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Life history parameters and diet of Risso's dolphins, *Grampus griseus*, from southeastern South Africa

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Abstract

The life history of Risso's dolphins (*Grampus griseus*) remains poorly known and data from strandings can help provide important information. Data from 126 Risso's dolphins stranded or bycaught along the southeastern coastline of South Africa between 1958 and 2017 were analyzed in relation to their sex, age structure, and diet. Mean estimated length at birth was 146.9 cm, while maximum length was 325 cm for males and 313 cm for females; small sample sizes precluded detailed examination of sexual dimorphism. Age estimates for 33 individuals (14 males, 17 females, 2 unknown sex) indicated a maximum age of 13 years (males) and 17 years (females), respectively; the oldest animal was 19 years (unknown sex). Mean length and age at attainment of sexual maturity were estimated at 280 cm and 7.1 years in males and at 282 cm and 7.7 years in females. Stomach contents from 27 individuals showed that diets of immature and mature males and females overlapped and consisted predominantly of cephalopods. Reported strandings decreased between 2000 and 2017, possibly due to a lack of reporting associated with a ban on driving on beaches or related to the collapse of the local "chokka" squid (*Loligo reynaudii*) fishery in 2014–2015.

KEYWORDS

age estimation, Cephalopoda, *Grampus griseus*, growth layer groups, life history, Risso's dolphin, stomach content analysis, strandings

1 | INTRODUCTION

Knowledge of the life history and diet of a species is fundamental for conservation management; without the understanding of demography, age at sexual maturity, age at first reproduction, and natural longevity, the dynamics of a population cannot be determined (Myrick, Hohn, Sloan, Kimura, & Stanley, 1983). However, such information is difficult to obtain for many cetacean species due to their long-lived nature and relative inaccessibility. Detailed knowledge on the foraging ecology of cetaceans is hindered by the difficulty of direct observational data in the wild. Thus, dietary patterns have generally been studied through stomach content analysis (Santos, Clarke, & Pierce, 2001; Sekiguchi, Klages, & Best, 1992), and by using stable isotope and fatty acid analysis in recent years (Evacitas, Kao, & Worthy, 2017). Samples and data from stranded specimens present an opportunity to obtain basic life history parameters and information on diet, particularly for species that are often inaccessible and/or considered less common, are otherwise difficult to study and therefore data deficient.

Risso's dolphins, *Grampus griseus* (Cuvier, 1812), are medium-sized pelagic dolphins that reach lengths of up to 3.8 m and attain a maximum weight of up to 500 kg (Baird, 2009; Jefferson, Leatherwood, & Webber, 1993). These dolphins are widely distributed and are mostly found inhabiting deep oceanic and continental slope waters (Best, 2007; Cockcroft, Haschick, & Klages, 1993; Jefferson et al., 1993) between 200 and 1,530 m in depth (Jennings, 1982; Olavarría, Aguayo-Lobo, & Bernal, 2001). Globally, their geographical distribution ranges from the tropics to temperate regions (Jefferson et al., 1993). Despite their cosmopolitan distribution, little is known about the life history of Risso's dolphins, particularly in the Southern Hemisphere (Baird, 2009; Bloch, Desportes, Harvey, Lockyer, & Mikkelsen, 2012; Chen, Watson, & Chou, 2011; Evacitas et al., 2017). The biology of the species off South Africa remains poorly known. Previous data on the life history of Risso's dolphin are limited (Ross, 1984) and to date their age-length relationship for South African waters has not been described (Best, 2007).

Observations in the Gulf of Mexico indicate that Risso's dolphins prefer a narrow depth range between the 350 m and 975 m isobaths (Baumgartner, 1997; Olavarría et al., 2001). Although the species feeds almost entirely on cephalopods (Baird, 2009; Cockcroft et al., 1993; Orr, 1966; Öztürk, Salman, Öztürk, & Tonay, 2007; Stroud, 1978), fish may occasionally also be taken (Olavarría et al., 2001). Previous work on the diet of Risso's dolphin from South African waters indicates that the diversity of the consumed prey differed between males and females as well as between dolphin size classes (Cockcroft et al., 1993). Recent investigations by Evacitas et al. (2017), examining stable isotope values in individual growth layer groups (GLGs) of teeth of Risso's dolphins from Taiwan, also indicated an ontogenetic shift in diet, as would be typical for many odontocetes (Newsome, Etnier, Monson, & Fogel, 2009; Riccialdelli et al., 2013).

The aim of the present study was, therefore, to investigate the age structure, growth rates, sexual maturity, and diet of Risso's dolphins from southeastern South African waters and determine if differential selection for prey was related to age, thus contributing to the knowledge of the feeding ecology of this poorly studied species.

