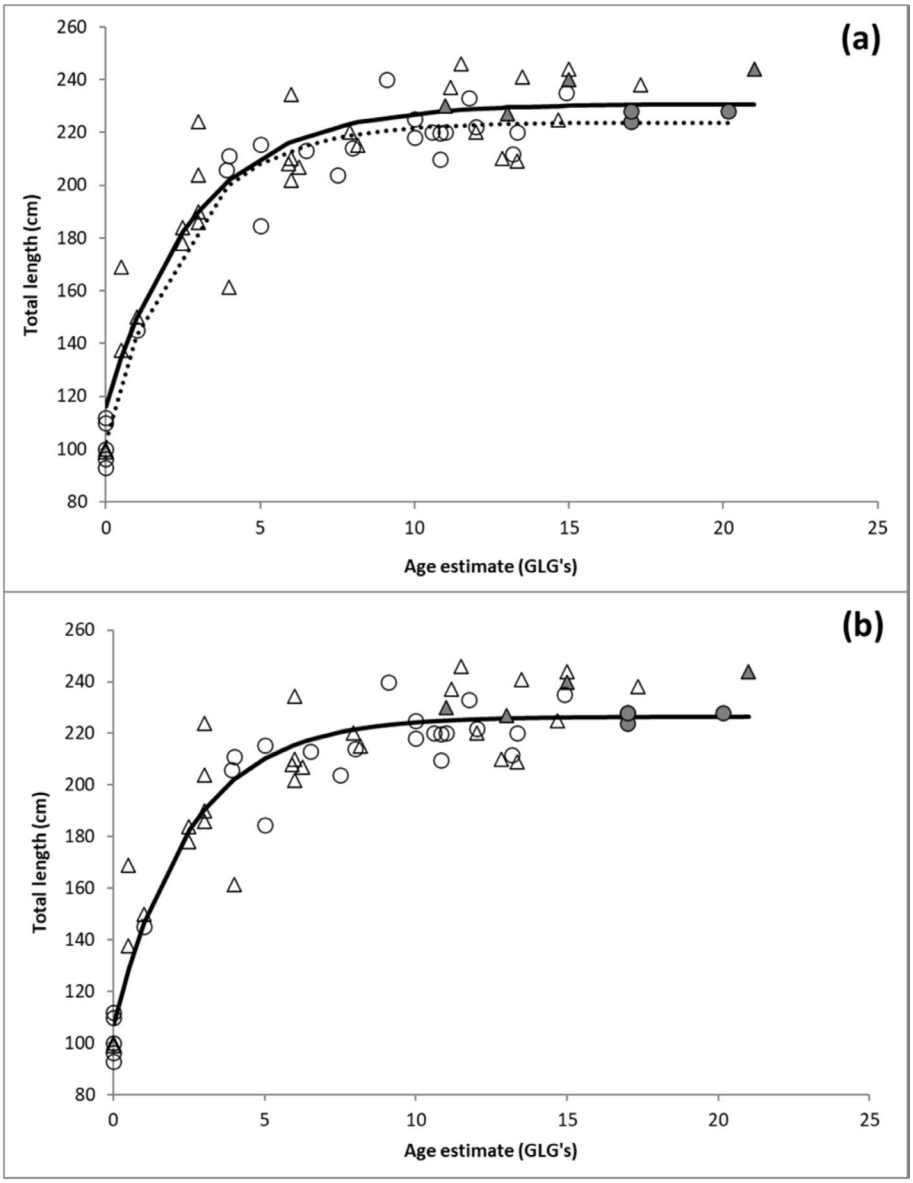

FIGURE 3 | Von Bertalanffy growth curve fitted to length-at-age data of *Stenella coeruleoalba* for males and females separately (a) and males and females combined (b). The triangles represent males, the circles represent females, and the shaded shapes represent specimens where cemental counts were used after occlusion of the pulp cavity ($r^2 = 0.840$ [males], $r^2 = 0.963$ [females], and $r^2 = 0.900$ [combined]).

TABLE 1 | Parameters derived from a von Bertalanffy growth curve fitted to age-length and age-weight data for male and female *Stenella coeruleoalba* stranded off the southeast coast of South Africa.

	Male		Female		Combined sexes	
Parameter	**Length (cm)**	**Mass (kg)**	**Length (cm)**	**Mass (kg)**	**Length (cm)**	**Mass (kg)**
L_1	99	8.6	93	7	93	7
L_2	244	157	235	135	244	157
$L\infty$	230.8	128	223.8	124.2	226.4	124.4
to	116.2	19.8	102.7	11.1	107.4	14.1
k	0.34	0.17	0.41	0.22	0.40	0.20
n	32	22	29	22	61	44
r^2	0.840	0.832	0.963	0.934	0.900	0.886

Note: L_1, smallest length/mass in the sample; k, growth constant; L_2, largest length/mass in the sample; n, sample size; $L\infty$, asymptotic length/mass; r^2, goodness of fit; to, length/mass at birth.

