Advances in MARINE BIOLOGY

SPECIAL VOLUME ON *KOGIA* BIOLOGY: PART 3

VOLUME 100

Edited by
Stephanie Plön

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VOLUME ONE HUNDRED

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Special Volume on *Kogia* Biology: Part 3

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Special Volume on *Kogia* Biology: Part 3

Edited by

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Preface

As we are now into its unexpected third Part of the Special Volume on *Kogia* Biology (originally only one Part was planned), a preface to the series is overdue.

Sperm whales present one of the most interesting taxa within the Cetacea - and the genus *Kogia*/family Kogiidae is even more fascinating. Having originally started on a completely different project, I ended up studying the life history of both *Kogia* species more or less by accident as this was simply the group for which there were the most samples available. Globally, South Africa along with Florida (USA), Japan and New Zealand, present stranding hotspots for the two species, but despite this, little remains known about the life of these two small, offshore, predominantly solitary species.

My research allowed me to gain new insights into stranding patterns along the South African coastline, the age structure of stranded animals, as well as the reproductive biology, diet and even the population genetic structure of the two species in the Southern Hemisphere (Plön et al., 2023). This was largely based on Ross' (1979, 1984) seminal works on the species from South Africa, but also other student research works from Florida, USA. It was an exciting journey to be able to study most of the life history of previously little known mammals. And after more than 20 years of being interested in all things related to *Kogia*, these critters never cease to surprise.

Unlike other odontocetes of similar size, we see an accelerated life history, high reproductive rates and a short lifespan (Plön et al., this volume) in these species, a diverse diet consisting mainly of cephalopods that live between 500 and 800m depth (Beatson 2007, Staudinger et al., 2013, West et al., 2009) and a unique microbiome (Erwin et al., 2017) which may, in part, explain the unusual 'inking' behaviour observed in the genus (Scott et al., 2001, Plön, 2022). But other aspects of the biology of these species are equally as puzzling, for example the observed host-parasite interactions (Keenan-Bateman et al., 2016). And all this in species which are notoriously difficult to study at sea (Hodge et al., 2018) due to long and deep dives and a low profile while 'logging' on the surface (Baird et al., 2022).

Kogia are not species that are high on the conservation agenda nor do they have a 'cutsie' factor, which puts them high on the research agenda. Nevertheless, their intriguing lifestyle demands to keep them in the 'desirable-to-study' drawer as one may never know what exciting new

knowledge may be discovered. Thus, for the Special Volume on their biology (four parts in total), I aimed to bring to light new information on the genus and contaced a number of colleagues whom I suspected to have substantial data on the genus, which may simply not see the publishing light as too many other things keep them busy. Subsequently, we have been able to publish contributions from diverse regions, such as Japan, the Carribbean, the Canary Islands and the Indian Ocean, and on such diverse topics as molecular analysis of population structure, parasites, diet, behaviour, stranding patterns and facial hair follicles. With a fourth (and likely final!) part still planned for early 2026, there will be more exciting information and new insights emerging into the fascinating biology of these two, still little known whale species.

Stephanie Plön
Husum, Germany, 22. June 2025

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CHAPTER ONE

Historical data on age, growth and reproduction of pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whales stranded along the Southern African coastline, with additional information from Australian specimens

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Abstract

South Africa has one of the highest stranding records in the world for both pygmy (*Kogia breviceps*) and dwarf (*K. sima*) sperm whales and as such offers a unique opportunity to study these little-known species. Data and samples from animals stranded along the South African and Namibian coastline between 1960 and 1999 were analysed to determine basic life history parameters for the two species.