2 | MATERIALS AND METHODS

Data and samples from 126 Risso's dolphins either found stranded along the Eastern Cape coastline or incidentally bycaught (three in shark nets off KwaZulu-Natal, one in a trawl net) off South Africa between 1958 and 2017 and accessioned to the Graham Ross marine mammal collection at the Port Elizabeth Museum (PEM), South Africa, were studied (Figure 1). Standard external measurements (Norris, 1961), as well as sex, date of collection, and location were recorded and accessioned. Teeth were collected and stored dry and stomachs were removed and stored frozen until further analysis. Available reproductive organs for both males and females were examined. For some females, data on the reproductive state (i.e., lactation and pregnancy) were also available. Teeth, reproductive organs, and/or stomach samples were not available for all individuals, resulting in differing sample sizes for the various analyses. No body weight measurements were available.
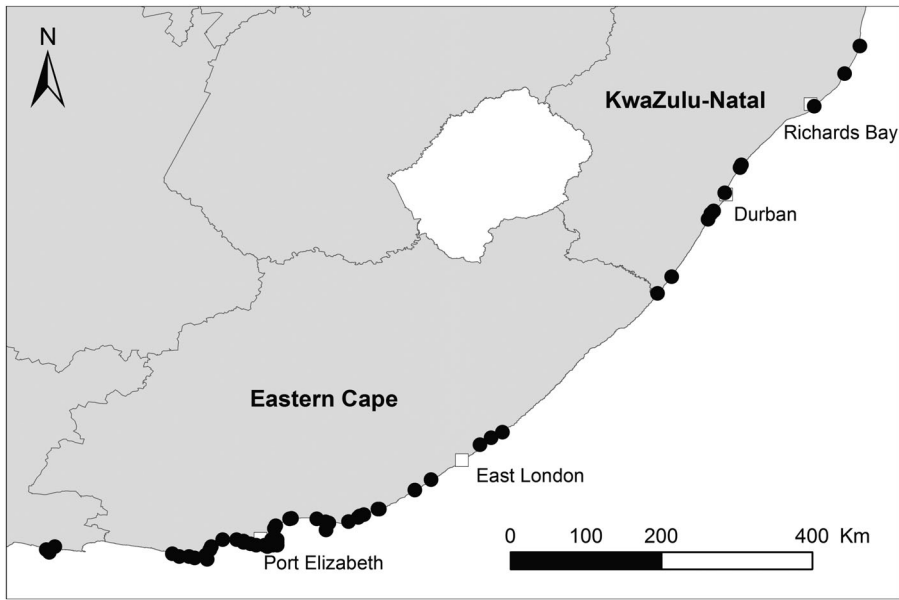
FIGURE 1 Location of stranded and bycaught (*n* = 2) Risso's dolphins, *Grampus griseus*, along the southeastern coast of South Africa between 1958 and 2017 (*n* = 126).

2.1 | Age determination and attainment of sexual maturity

Teeth for age determination were available for 33 animals (14 males, 17 females, 2 unknown sex). In addition, previous age estimates from Ross (1984) for nine specimens (four males, three females, two unknown sex) from the same region were included in the analyses, bringing the total to 42. Age estimates were obtained through counting the number of GLGs in histological preparations of longitudinally sectioned teeth (Perrin & Myrick, 1980). One tooth per animal was selected for age determination and chosen on the basis of being the largest and straightest tooth, showing the least wear, and without curving in more than one plane (Hohn, 1980).

Selected teeth were bisected longitudinally through the midline, using a Buehler "Isomet" saw with a diamond blade. Sectioned teeth were ground to thin, even sections of 100–180 µm thickness, using waterproof silicon carbide paper, until translucent. Sections were cleared in xylene and mounted on slides. Prepared sections were examined under a Leica EZ4D stereomicroscope (magnification 80×) with transmitted, polarized light (Figure 2). The GLGs were read blindly, three times each by two independent readers and a trimmed mean (the mean of those GLG counts that were within 15% of each other) was calculated. The extent of the last, incomplete layer was calculated as a percentage of the previous complete layer. In the absence of any age validation, one GLG was taken as equivalent to one year, as has been done previously for Risso's dolphins (Amano & Miyazaki, 2004; Bloch et al., 2012; Kruse, Caldwell, & Caldwell, 1999). For teeth in which the pulp cavity was occluded, readings of cemental GLGs were also performed.

The onset of sexual maturity was determined from macroscopic examination of the reproductive organs (Cockcroft & Ross, 1990). For this purpose, data on the combined testis weight of nine male Risso's dolphins and corpora counts from 22 ovaries of female Risso's dolphins were examined in relation to body length and age estimate of the animals. Onset of sexual maturity was defined as the age/length at which a rapid increase of combined testis weight could be observed in males (Hohn, Chivers, & Barlow, 1985; Kasuya & Tai, 1993); in females, the age/length at which a female has ovulated at least once, as evidenced by the presence of at least one corpus (following descriptions and definitions in Perrin & Reilly, 1984) in its ovaries, was taken as the onset of sexual maturity.
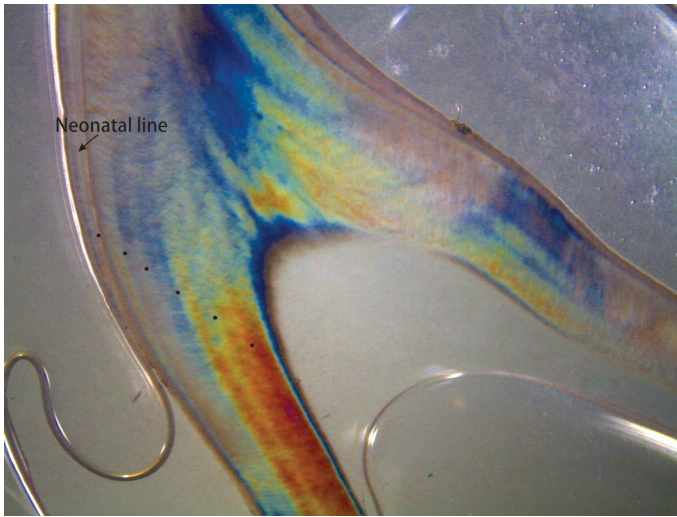
FIGURE 2 Longitudinal section of a Risso's dolphin, *Grampus griseus*, tooth showing the neonatal line; additional dots delineate individual growth layer groups (GLGs). Six complete GLGs can be counted (excluding the neonatal line), indicating that the animal was 6 years of age.

2.2 | Growth analyses

The growth of Risso's dolphins was modelled using the von Bertalanffy growth model:

$$L(t) = L_\infty \left[1 - e^{-k(t-t_0)} \right] \tag{1}$$

where L_∞ is the asymptotic length, k is the growth rate constant, and t_0 is the age that corresponds to zero length. This model was used for comparative purposes as growth in most other odontocetes is described using the von Bertalanffy model (Amano & Miyakazi, 2004; Denuncio, Negri, Bastida, & Rodríguez, 2017).