7 kg (Table 1). Initial length increase is rapid up to about 5 years of age and 210 cm in length in males and about 4 years of age and 200 cm in length in females (Figure 3). The initial weight increase is less rapid. Weight increase is the fastest in the first 6 and 7 years for males and females, respectively (Figure S1). Individuals were considered physically mature if they had a TBL/weight equal to or greater than the asymptotic value of 230.8 cm and 128 kg for males and 223.8 cm and 124.2 kg for females generated by the von Bertalanffy equation (Table 1). Based on the von Bertalanffy growth curve, males reach physical maturity at a length of 231 cm, an age of 21 years, and a weight of 125 kg, while females reach physical maturity at 224 cm, an age of 20 years, and a weight of 123 kg.

3.2 | Male Reproductive Biology

The histological appearance of the testes was classified as mature and immature following Hohn et al. (1985). A dependent paired *t*-test showed no significant difference in weight between left and right testicles ($n = 8$; $p = 0.492$). Thus, either testis could be examined to determine sexual maturity. In general, immature individuals had small, thin, elongated testes (mean testis length: 6.5 cm [range: 2.1–8.4 cm]; Table 2), while mature individuals had large, thick, elongated testes (mean testis length: 12.1 cm [range: 10–14.4 cm]; Table 2). Table 2 summarizes the mean and range of testis weight, length, and seminiferous tubule diameter for immature and mature individuals. Mean seminiferous tubule diameter was plotted against total body length, body weight, and estimated age (Figure 4). Mature individuals all had a seminiferous tubule diameter greater than 72 μm, a body length greater than 224.8 cm, a body weight over 98 kg, and an estimated age of 10 years or more (Figure 4). One individual (N289) was determined to be inactive; this individual measured 244 cm in length, had an estimated age of 15 years, and weighed 131 kg. The mean testis length was 10.5 cm, and the mean seminiferous tubule diameter was 54.54 μm.

The sample size was too small to statistically estimate the age at 50% sexual maturity. However, a range of age and length at sexual maturity could be determined using the range between the oldest/longest immature individual and the youngest/shortest mature individual (Table S2). A mean age at ASM could also be determined by extrapolating it from the growth curve using the average body length (227.5 cm) and weight (112.6 kg) at ASM, calculated (Table S2). These data correspond to the ages between 10 and 11 years, indicating the average age at ASM for male striped dolphins.

TABLE 2 | Measurements of testis weight (g), testis length (cm), and seminiferous tubule diameter (μm) for immature and mature male *Stenella coeruleoalba*.

Maturity stage	Mean (±SD)	Range	Sample size
Single testicle weight (g)			
Immature	8.0 (0)	—	1
Mature	72.0 (58.9)	19.8–200	6
Combined testis weight (g)			
Immature	16 (0)	—	1
Mature	144.0 (123)	41.4–376	6
Mean testis length (cm)			
Immature	6.5 (2.1)	2.1–8.4	8
Mature	12.1 (1.4)	10–14.4	7
Seminiferous tubule diameter (μm)			
Immature	41.7 (15.9)	23.8–69.6	7
Mature	74.7 (23.3)	43.5–110.6	9