Teeth from 80 *K. breviceps* and 45 *K. sima* from South Africa and an additional 27 *K. breviceps* and one *K. sima* from Australia were available for age determination. A good correlation between cemental and dentinal age estimates was found for both species, although cemental readings may not be as reliable in *K. sima* as they are for *K. breviceps*. Length at birth for *K. breviceps* was about 120 cm and the weight around 53 kg, while it was about 103 cm and 14 kg for *K. sima*. The asymptotic length for *K. breviceps* was calculated as 306.04 cm by 286.08 cm for females and males. Assuming one growth layer group (GLG) to be equal to one year, both sexes reached physical maturity at about the same age of 15 years. A life expectancy between 16 and 23 years was determined for the species.

For *K. sima*, the asymptotic length was 249.14 cm in females and 263.75 cm in males. This corresponds to 13 and 16 years of age for females and males, respectively. A life expectancy of 17–22 years was determined for *K. sima*. Reversed sexual dimorphism is suggested for *K. breviceps*, while there appears to be little size difference between the sexes in *K. sima*.

Reproductive organs from 19 male and 25 female *K. breviceps* and 19 male and 26 female *K. sima* were examined to determine reproductive status. The onset of sexual maturity was estimated to be at about 262 cm and around five years in female *K. breviceps* and at about 215 cm and around five GLGs in female *K. sima*.

The ovulation rate of 0.9 per year for *K. breviceps* indicated that, on average, ovulations occurred about every 13.3 months. The gestation length is approximately 11 months and conceptions occur from April to September and births possibly occurring from March to August in *K. breviceps*.

In *K. sima*, the ovulation rate of 0.7 per year indicates that ovulations occur about every 17.1 months (or roughly one and a half years) and gestation length is 11–12 months. Both conceptions and births occurred between December and March and 11.5 % of mature females were found to be simultaneously lactating and pregnant. These data indicated that *K. sima* may also show annual reproduction, if the conditions are right, although that may be facultative and some animals may only reproduce every two years. The reproductive strategy determined for both *Kogia* species indicated that a relatively high percentage of females was simultaneously lactating and pregnant, but the accumulation rate of *corpora* showed that although *K. breviceps* may have an annual reproduction, at least some *K. sima* females may only reproduce every two years. Both species exhibited seasonal reproduction, but while *K. breviceps* appeared to have a protracted mating and calving season of six months, *K. sima* exhibits a shorter mating and calving season over the period of four months with births occurring during the warmest part of the year.

Reproductive organs from 19 *K. breviceps* and 19 *K. sima* males were examined to determine their reproductive status. In male *K. breviceps,* attainment of sexual maturity (ASM) occurred between 2.5 and 5 years, 241–242 cm and 210.0–233.6 kg, while it occurred between 2.55 and three years of age in male *K. sima*, a body length of 197 cm and body weights between 111.8 kg–124.0 kg. The maximum combined testis weight made up 1.04 % of the total body weight in *K. breviceps* and 2.00 % in *K. sima*. Based on data on testes size, sexual size dimorphism, signs of intraspecific fighting, and group size a polygynous mating system with a roving male strategy was proposed for both species.

1. Introduction

Little is known about the natural history of pygmy (*Kogia breviceps*) and dwarf (*K. sima*) sperm whales. The holotype of a pygmy sperm whale was described by de Blainville in 1838 from a skull found at the Cape of Good Hope (Ross, 1979). Since then more information about the genus *Kogia* has been gathered, mainly from occasional strandings around the world (Hale, 1947, 1959, 1962, 1963; Caldwell et al., 1960, 1973; Omura and Takahashi, 1981;