To determine if sex-specific von Bertalanffy growth curves were required to fit the age and length data, a likelihood ratio test was performed using the *vblrt* function in the fishmethods package in R (Nelson, 2017; R Core Team, 2017). To perform the test, the general von Bertalanffy model, with the same L_∞, k, and t_0 values for males and females were compared to four submodels fitted with sex-specific starting terms. Starting terms were estimated from Walford lines (Nelson, 2017). Likelihood ratios were then calculated for each general submodel comparison and tested using chi-square statistics. Subsequent to failing to find a difference between males and females in growth parameters, a single von Bertalanffy model was fitted to the pooled male and female data using the function *nls* (nonlinear squares) from the fisheries stock analysis package (FSA; Ogle, 2017) in R.

2.3 | Stomach content analysis

To avoid any possible bias, only stomach contents from stranded animals were included in the analyses. Stomach contents of 77 Risso's dolphins stranded between 1969 and 2000 were available for analysis; additional raw data from a previous analysis (Cockcroft et al., 1993) were also included in the study (courtesy of Norbert Klages, formerly PE Museum). Stomachs were thawed and intact prey and visible cephalopod beaks were removed for later identification. The remaining stomach contents were washed through a 2-mm mesh sieve and any hard remains removed. Clean cephalopod beaks were fixed in formalin for 2 hr, drained and stored in 70% ethanol. Cephalopod beaks were identified using both the reference collection of the PEM and Clarke (1986). To determine the mantle length and reconstituted weight of the prey, the lower rostral length (LRL) of the cephalopod beaks and the crest lengths (CL) of the order Octopoda were measured. Reconstituted mantle lengths and weight were calculated using the appropriate

regression from the PEM reference collection, Clarke (1986) and Smale, Clarke, Klages and Roeleveld (1993). From the identified cephalopod remains, an Index of Relative Importance (IRI) was calculated (Equation 2; Pinkas, Oliphant, & Iverson, 1971):

$$IRI = (\%N + \%W)\%F \tag{2}$$

where %N is the numerical percentage of each prey in relation to the total number of individual prey found in the stomachs, %W represents the percentage of the individual prey weight in relation to the total reconstructed prey weight, and %F the frequency of occurrence of each prey type in relation to the total prey. Stomach contents were analyzed according to sex and maturity of the dolphins. For this purpose, immature animals were those that were sexually immature based on the reproductive parameters determined in this study and using body length as the indicator when reproductive organs were not available; mature individuals were those that were deemed to be sexually mature based on the same criteria.

Following a detailed exploratory data analysis (Zuur, Hilbe, & Ieno, 2013), the effect of dolphin length as a function of sex on prey length was analyzed with a generalized additive model (GAM) using Gaussian distribution with an identity link function applying the *mgcv* package in R (Wood, S. N. 2019). The GAM was defined by:

$$PL_i = \alpha + \beta \times Sex_i + f(Dolphin\ length_i) : Sex_i + \varepsilon_i \tag{3}$$

where PL_i represents the prey length from individual i, α represents the intercept, β the coefficient of the covariate *Sex*, $f(Dolphin\ length_i)$: Sex_i is the smooth term of the relationship between *PL* and *Dolphin length* for males and females, and ε_i represents residuals, assumed to be normally distributed, with mean of zero and variance σ^2.

As no effect of sex on the relationship between prey length and dolphin length was found, sex was dropped and the data modeled according to Equation 4, where $f(Dolphin\ length_i)$ is the smoothed function of *Dolphin length*:

$$PL_i = \alpha + f(Dolphin\ length_i) + \varepsilon_i. \tag{4}$$

To determine if the diets of Risso's dolphins differed with sex and age, a permutational multivariate analysis of variance (PERMANOVA) in PRIMER v6 with PERMANOVA+ add on (Anderson, Gorley, & Clarke, 2008) was performed on the prey abundance and prey biomass data from the stomach content analysis. The two factor design tested the hypothesis that age ("maturity," fixed: two levels, *immature* vs. *mature*) and sex ("sex," fixed: two levels, *male* vs. *female*) influenced prey selection. The data were first square root transformed before a Bray–Curtis similarity matrix was calculated. The analyses were based on 9,999 permutations of residuals under a reduced model, with type III sum of squares (Anderson et al., 2008).

3 | RESULTS

Out of the total of 126 animals stranded and bycaught along the southeastern coastline of South Africa, information on total length and sex were available for 107 specimens (45 males, 53 females, 9 unknown sex) in the PEM records. The majority of animals measured between 150 and 300 cm in length (Figure 3). The smallest male and the smallest female measured 135 cm and 124 cm, respectively (Figure 3).