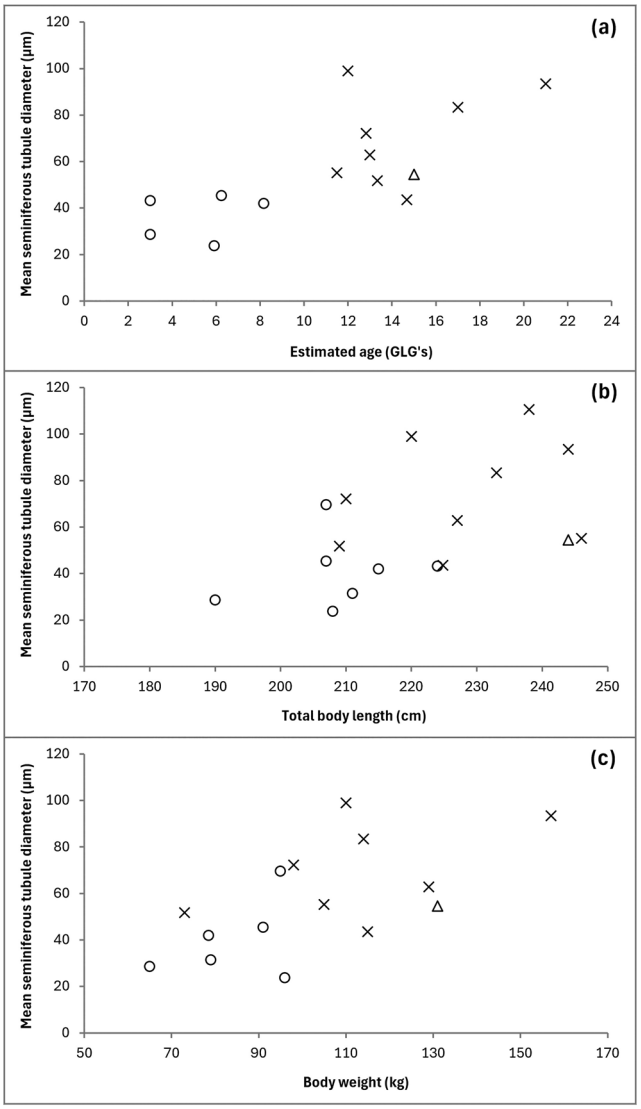

FIGURE 4 | Mean seminiferous tubule diameters for male *Stenella coeruleoalba* of different maturity stages in relation to (a) estimated age (GLGs; $n = 14$), (b) total body length (cm; $n = 17$), and (c) total body weight (kg) ($n = 15$). Crosses represent sexually mature individuals, circles sexually immature individuals, and the triangle a sexually inactive individual.

Seasonal variation of the mean seminiferous tubule diameter and combined testis weight is shown in Figure S2. No individuals were available for the month of March. Mature individuals were found in every month, except April, September, and October, showing a fluctuation in tubule diameter and testis weight throughout the year. Tubule diameter peaked in May and December with a corresponding peak in testis weight in May (no testis weight measurements were recorded for individuals stranded in December; Figure S2).

3.3 | Female Reproductive Biology

Data on ovarian weight indicated that in mature animals, one ovary was consistently larger in size and weight than the other; where available, the data indicated that the left ovary was usually the larger/heavier one, and this was statistically significant at the 5% level ($p=0.017$, $n=9$). In immature animals, no size difference was detected between the two ovaries. A paired *t*-test to ascertain if ovulations occurred equally in both ovaries indicated that ovulations occurred significantly more often in the left ovary than the right ovary (*t*-value = 3.95, $p=0.002$, $n=9$). Furthermore, CAs were only found in the right ovary in females older than 10 years of age and longer than 220 cm in total body length.

CLs presented themselves as a protrusion from the surface of the ovaries. Two types of CLs were identified, one with no lumen and one with a gelatinous lumen. No relationship was found between the type of CL present and the progress of pregnancy. In cases where left and right ovaries could be identified, the CL was always found in the left ovary. CAs presented themselves as either a small protrusion or as a scar on the surface of the ovary. Five individuals had only one *corpus* present, and these individuals ranged from 209.8 to 240 cm in length and 9 to 11 years of age (Figure S3). Two of the five individuals were pregnant with a CL present, indicating that individuals can become pregnant on their first ovulation. A regression of estimated age against the number of *corpora* was described by the equation $y=0.3196x-0.3556$, which gave an ovulation rate of 0.32 per year (least squares regression method). This suggests that ovulation occurs, on average, every 3.1 years (or 37.2 months). A low coefficient of determination (0.39) was calculated between age and the number of ovarian *corpora* (Figure S3).

There were too few ovaries available to statistically estimate the age at 50% sexual maturity. However, a range of age and length at sexual maturity could be determined using the largest/oldest immature individual and the smallest/youngest mature individual (Table S3). All individuals with a combined ovary weight of 5 g, a body length over 216 cm, an age estimate older than 8 years, and a body weight above 93 kg (Figure 5) were sexually mature. The youngest mature individual (6.5 years) was a pregnant female with a combined ovary weight of 11 g, while the oldest (7.5 years) immature individual had a combined ovary weight of 3 g (Figure 5). A lactating female with an estimated age of 14.9 years had the highest combined ovary weight of 13 g (Figure 5).

Various other reproductive parameters calculated are presented in Table 3. A total of 7 out of 27 females were pregnant. Unfortunately, it was not possible to calculate the lactation period due to a lack of data.