Sylvestre, 1983, 1988; Pinedo, 1987; Baccetti et al., 1991; Baird et al., 1996; Valverde and Caminas, 1996), although in recent years the number of studies in the wild has increased (Baird et al. 2022; Dulau et al., 2024; Kiszka et al., 2024; Martin et al., 2024). Both *Kogia* species occur in temperate, subtropical and tropical waters of both the Northern and Southern Hemisphere, with *K. sima* preferring slightly warmer waters (Leatherwood and Reeves, 1983; Carwardine, 1995; Baird et al.,1996). While juvenile and immature animals of *Kogia*, particularly those of *K. sima*, are thought to live closer inshore than adults, probably over the outer part of the continental shelf and upper part of the slope, adults are found over deeper water (Ross, 1984). Up to seven species of *Kogia* were described (Flower and Lydekker, 1891) until Handley (1966) delineated two distinct species. The most comprehensive work on the biology and natural history of these two species to date was carried out by Ross (1979, 1984), who examined specimens from Southern Africa. Although previously thought to be rare, increasing evidence from cetacean surveys, locally high stranding rates, and a number of field studies suggest that the two species are quite common locally, although somewhat elusive due to their shyness and diving behaviour (Barlow and Sexton, 1996; Credle, 1988; Hodge et al., 2018). *K. breviceps* is reported to be the most commonly stranded cetacean along the Florida coastline after the bottlenose dolphin *Tursiops truncatus* (Odell et al., 1984; Hodge et al., 2018) and along the New Zealand coastline (Tuohy et al., 2001) and high stranding rates have also been reported for Japan (T. Yamada, *pers. com.*). South Africa has a high stranding rate for both *Kogia* species and thus offers opportunities for further studies on the natural history of the genus. These investigations are a necessary prerequisite if we are to find out more about the population dynamics of these animals and the possible effects of habitat destruction, pollution, overfishing and other anthropogenic activities.

For the present study, data and samples for both *K. breviceps* and *K. sima* stranded along the entire South African coastline and part of the Namibian coast between 1960 and 1999 were examined to determine basic life history parameters for the two species.

2. Materials and methods

2.1 Study area

Data and samples for the two *Kogia* species stranded between 1960 and 1999 and held in the marine mammal collections of the Port Elizabeth Museum (Graham Ross Marine Mammal Collection), Port Elizabeth/Gqeberha, and

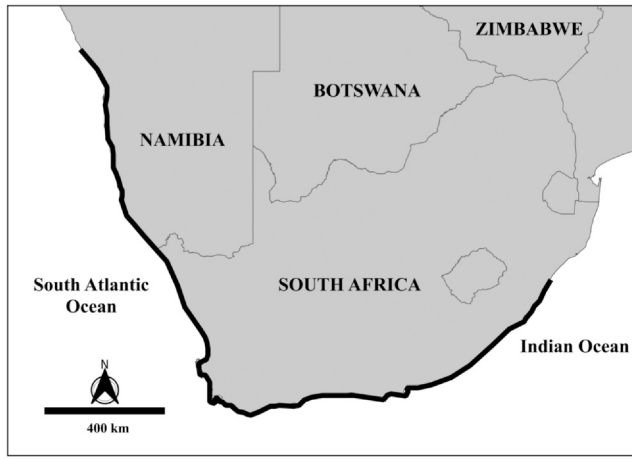

Fig. 1 Study area, stretching from Dunrissa Bay, Namibia, in the West to Central Beach Durban, South Africa in the East.

the South African Museum/Iziko Museum in Cape Town were analysed. The location of the strandings extend from Dunrissa Bay in Namibia on the western Southern African coastline (21°15′S and 13°14′E) to Central Beach, Durban, on the east coast of South Africa, approximately 500 km south of the border with Mozambique (29°50′S and 31°02′E; Fig. 1).

2.2 Sample

Standard length and weight measurements of stranded specimens were taken upon necropsy (following Norris, 1961) and the sex was determined. Teeth were extracted and stored dry after maceration. Reproductive organs were collected and preserved in 10 % buffered formalin.

For *K. breviceps*, teeth from 62 animals and reproductive organs from 41 animals (22 females, 19 males) were examined, whereas for *K. sima*, teeth from 48 animals and reproductive organs from 43 animals (24 females, 19 males) were analysed. In some cases, the original tissue samples were not available, but weights and measurements were obtained from data sheets, accounting for discrepancies in sample sizes between tables and figures. To increase the sample size, results from Ross (1979, 1984) were included in the analyses. Furthermore, teeth were also available for 24 *K. breviceps* (12 females, 12 males) and one *K. sima* female from Australia.