The frequency of reported strandings of Risso's dolphins peaked in the 1980s (Figure 3), with a mean of 5.6 ± 4.7 animals stranded per annum during that decade (Table 1). The following two decades saw a decline in the number of reported strandings, and only 0.4 ± 0.7 animals/year were recorded stranded in the period 2000–2017 (Figure 3, Table 1); no strandings of Risso's dolphins were documented between 2013 and 2017 and no change in length or age distribution over time could be determined.
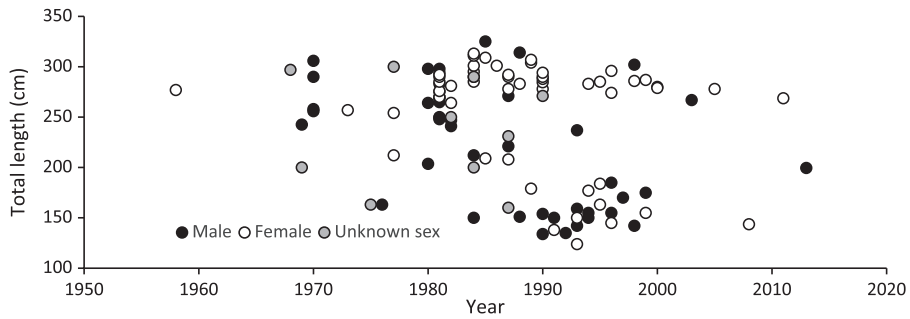
FIGURE 3 Total length and temporal distribution of stranded and bycaught (*n* = 1) Risso's dolphins, *Grampus griseus*, along the south-eastern coastline of South Africa between 1958 and 2017 (*n* = 107; black circles: males (*n* = 45), white circles: females (*n* = 53), gray circles: unknown sex (*n* = 10).

TABLE 1 Total and average number of Risso's dolphins, *G. griseus*, stranded along the southeastern coastline of South Africa between 1970 and 2017 (*n* = 118).

Decade	Total stranded animals	Mean/annum (± *SD*)
1970–1979	17	1.7 ± 1.7
1980–1989	56	5.6 ± 4.7
1990–1999	36	3.6 ± 2
2000–2009	6	0.6 ± 0.7
2010–2017	3	0.4 ± 0.7

3.1 | Age and attainment of sexual maturity

In males, an increase of combined testis weight could be observed between 260 and 300 cm (Table 2), thus the mean length of 280 cm was taken as the onset of sexual maturity; this corresponded to an age of around 7 years when extrapolated from the growth curve (Figure 4; 290.88 × {1 − exp[−0.35 × (7.1 + 2.20)]} = 280.1 cm). The length of the smallest female that showed signs of being reproductively active (lactating and two corpora in its ovaries) was 264 cm (Table 3). The longest female with no evidence of reproductive activity was 301 cm. The mean length between those two females was 282.5 cm, and therefore all females smaller than 282 cm (Table 3) were considered sexually immature, which corresponds to 7.7 GLGs when extrapolated from the growth curve (Figure 4; 290.88 × {1 − exp[−0.35 × (7.7 + 2.20)]} = 282.2 cm). This is supported by additional females with total body lengths of 278 cm and an age estimate of eight GLGs and 257 cm and 7.5 GLGs, which showed zero and two corpora in their ovaries, respectively, while another female of 290 cm length with an age estimate of 7.5 GLGs had two scars in its ovaries (Table 3). Small sample sizes precluded a calculation of ovulation rate for the species, but a 9-year-old female with 11 corpora present in its ovaries (Table 3) suggests multiple ovulations occur at the onset of sexual maturity in this species as is common in many small cetaceans (Perrin & Reilly, 1984). Alternatively, it may indicate a failure to conceive in this individual.
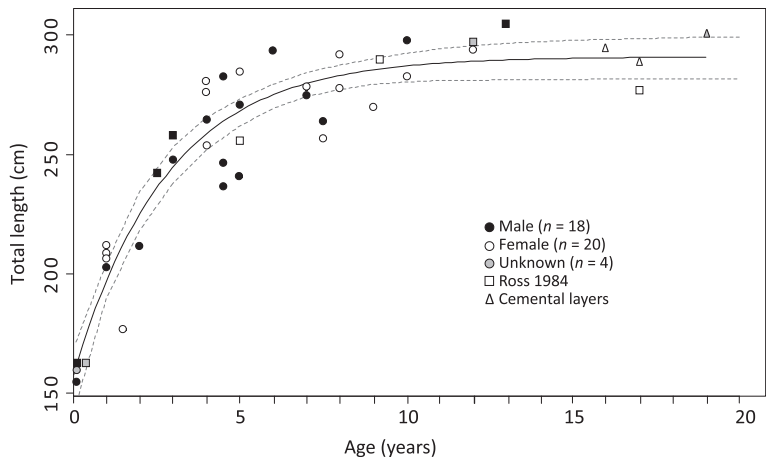
3.2 | Growth

Comparison of the different male and female von Bertalanffy growth models indicated that models which shared the same starting terms did not differ from models with sex-specific starting terms (Table 4). The absence of any statistical difference between the sex-specific models suggests similar growth rates for male and female Risso's dolphins off the southeast coast of South Africa (Figure 4). Body weights were only available for five individuals: two males

TABLE 2   Combined testis weights in relation to body length and age for male Risso's dolphins, *Grampus griseus*, from the southeastern coast of South Africa.

PEM No.	Total body length (cm)	Estimated age (GLGs)	Combined testis weight (g)
N14	264	7.5	180
N298	163	—	9.4
N697	283	4.5	108
N704	298	10	670
N710	248	3	47
N1218	325	—	4,545
N1982	135	—	12
N2613	185	—	13.2

FIGURE 4   Von Bertalanffy growth curve, $y = 290.88 \times \{1 - \exp[-0.35 \times (x + 2.20)]\}$, using growth layer groups (as proxy for age) for male and female Risso's dolphins, *Grampus griseus*, from the south-eastern coastline of South Africa (total $n = 42$; $n = 33$ for present study, $n = 9$ from Ross 1984). Dashed lines show 95% confidence intervals.

(142 cm weighing 28 kg and 302 cm weighing 302 kg) and three females (155 cm and weighing 42 kg, 278 cm and weighing 220 kg, 287 cm and weighing 250 kg); unfortunately, no age estimates were available for these individuals.