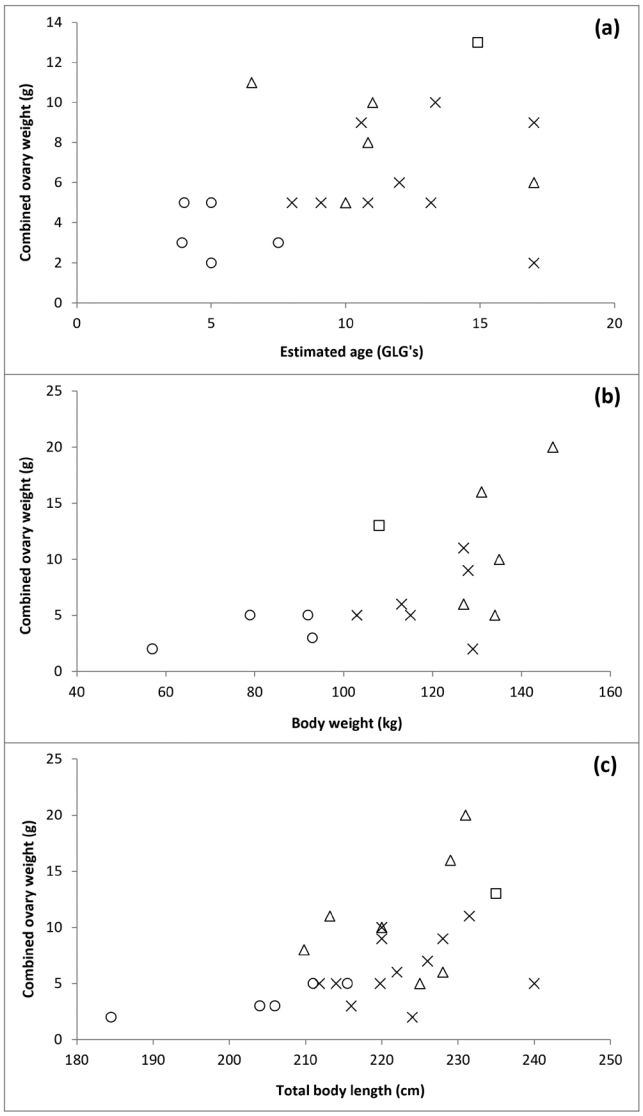

FIGURE 5 | Increase in combined ovary weight with (a) estimated age (GLGs) ($n=20$), (b) body weight ($n=17$), and (c) body length ($n=25$) in *Stenella coeruleoalba*. Circles represent immature individuals, crosses mature resting individuals, triangles mature pregnant individuals, and squares mature lactating individuals.

The occurrence of fetuses, neonates, and calves up to and including an age of 1 year in relation to time of year is shown in Figure 6. It is difficult to ascertain whether there is seasonality in conceptions and births due to the small sample size, but there is a possibility of two cohorts of pregnancies per year, one starting in August and the other in December/January. Although the data are sparse, there appear to be more neonates in the last 6 months of the year.

4 | Discussion

Several aspects of the biology of the striped dolphin were assessed in this study, and using this information, inferences can be made about population parameters. All animals sampled in this study were stranded, and samples have been collected over a long period and a wide geographic area. The cause of death was usually unknown, and it is thought that stranded dolphins may

TABLE 3 | Summary of the values obtained for a number of reproductive parameters for mature female *Stenella coeruleoalba*.

Reproductive parameter	Calculation	Value
Annual pregnancy rate	$APR = P/T_G$	25.9%
Proportion pregnant (P)	7/27 = 0.259	
	(0.259/1) = 0.259 × 100%	
Calving interval	CI = 1/APR 1/0.259	3.86 years
Resting period	$T_R = T_G \times R/P$	1.86 years
Proportion pregnant (P)	7/27 = 0.259	
Proportion resting (R)	13/27 = 0.481	
	1 × 0.481/0.259	
Ovulation rate	$y = 0.3196x - 0.3556$	0.32
Regression equation (least squares method)	Slope of equation = 0.3196	

Note: T_G, length of gestation assumed to be 1 year (12 months).

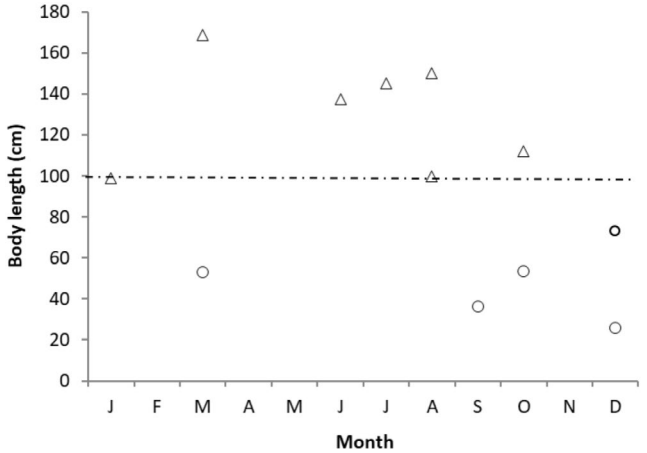

FIGURE 6 | Occurrence of *Stenella coeruleoalba* fetuses ($n = 5$) and calves ($n = 7$) up to and including the age of 1 year in relation to month. The circles represent fetuses, the triangles represent neonates and calves, and the dotted line indicates length at birth.

not reflect the "normal" population, as the animals may not be healthy, leading to strandings.

4.1 | Age and Growth

In the present study, length and mass at birth were predicted to be 116.2 cm and 19.8 kg, and 102.7 cm and 11.1 kg for males and females, respectively, based on the von Bertalanffy growth equation (Table 1). These values are most likely overestimates, as a result of having only a few younger individuals present in the sample (10 males, 7 females < 200 cm TBL), the shortest male measuring 99 cm and weighing 8.6 kg, and the shortest female measuring 93 cm and weighing 7 kg. The smallest individual in the sample measured 93 cm (no teeth were available for age determination for this individual), indicating that striped dolphins may be born at lengths shorter than reported previously. This is similar to animals from the Mediterranean (92.5–95 cm; Aguilar 1991; Calzada et al. 1996; Di-Meglio et al. 1996) and western North Pacific (100 cm; Kasuya 1972; Miyazaki 1977a), with calf length in South African waters ranging from 91.2 to 107.7 cm (Best 2007; Kroese 1993). Miyazaki (1977b) obtained a value of 100 cm for the mean length at birth for male and female Japanese striped dolphins (Table 4).

The initial increase in length and weight after birth is rapid for male and female striped dolphins. Males measure between 148 and 149 cm, and females between 144 and 147 cm by the end of their first year. The large initial increase in body length after birth reflects the rapid development of the calf, which is needed to reach thermoregulatory equilibrium and social and motor independence from its mother (Cockcroft and Ross 1990). These results concur with data from the Northeast Atlantic Ocean, where male and female striped dolphins attain a size of about 148 cm by the end of their first year (Di-Meglio et al. 1996). However, shorter lengths of approximately 138 and 120 cm for males and females, respectively, were reported for the Mediterranean Sea population (Di-Meglio et al. 1996). In the Japanese population, males and females reached a longer body length of 166 cm by the end of their first year (Miyazaki 1977a), suggesting that this population has a higher growth rate, which could be linked to a number of factors, such as environmental productivity, fattier milk provided by the mothers, or population differences.

Once animals reach asymptotic length and weight, they are physically mature (Kroese 1993). Striped dolphins in the southwestern Indian Ocean are estimated to reach physical maturity at 231 cm and 127.98 kg and 224 cm and 124.21 kg for males and females, respectively, indicating that females are slightly smaller than males in the subregion (Kroese 1993). Di-Meglio et al. (1996) used stranded dolphins to study the northeast Atlantic ($n = 52$) and Mediterranean ($n = 44$) populations and found that these populations reach physical maturity earlier. Physical maturity was reached at 216 cm and 104.2 kg and 200 cm and 90.5 kg for males and females, respectively, in the northeast Atlantic population, and at 191 cm and 78.1 kg and 195 cm and 78.9 kg for males and females, respectively, in the Mediterranean population (Di-Meglio et al. 1996; Table 4). The differences suggest that striped dolphins in the southwestern Indian Ocean have a larger overall body size compared to the northeast Atlantic and Mediterranean populations. The differences in asymptotic length, mass, and growth rates between the populations may be due to varying environmental conditions, particularly temperature and/or food availability, both of which can influence body size and growth of cetaceans (Cockcroft and Ross 1990; Di-Meglio et al. 1996; Table 4).

Female striped dolphins in the southwestern Indian Ocean reach physical maturity at a shorter length, lower body weight, and younger age than their male counterparts. Males reach physical maturity at an estimated 21 years of age, while females attain physical maturity at about 18 years of age. Similar findings are reported for the Japanese population, where the males reach asymptotic lengths at 21 years and females at 17 years, respectively (Kasuya 1976; Table 4). According to Best (2007) and Kroese (1993), lengths of up to 2.7 m have been recorded for adult males, while adult females

TABLE 4 | Geographical differences in *Stenella coeruleoalba* life history parameters.

Parameter	Sex	SW Indian Ocean[a]	SW Indian Ocean[b]	NW Pacific Ocean[c,d,e,f]	NE Atlantic Ocean[g]	Mediterranean Sea[g,h,i,j]
Length at birth (cm)	♂	116.2	108	100	—	92.5–95
	♀	102.7	91.2	100	—	92.5–95
Max length (cm)	♂	244	245	245	240	210
	♀	235	230	235	210	208
Max age (GLG)	♂	21	47	50	29	25
	♀	20.2	42	49	23	22
Length at physical maturity (cm)	♂	231	246	236	216	191
	♀	224	230	225	200	195
Age at physical maturity (GLG)	♂	21	25	21	8–9	—
	♀	20	20	17	5–6	—
Length at sexual maturity (cm)	♂	209–224	210–230	200–240	—	190
	♀	209–215.2	200–240	190–220	—	182–194
Age at sexual maturity (GLG)	♂	8.17–11.5	10–12	6.5–14.5	—	11
	♀	6.5–7.5	8.6	4.5–12.5	—	10–15
Gestation period (months)		12	—	12–13	—	12
Annual pregnancy rate (%)		25.9	34	42–45	—	25
Ovulation rate per year		0.32 (3.1 years)	0.43 (2.3 years)	0.41–0.69 (1.4–2.4 years)	—	0.40 (2.5 years)
Calving interval (years)		3.86	2.3	3.2	—	4
Reproductive seasonality		Possible	No	Yes	—	—
Sexual dimorphism		Limited	—	—	—	—

[a]Present study.
[b]Kroese (1993).
[c]Kasuya (1976).
[d]Kasuya and Miyazaki (1976).
[e]Miyazaki (1977a).
[f]Miyazaki (1984).
[g]Aguilar (2000).
[h]Calzada et al. (1996).
[i]Di-Meglio et al. (1996).
[j]Guarino et al. (2021).

reach lengths of up to 2.4 m in the southern African subregion. Allocation of resources and energy toward reproduction rather than growth in females may account for this difference between the sexes. The difference between maximum recorded lengths and asymptotic lengths in males and females may suggest sexual dimorphism. However, in the same population, no distinct sexual dimorphism in size and shape was found, but the males possess significantly larger appendages (Bishop 2014). Additionally, no significant differences in cranial size and shape between the sexes were demonstrated for the same population (Conry et al. 2016).