The von Bertalanffy growth curve estimated length at birth to be 158 cm (Figure 4), while data from stranded neonates in which fetal folds and umbilical cords were present indicated an average size at birth of 146.9 ± 15.9 cm ($n = 9$; 124–177 cm; Table 5). The oldest male for which an age estimate was available had 13 GLGs and measured 305 cm in length. The oldest female had 17 GLGs and was 290 cm in length (Figure 4); however, the oldest age estimate was obtained for a 300-cm-long animal of unknown sex, which had 19 cemental GLGs. Only four animals showed occluded pulp cavities, requiring an examination of the cemental GLGs. The asymptotic length (L_∞) for both sexes was estimated at 291 cm from the von Bertalanffy growth model (95% CI [281, 301.3]), and k was estimated at 0.35 (95% CI [0.25, 0.46]; Figure 4, Table 5).

3.3 | Stomach content analysis

In total, 77 stomachs were available for examination, of which 46 were empty and therefore not considered in the analysis. Two stomachs contained only the pelagic octopus *Japetella* sp., for which no length regression exists, and a further two samples had no associated information on the sex of the dolphins, thus these were excluded from

TABLE 3 Total corpora counts in relation to body length and age for female Risso's dolphins, *Grampus griseus*, from the southeastern coast of South Africa.

PEM no.	Total body length (cm)	Estimated age (GLGs)	Total number of corpora
N112	290	7.5	2
N117	256	—	0
N198	257	7.5	0
N319	254	4	0
N325	212	—	0
N700	270	9	0
N707	276	4	0
N772	285	5	0
N842	264	—	2
N1069	290	—	14
N1076	295	9	11
N1077	311	—	11
N1217	309	—	12
N1287	301	—	0
N1327	304	—	9
N1328	292	—	6
N1689	288	—	8
N1806	278	8	0
N2242	283	10	6
N2779	287	—	13
N2793	279	—	0

TABLE 4 Results from the likelihood ratio tests on the different sex-specific von Bertalanffy models fitted with nonlinear squares.

Tests	Hypothesis	Chi-squared	df	p
H_0 vs. H_1	$L_\infty(F) = L_\infty(M)$	0.58	1	.446
H_0 vs. H_2	$k(F) = k(M)$	0.3	1	.584
H_0 vs. H_3	$t_0(F) = t_0(M)$	0	1	1
H_0 vs. H_4	$L_\infty(F) = L_\infty(M)$, $k(F) = k(M)$, $t_0(F) = t_0(M)$	2.68	3	.444

Note: L_∞ = asymptotic length, k = growth constant, and t_0 = age that corresponds to zero length; (F) = females; (M) = males; df = degrees of freedom.

further analyses. Analyses were therefore conducted on the remaining 27 stomachs (10 immature males, five mature males, five immature females, and seven mature females).

In total, 19 cephalopod taxa were identified, 12 to species and seven to genus. Based on IRI, the three most important prey species in the diets of mature male Risso's dolphins were the three squid species *Lycoteuthis lorigera* (3,036.9), *Ancistrocheirus lesueurii* (2,737.2), and *Teuthowenia pellucida* (1,142.4; Table S1). Collectively, these three species represented 57.2% of the reconstituted weight of the diet of male dolphins (Table S1). *Ancistrocheirus lesueurii* and *Lycoteuthis lorigera* were the most frequently consumed prey items in mature male diets (75% frequency

TABLE 5 Life history parameters for Risso's dolphins, *Grampus griseus*, from the southeastern coastline of South Africa. GLGs: growth layer groups.

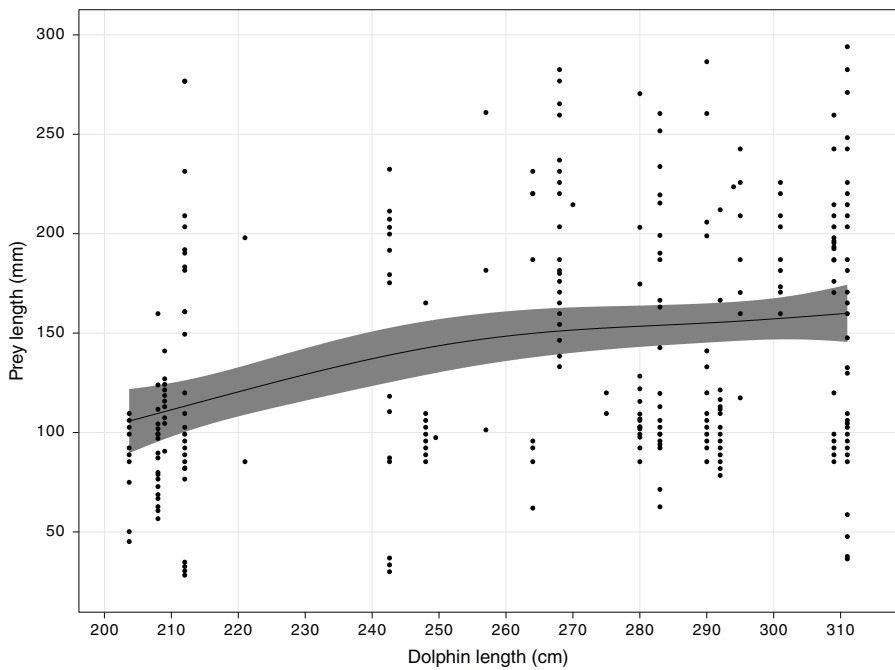| Parameter	
Shortest male	135 cm
Shortest female	124 cm
Longest male	325 cm
Longest female	313 cm
Length at birth:	
mean neonate length (*n* = 9)	146.9 cm
growth curve estimate (*L* at age 0)	158 cm
Length at sexual maturity (males)	280 cm
Length at sexual maturity (females)	282 cm
Asymptotic length (L_∞ both sexes)	291 cm
Growth rate constant (*k*)	0.35
Oldest male	13 GLGs, 305 cm
Oldest female	17 GLGs, 290 cm

FIGURE 5 Predicted values from the generalized additive model illustrating the relationship between dolphin length and prey length. The dots represent the observed data, the black line is the predicted trend line and the gray area presents the approximate 95% confidence intervals.

each; Table S1), although *Lycoteuthis lorigera* presented the highest percentage numerically (39.4%), while *A. lesuerii* made up the highest percentage in mass (37.2%; Table S1).

Mature females most often selected the squid species *Lycoteuthis lorigera* (3,732.7 IRI) and *Loligo reynaudii* (3,071.3 IRI), with the octopus *Enteroctopus magnificus* (1,551.8 IRI) also being well represented (Table S2).

TABLE 6 PERMANOVA results for the effects of sex and maturity on the stomach contents of Risso's dolphin, *Grampus griseus*. Pairwise analyses of prey items are between sexes within maturity levels (immature or mature) and between maturity levels within the different sexes.

	Source	df	PERMANOVA MS	Pseudo-F	P(perm)	Pairwise (sex comparison)	t	P	Pairwise (maturity comparison)	t	P
Abundance	Sex	1	3,197.9	0.9826	.4222	Immature	1.2089	0.179	Male	1.524	**.0365**
	Maturity	1	3,980.8	1.2231	.2604	Mature	1.3001	0.1247	Female	1.068	.3367
	Sex × Maturity	1	7,015.1	2.1554	**.0492**						
Biomass	Sex	1	4,139.1	1.2238	.2692						
	Maturity	1	5,963.3	1.7632	.0921						
	Sex × Maturity	1	6,253.1	1.8489	.0739						

Note. Values indicated in bold represent a significant effect. df = degrees of freedom; MS = mean square; Pseudo-F = F ratio; P(perm) = probability level based on permutations; t = t statistic.

TABLE 7 Diet overlap between different demographic groups of Risso's dolphins.

Group and no. of prey species found in diet	Group and no. of prey species found in diet	Total no. of prey species combined	Shared no. of prey species	% overlap
Adult males 10	Adult females 12	6	16	37.50
Adult males 10	Juvenile males 10	5	15	33.33
Adult males 10	Juvenile females 10	5	15	33.33
Adult females 12	Juvenile females 10	7	15	46.67
Adult females 12	Juvenile males 10	8	14	57.14
Juvenile males 10	Juvenile females 10	6	14	42.86

Enteroctopus magnificus and *Loligo reynaudii* comprised 38.3% and 32.0%, respectively, of the total weight consumed by mature females, while *Lycoteuthis lorigera* was the most frequently consumed prey item (62.5%; Table S2).

Immature male dolphins consumed mainly *Loligo reynaudii* (5,925.3 IRI), followed by *Lycoteuthis lorigera* (3,217.4 IRI) by IRI (Table S3). Although both in terms of frequency (60% for both) and numerically (41.8% and 42.6%, respectively) these two species contributed a similar percentage to the diet, *Loligo reynaudii* made up a substantially larger amount of the diet in mass (57%) than *Lycoteuthis lorigera* (11%; Table S3).

In contrast to the mature female and male dolphins, the diet of immature females consisted mostly of *Cranchia scabra* (2,475.2 IRI), *Lycoteuthis lorigera* (1,609.7 IRI) and also *Octopoteuthis* sp. (1,584.6 IRI; Table S2). *Cranchia scabra* was not only numerically the most important prey item in the diet of immature females, but was also observed in four out of five immature female stomachs (Table S4). Compared to the diets of immature and mature males, two prey species that were of high importance, *Loligo reynaudii* and *A. lesueurii*, were very rarely selected by immature females (IRI: 568.8 and 44.3, respectively; Table S4). However, immature female *G. griseus* was the only group that had been feeding on Sepiids (Table S4).

To determine whether the length of the prey increased with the total length of the dolphin, we employed a GAM. Initially, sex was included as a covariate (Equation 3), but no effect of sex on the relationship between prey and dolphin length was observed ($F_1 = 0.41$; $p = .522$). The results from the GAM, excluding the covariate sex, indicated an initial significant positive relationship between prey length and dolphin length, which plateaued at a dolphin length of about 270 cm and prey length of roughly 150 mm ($F_{2.032} = 11.46$; $p < .001$; Figure 5).

The PERMANOVA analysis on the stomach contents of Rissos's dolphins indicated a significant interaction effect between sex and maturity for the abundance data (Table 6). Pairwise analyses between mature and immature dolphins within the factor "sex" indicated significantly different diets for the male dolphins, but no difference was found between the mature and immature females (Table 6). When considering dietary overlap, immature and mature males only shared 33% of the species in their diet, compared to immature and mature females, which shared 47% of the species in their diet (Table 7).

4 | DISCUSSION

The present study allowed the establishment of age and growth parameters for Risso's dolphins for the subregion and refines previous life history parameters made by Ross (1984), which aided our understanding of the life history of *Grampus* worldwide. Although the earliest reported stranding of a Risso's dolphin along the southeastern coastline of South Africa was in 1958, reliable stranding response effort only started in the late 1960s and thus the majority of length measurements are available from then onwards (Figure 3). The apparent drop-off in strandings after 2000 (Table 1) may be indicative of the "beach ban" of vehicles driving on the beach, implemented in 2002 (Republic of South Africa, 2001), which may have led to a reduction in strandings being reported, particularly in remote areas. In addition, the "chokka" squid, *Loligo reynaudii* forms an important component of the diet of Risso's dolphins found off South Africa (see below) and a significant decline in catches of the chokka squid fishery in 2013 along the Eastern Cape coastline (Githaiga-Mwicigi & van der Westuizen, 2017), indicative of reduced numbers of squid, may have resulted in Risso's dolphins foraging further offshore, rendering them less prone to strand or wash up dead.