There was a good correlation between dentinal and cemental age estimates up to an age of about 11 years, after which the pulp cavity starts to become occluded. Similarly, occlusion of the pulp cavity occurred from about 11 years of age in the Japanese population (Kasuya 1976). Difficulties in reading the last few dentinal GLGs in teeth close to occlusion may result in age estimates of older individuals being underestimated. The maximum age estimates obtained during the present study were 21 years for males and 20.2 years for females. Similarly, maximum age estimates of 25 and 22 years were obtained for males and females of the population from the Mediterranean Sea, respectively, using dentinal

and cemental GLGs (Di-Meglio et al. 1996; Table 4). Di-Meglio et al. (1996) also examined the northeast Atlantic population and found the maximum ages to be 29 and 23 years old for males and females, respectively. Similar findings were reported for the Japanese population using age estimates obtained from dentinal layers only, where the oldest male was 29 years and the oldest female 27.5 years (Miyazaki 1977a). However, when both dentinal and cemental layers were used, the age estimates for this population were much higher, reaching 50 years and 49 years for males and females, respectively (Kasuya 1976; Table 4). Similarly, for the South African population, Kroese (1993) had much higher estimates of 47 and 42 years for males and females, respectively, based on cemental readings. Because striped dolphin teeth have numerous accessory lines, it is easy to misinterpret GLGs in this species (Hohn et al. 1989), and thus these ages could be overestimated. The age estimates in our study were confirmed by three independent readers and were in the range previously reported by Ross (1984), suggesting that the age estimates obtained here for dentinal layers were consistent.

4.2 | Reproductive Biology

Limitations occurred due to poor tissue preservation, which resulted in the lack of some reproductive data being collected. The ASM for males occurred at a combined testis weight between 16 and 41.2 g, 8.4–10 cm testis length, and 43.54–69.61 μm seminiferous tubule diameter (Table 2). Maturity occurs at a smaller seminiferous tubule diameter between 34.0 and 45.0 μm in the Japanese population (Miyazaki 1977a). That population is highly exploited (Miyazaki 1977a), which could account for the differences in reproductive parameters, particularly given the similarity in age and growth structure between the Japanese and South African populations. The combined testis weight of mature individuals ranged from 41.4 to 376.0 g (Table 2). The wide range in testes weights observed in mature males during this study is not unexpected, as testes of short-beaked common dolphins from the eastern North Atlantic ranged from 70.0 to 800.0 g (Collet and Girons 1984). Generally, cetaceans possess testes that comprise more than 1% of their total body weight (Kenagy and Trombulak 1986; Plön and Bernard 2007); yet in the present study, the maximum combined testis weight comprised only 0.24% of the total body weight. This is not unusual as some dolphins (Indian Ocean humpback dolphin *Sousa plumbea*, common bottlenose dolphin *Tursiops aduncus*, and Franciscana dolphin *Pontoporia blainvillei*; Cockcroft 1993; Plön and Bernard 2007) and several baleen whales (humpback whale *Megaptera novaeangliae*, gray whale *Eschrichtius robustus*, and sperm whale *Physeter macrocephalus*; Plön and Bernard 2007) also possess testes that comprise less than 1% of their total body weight. In contrast, other odontocetes, such as the harbor porpoise *Phocoena phocoena* (Gaskin et al. 1984; Read 1990), short-beaked common dolphin *Delphinus delphis* (Cockcroft 1993), vaquita *Phocoena sinus* (Hohn et al. 1996), and dusky dolphin *Lagenorhynchus obscurus* (van Waerebeek and Read 1994), all have testes that comprise more than 1% of their total body weight, which suggests that the striped dolphin has small testes in relation to their body size compared to other odontocetes. It has been suggested that species with relatively small testes have uni-male breeding systems, either monogamous or polygynous (Harcourt et al. 1981; Plön and Bernard 2007), whereas species with relatively large testes have multi-male breeding systems and exhibit promiscuity (Jefferson 1990; Plön and Bernard 2007). This suggests that striped dolphins from this study area could display monogamy or polygyny.

Our data indicate that the left ovary attains maturity before the right ovary in striped dolphins, which indicates that the ovaries are not equally functional. Only females older than 10 years and greater than 220 cm in length showed *corpora* in the smaller, right ovary. This prevalence of ovulation in one ovary is not unusual and has been previously reported by Ohsumi (1964) and Hirose et al. (1970). Hirose et al. (1970) reported that ovulations occur in the left ovary only in dolphins while they are young, and only at a later age do ovulations become more frequent in the right ovary. This pattern of asymmetry of sexual maturity fits the type III accumulation rate described by Ohsumi (1964). The onset of sexual maturity in females occurred at a combined ovary weight of between 5 and 8 g. However, ovarian weight was not a good indicator of sexual maturity due to the high variation resulting from the size of the CL.