4.1 | Life history parameters

Data on the length at sexual maturity for male *G. griseus* are variable. Ross (1984) suggested maturity occurs between 260 and 300 cm based on histological and macroscopic data from two males from southeastern South Africa and other published data from populations elsewhere. The 280 cm estimated in the present study falls in the center of this range. Males from Japanese coastal waters are reported to attain sexual maturity at 270 cm, corresponding to 10–12 years of age (Amano & Miyazaki, 2004); the latter is somewhat higher than the seven years estimated for attainment of sexual maturity in males for the present study. In contrast, Aguayo-Lobo (1975) and Leatherwood and Reeves (1987) concluded that males reach sexual maturity at 300 cm, which is the same as Best (2007) suggested for animals from South Africa.

The length at sexual maturity for females in this study (282 cm) refines the previous estimate for a subset of the present sample analyzed by Ross (1984), which suggested sexual maturity occurred between 257 cm and 277 cm. Bloch et al. (2012) reported similar values of between 268 cm and 277 cm for animals from the Faroe Islands as did Amano and Miyazaki (2004) with 270 cm for Japan. By contrast, Best (2007) suggested 280 cm for length at sexual maturity, while it was estimated to occur between 240 and 255 cm for animals from Taiwan (Chen et al., 2011). Our estimated age at sexual maturity for female Risso's dolphins of 8 years agrees with Bloch et al. (2012), who indicated sexual maturity for females between 2 and 8 years from a similarly small sample size. Other studies suggest between 8 and 10 years of age for females from Japan (Amano & Miyazaki, 2004) and 10 years for females from Taiwan (Chen et al., 2011).

Data available on length at birth for Risso's dolphins are sparse, particularly for the Southern African subregion. Ross (1984) states that length at birth is unknown, while Best (2007) suggests 130 cm based on an estimate determined from a single calf. In the present study, length at birth, as estimated by the von Bertalanffy growth curve, was 158 cm for both sexes combined; this might be somewhat of an overestimate, since the average length of nine neonates is 146.9 cm (range 124–177, *n* = 9), although it is possible that some of these specimens may have been

aborted fetuses close to term. Perrin and Reilly (1984) estimated length at birth to be between 110 and 150 cm based on the available literature at the time. The shortest male neonate in the present study measured 135 cm and the shortest female 124 cm, which fall well within the range published by Perrin and Reilly (1984) and add new information for length at birth for Risso's dolphins from Southern Africa.

Both the maximum recorded lengths (325 cm for males and 313 cm for females) and minimum recorded lengths (135 cm for males and 124 cm for females) for stranded Risso's dolphins along the southeastern coastline of South Africa suggest that males are longer than females. This is in line with previous data from Best (2007), who reported that 20% of males recorded from the South African coastline exceeded the longest female in length, concluding that the species has sexual size dimorphism. Comparisons of the sex-specific von Bertalanffy models in the present study, however, found no statistically significant difference between males and females, suggesting an absence of sexual dimorphism as was also suggested by Ross (1984) for 19 males and 14 females from the same sample. Kruse et al. (1999) report a lack of evidence for sexual dimorphism for the species as do Chen et al. (2011) for Taiwan. By contrast, males grow larger and become heavier than females off the Faroe Islands (Bloch et al., 2012). Both the relatively small sample size as well as the skewedness of the sample towards mature females and immature animals of both sexes in the present study (Figure 4) may explain the conflicting conclusions regarding sexual size dimorphism for the species off southeastern South Africa. The social structure of the species may be such that mature and thus larger males may be solitary or form separate groups and consequently be found elsewhere as studies by Hartman, Visser and Hendricks (2008) and Hartman, Fernandez and Azevedo (2014) suggest. As a result, mature males may have a more offshore distribution than mature females and immature animals of both sexes and subsequently may not strand as frequently. In addition, strandings from the Western Cape may be part of a different population to the one found off the Eastern Cape and KwaZulu-Natal, as was previously suggested for striped dolphins *Stenella coeruleoalba* (Conry, Pistorius, Plön, & Hofmeyr, 2016).

Based on anecdotal evidence, Aguayo-Lobo (1975) reported that Risso's dolphins live for at least 24 years. Amano and Miyazaki (2004) reported maximum GLG readings of 16.5 and 34.5 years for males and females, respectively, while Kruse et al. (1999) suggested at least 30 years for males. Similarly, Bloch et al. (2012) reported maximum ages of 27 years for males and 31 years for females from the Faroe Islands. In our study, the oldest specimen (19 years) was an animal of unknown sex, measuring 300 cm in length. Considering that the species attains body lengths of up to 325 cm off south-eastern coastline of South Africa (Ross, 1984), and thus this specimen was not fully grown, these animals could have a longer life expectancy than suggested by the maximum age estimate determined in the present study.

It is worth noting that all studies conducted on age determination of Risso's dolphins report higher maximum age estimates for females than males (Amano & Miyazaki, 2004; Bloch et al., 2012; present study). Again, this may be indicative of the social segregation that has been suggested for the species, with mature males forming separate groups (Amano & Miyazaki, 2004; Bloch et al., 2012; Hartman et al., 2008, 2014). The skewedness of the present sample towards mature females and immature animals of both sexes would support such a scenario and explain the higher age estimates for female Risso's dolphins.

The asymptotic length of animals from the present study was estimated as 291 cm by the von Bertalanffy equation. This estimate is close to the asymptotic body length of 270 cm suggested for both sexes of Risso's dolphins off Japan (Amano & Miyazaki, 2004), although both studies lacked old males. In the present study, the largest Risso's dolphin recorded for southeastern South Africa was a male of 325 cm (Ross, 1984). Maximum lengths for the species have been reported to be between 380 cm and 400 cm (Aguayo-Lobo, 1975; Jefferson et al., 1993; Leatherwood & Reeves, 1987), although for South African specimens these were 341 cm for males and 318 cm for females (Best, 2007). It has been previously suggested that Risso's dolphins in South African waters may be smaller than elsewhere (Chen et al., 2011; Ross, 1984). In addition, the differences in length at birth and maximum body length between individuals from the Western and Eastern Cape may also point to different populations being present in the southeast Atlantic vs. the western Indian Ocean, respectively, as seen for other small odontocetes off South Africa (Conry et al., 2016). Chen et al. (2011) found that although the body size of the South African population is not significantly

different from the populations off Japan and Taiwan, all three populations showed smaller specimens than those from the northeast Pacific, northeast Atlantic, and the Mediterranean. Consequently, the degree of sexual dimorphism may also vary with population. However, an alternative is that this is due to small sample sizes for particular age classes.

4.2 | Diet

The preferred prey of cephalopods for Risso's dolphins reported in the present study is in agreement with data from stranded and incidentally caught individuals off Taiwan (Wang, Shao, Huang, & Chou, 2012). Studies of Risso's dolphin from the west coast of South Africa suggest that, in terms of number of items, Risso's dolphins feed preferentially on *Todaropsis eblanae*, *Loligo reynaudii*, *Argonauta nodosa*, and *Argonauta argo* (Best, 2007), although *Octopus* sp. and the anchovy *Engraulis capensis* were also considered important in terms of reconstituted mass (Sekiguchi et al., 1992). The inclusion of pelagic fish species and feeding on different cephalopods in that study is likely a reflection of the relative abundance of prey off the west coast.

The stomach content analysis for Risso's dolphins in the present study shows some contrasting results. Comparison of Indices of Relative Importance indicates that immature female dolphins have a "unique" diet, selecting smaller cephalopod species, such as *Cranchia scabra* and those from the Order Sepiida (Table S4). However, the multivariate analyses (PERMANOVA) failed to show a difference in the diet of mature and immature female dolphins, but showed a difference between the diets of the immature and mature males (Table 6). The validity of gut contents collected from stranded cetaceans as being representative of their normal diet has long been debated (De Pierrepont, Dubois, Desormonts, Santos, & Robin, 2005; Ross, 1979). Nonetheless, our data show that mature males and females select similar prey with some indication of possible ontogenic shifts in diet, especially in males. The two most important squid species consumed by males (both immature and mature) and mature females were *Loligo reynaudii* and *Lycoteuthis lorigera*, but were not of particular importance in the diet of immature females. Smaller cephalopod species, such as *Cranchia scabra* and those from the Order Sepiida, were only consumed by immature females (Table S4). In contrast, the diet of mature males indicated that species from the Order Octopoda constituted 29.3% of the total mass consumed (Table S1). Species from this order are generally considered large cephalopods; for example, *Octopus vulgaris* may reach weights of 4 kg in 290 days (Smale & Buchan, 1981). *Enteroctopus magnificus* is commonly taken in deeper continental shelf waters and attains a mantle length of at least 36 cm and a mass of at least 12 kg (Roeleveld, 1998; Villanueva, Sánchez, & Roeleveld, 1991). These larger species were absent from the diet of immature males, supporting the idea that differential selection of prey is related to ontogeny, with the immature animals taking smaller prey than the mature ones (Tables S1–S4). This supports previous findings of Cockcroft et al. (1993). Additional work in odontocetes using isotopic signatures from teeth has shown ontogenetic diet shift associated with preweaning (suckling) to post-weaning (Evacitas et al., 2017; Knoff, Hohn, & Macko, 2008; Niño-Torres, Gallo-Reynoso, Galván-Magaña, Escobar-Briones, & Macko, 2006), but few studies were able to show a change in diet from immature to mature age classes using stomach content analysis due to restrictions in sample size. In the present study, we expected an increase in prey length with increase in dolphin length, since ontogenetic shifts in diet are often related to a change in prey size. Our results did indicate some compositional changes in diet related to ontogeny, and also found that smaller dolphins fed on smaller prey and that prey size increased with increasing predator (dolphin) body length (Figure 5).

Initial work by Ross (1984) suggested that Risso's dolphins occur in small groups that are often part of a larger, widespread aggregation, possibly indicating segregation by sex and/or size. As the majority of stranding events analyzed in the present study involved single individuals, little can be said about segregation by sex and age for the species off the southeast coast of South Africa, as has been suggested elsewhere (Bloch et al., 2012; Hartman et al., 2008; Hartman, Fernandez, Wittich & Azevedo, 2015). In the Azores, individuals form long-term bonds of 2–12 animals of the same sex and similar age (Hartman et al., 2008) and exhibit sex-related differences in residency patterns

(Hartman et al., 2015). The data presented here on differences in diet between the sexes and age groups support a similar scenario off South Africa, with larger males potentially feeding further offshore due to social segregation. Risso's dolphins tend to remain with their natal group after weaning and leave later to form groups of immature animals at approximately 5 years of age (puberty; Amano & Miyazaki, 2004). Postweaning differences in stable isotope ratios between male and female Risso's dolphin from Taiwan reported by Evacitas et al. (2017) indicate that after leaving the natal group, males feed on different prey and/or utilize different foraging areas than females. This is supported in the present study by the significant difference between adult and juvenile male diets (Table 6).

Future studies on the feeding ecology and life history of Risso's dolphins off South Africa should attempt to examine ontogenetic changes in diet utilizing stable isotope data from GLGs to assess changes reported here on a finer scale. Historical data on stable isotope signatures of potential prey items could assist in this respect.

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