In the present study, sexual maturity is reached between 209 and 224 cm in body length in males and between 209 and 215.2 cm body length in females, indicating that males and females reach sexual maturity at a similar length. Previously, Kroese (1993) reported that the smallest mature males were 2.2 m in length and the largest immature one was 2.3 m, while the equivalent sizes in females were about 2 and 2.1 m. According to Ross (1984), South African striped dolphins reached sexual maturity at 2.1–2.2 m for males and 2.1 m for females. In the northwestern Pacific, Kasuya (1972) found that males reach sexual maturity between 200 and 240 cm in body length and females at a shorter length between 190 and 220 cm. However, the length at which 50% of the population were mature was 220 cm for males and 212 cm for females, which is within the range obtained in the present study. In the Mediterranean Sea, female striped dolphins reach sexual maturity at a shorter length between 182 and 194 cm in TBL, and the average length for ASM was 187 cm TBL ($n = 84$; Calzada et al. 1996). The differences in length at ASM between populations could be due to differences in sample sizes, genetically determined geographic variation, or differences in population densities (Perrin and Reilly 1984).

Our results indicate that the age at ASM for the striped dolphin in the southwestern Indian Ocean is between 8.17 and 11.5 years for males and between 6.5 and 7.5 years for females, respectively. This suggests that females attain sexual maturity at a younger age than males. Average ages at sexual maturity are 7–15 years for males and about 7 years for females in the western North Pacific (Archer et al. 2025). A number of studies on delphinids have demonstrated that females attain sexual maturity earlier than males (Cockcroft and Ross 1990; Miyazaki 1984; Perrin et al. 1977). In a previous study of striped dolphins conducted on the same population, the age estimates for ASM for males and females were slightly higher (males reached maturity between 10 and 12 years of age, and females earlier at 8.6 years of age) (Kroese 1993). These differences could be due to differences in the interpretation of GLGs or could suggest that the age at ASM has decreased slightly for the present population, indicating that

the population has undergone density-dependent changes in life history parameters (Kasuya 1985). Changes in population densities are caused by a decrease in food availability or by an increase in human threats (Kasuya 1985). The Japanese population is highly exploited through directed fishing, and the age at ASM has decreased since the 1970s due to overexploitation (Kasuya 1985). Therefore, the Japanese population reached sexual maturity earlier than the present population (males reached sexual maturity between 6.5 and 14.5 years and females between 4.5 and 12.5 years; Miyazaki 1984). Unfortunately, the sample examined here was too small to test for changes in parameters over time.

Assuming that our sample is a good representation of the free-ranging population in the southwestern Indian Ocean, 25.9% of striped dolphin females could be pregnant at any one time based on the APR. This estimate is similar to that for the Mediterranean Sea population (25%; Calzada et al. 1996) and for the spotted dolphin *Stenella attenuata* off the Pacific coast of Japan (23.8% and 25.4%; Kasuya 1976; Kasuya et al. 1974). The present estimate is slightly less than the previous estimate for the same population in 1993 (34%; Kroese 1993). The higher APR in 1993 could be due to the inclusion of West Coast animals in the earlier study. Alternatively, the decrease in APR could also indicate that food availability has decreased, and females do not have enough energy to invest in pregnancy. The APR in the present study is substantially lower than that for striped dolphins off the Pacific coast of Japan, where it is estimated to be 42.2% (Kasuya 1976) and 45.5% (Kasuya and Miyazaki 1976). The higher APR in the Japanese population could be due to the larger sample size. Due to the high exploitation of the Japanese population, the CI has declined, which may account for the higher APR (Kasuya 1985; Perrin and Reilly 1984). Higher estimates of 47% and 36% were also obtained for the spotted dolphin (Perrin et al. 1976) and the spinner dolphin, *Stenella longirostris* (Perrin et al. 1977), in the eastern tropical Pacific.

Estimates of ovulation rates vary among delphinids and within a species, depending on the region and physical condition (Perrin and Reilly 1984). An ovulation rate of 0.32 per annum in the present study indicated that, on average, ovulations occur every 3.1 years (37.2 months). In contrast, the ovulation rate of the striped dolphin off the Pacific coast of Japan was found to vary between 0.41 and 0.69 per year (Kasuya 1972, 1976; Miyazaki 1984), which has been suggested to be a direct result of exploitation (Miyazaki 1984). Similarly, in the Mediterranean Sea, the ovulation rate was estimated to be 0.40 per year (Calzada et al. 1996). In the present study, the poor correlation between the number of *corpora* and estimated age may indicate that there is either a decrease in the ovulation rate with age or variation in the number of ovulations per estrus period (Myrick et al. 1986), but caution must be taken due to the small sample size. Individual variability in ovulation rate has also been observed in the spotted dolphin (Kasuya et al. 1974; Myrick et al. 1986; Perrin et al. 1976).

The resting period, defined as the time between weaning and the next pregnancy (Perrin and Reilly 1984), was estimated to be 1.86 years (22.3 months) in the present study. This is much higher than that obtained by Kasuya (1972), who estimated a resting period of between 3.6 and 6 months for the striped dolphin off the Pacific coast of Japan. The resting period has decreased to between 2.4 and 3.6 months under heavy exploitation in Japanese waters (Kasuya 1985). The resting period of almost 2 years in the present study could be an artifact of a small sample size, although previous findings reported a typical gap of 2–3 years between calvings, with a 13.4-month gestation period and 16.5 months of lactation (Kroese 1993). Differences in the resting period between populations may reflect small sample sizes or varying population densities (Perrin and Reilly 1984). The resting period for the spotted dolphin off the Pacific coast of Japan was longer than reported for the striped dolphin in the same region, lasting 8.1 months (Kasuya et al. 1974), and in a later study, 9 months (Kasuya 1976).

The CI of 3.86 years estimated during the present study is similar to the CI in the northwest Pacific Ocean (3.2 years) (Miyazaki 1984) and Mediterranean Sea populations (4 years; Calzada et al. 1996; Di-Meglio et al. 1996), but higher than the previously estimated 2.3 years for the South African population (Kroese 1993). It is worth noting that the previous estimate was suggested to be an underestimate due to the inclusion of West Coast animals in the analysis (Kroese 1993). Off the Pacific coast of Japan, the CI decreased from 3 to 2.37 years between 1972 and 1976 (Kasuya 1972, 1976). It has been proposed that when a population is depleted through exploitation, such as the Japanese population, the pregnancy rate and the CI change in order to increase recruitment (Laws 1961), which was assumed to be the case for the Japanese population.

Unfortunately, the small sample size precluded any definite conclusions from being drawn on reproductive seasonality in the present study. Kroese (1993) previously indicated that births may occur in the austral winter (May–August) or summer (January–February) in the southern African subregion. Our results indicate that spermatogenesis seemed to occur year-round; however, testis weight and seminiferous tubule diameters fluctuated throughout the year, and there is a possibility of two resting periods in April and September/October. Additionally, fetus and calf lengths indicated the possibility of two cohorts, with conceptions occurring in August and December/January, although the second half of the year showed more neonates. This aligns with the peak in seminiferous tubule diameter during the month of December, although the peak in May is earlier than the cohort starting in August. These data could suggest reproductive seasonality, but a larger sample size is needed to support this. Diffuse breeding, with peaks at certain times of the year, is known for other delphinids within the subregion, such as the common bottlenose dolphin (Cockcroft and Ross 1990). On the other hand, clear reproductive seasonality was observed for the northwest Pacific population of the striped dolphin (Kasuya 1972; Miyazaki 1977a, 1984). Three breeding seasons were reported for this population: one from February to May, another from July to September, and the last one in December (Miyazaki 1977a). Differences observed in reproductive seasonality are likely due to geographic variations in environmental conditions, such as food availability, water temperature, etc. (Bronson 1989).

In conclusion, the life history parameters determined for the population in the southwestern Indian Ocean presented here provide vital information for a species that is currently classified as "least concern" by the IUCN globally and off Southern Africa (but "vulnerable" for the Mediterranean population). However, further studies with larger sample sizes are required to address

possible artifacts caused by the small sample size. Further examinations and monitoring of life history parameters are important, as changes in these parameters can indicate changes in population densities with implications for the conservation of the species.

Author Contributions

Stephanie Plön: conceptualization, funding acquisition, methodology, writing – review and editing, data curation, supervision, resources, validation. **Marcel Kroese:** writing – review and editing. **Amy Bishop:** investigation, writing – original draft, formal analysis, visualization, methodology. **William P. Froneman:** supervision, resources, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Von Bertalanffy growth curve fitted to weight-at-age data of *S. coeruleoabla* for males and females separately (a) and males and females combined (b). The triangles represent males, the circles represent females, and the filled shapes represent specimens where cemental counts were used after occlusion of the pulp cavity ($r^2 = 0.832$ [males], $r^2 = 0.934$ [females], and $r^2 = 0.886$ [combined]). **Figure S2:** Monthly plot of (a) mean seminiferous tubule diameter (μm) and (b) combined testis weight (g) for mature and immature male *S. coeruleoalba*. Crosses represent sexually mature individuals, circles sexually immature individuals and the triangle an inactive individual. **Figure S3:** Attainment of sexual maturity in relation to (a) total body length ($n = 27$) and (b) estimated age (GLGs) ($n = 22$). The solid line in (b) represents the regression (least squares method) between the number of corpora and the age ($y = 0.3196x - 0.3556$; $r^2 = 0.3875$). Circles represent immature individuals, crosses mature resting individuals, triangles mature pregnant individuals, and squares mature lactating individuals. **Table S1:** Comparison of dentinal age estimates between the present study and Ross (1984). **Table S2:** Summary of the size and estimated ages for different maturity stages for male *S. coeruleoalba*. **Table S3:** Summary of the size and estimated ages for different maturity stages of female *S. coeruleoalba*.