The length-frequency distribution of the available sample showed a clear bias towards females between 300–320 cm in total body length and males

between 180–200 cm in *K. breviceps*. This has to be kept in mind during further analyses. For *K. sima,* however, no skewness could be determined in the sample; males stranded most frequently around 220 cm total body length, while females stranded most frequently at around 240 cm.

2.3 Age determination

One tooth was selected per animal for age determination and teeth were selected on the basis of greatest size, least curving (in no more than one plane), and least wear. Due to the curvature of *Kogia* teeth, best results were obtained when teeth were ground down from either side towards the midline by hand. Teeth were ground into 300 μm thick longitudinal sections using waterproof silicon carbide paper, initially to a thickness of 1300 μm using grit size P120, then to 500 μm using grit size P320. Ground sections were stored in absolute alcohol overnight, cleared in xylene for five minutes and mounted on slides using DPX mounting medium.

A dissecting microscope with polarizing filters was used to count the growth layer groups (GLGs) using 6x magnification for *K. breviceps* sections and at 12x magnification for *K. sima*. Dentinal layers were read as complete GLGs plus an increment consisting of the last incomplete layer. For this, the last complete GLG was measured using a micrometer under 12x magnification and the increment was calculated as a percentage of the last complete GLG. Cemental GLGs were read at a magnification of 40x.

To obtain an age estimate for teeth with osteodentine, the number of GLGs occupied by the osteodentine was estimated by measuring the length of the part of the tooth occupied by secondary dentine divided by the mean width of the last three complete GLGs prior to the osteodentine as an estimate of the mean GLG width. In addition, counts of cemental GLGs were also carried out in those teeth and for specimens with a closed pulp cavity.

For animals with less than one GLG, the average width of the first GLG was determined from animals between one and two years of age. Then the increment of dentine laid down after the neonatal line was measured and used to calculate the age as a percentage of an average GLG.

Tooth sections were read five times by each of two independent observers (WHO and SP) and the trimmed mean values of both dentine and cementum readings were calculated. Only estimates within 15 % of each other were used. If no clear neonatal line was visible due to tooth wear, the first layer was assumed to be the first GLG. Cemental layers were only read by a second observer (WHO) when osteodentine was present. In these cases the cemental readings were used as age estimates.

If GLG counts were not within 15 % of each other, revised counts were carried out by the two observers and an agreement on the age estimate was reached. Tooth sections were read 'blind' i.e. without any additional information on the specimens, such as body length, which could have influenced the counts.

Two methods for age estimation were examined. Method 1 examined the correlation between cemental and dentinal readings where only complete GLGs were counted. Method 2 examined the correlation between cemental readings and complete GLGs plus an increment. In teeth where the pulp cavity was closed, the cemental reading was taken as an estimate of age. The percentage closure of the pulp cavity was calculated by measuring the length of the open pulp cavity as a percentage of the total length of the tooth. For this exercise, only animals with pulp cavities that appeared just closed were included; no animals with extensive osteodentine were included.

Although GLGs have not been calibrated in either species of *Kogia,* it is assumed that one GLG is laid down per year as this was found to be the case in other odontocete species for which calibration of GLGs have been carried out. Therefore, subsequently GLGs and years may be used interchangeably.

2.4 Growth curve

To obtain growth curves for both species, the estimated ages of the animals were plotted versus body length. The computer package 'PC-Yield II', Version 2.2 (Punt, 1992) was used to fit the von Bertalanffy equation to the data as this gave the best fit. The growth model was used to provide data on asymptotic length (or length at physical maturity) and age.

The von Bertalanffy equation describes the growth curve as follows:

$$l(t) = L_{\text{inf}} \left(1 - e^{-k(t-t_0)}\right)^p$$

where:

L_{inf} is the asymptotic length or mass.
k is the constant of metabolism or growth constant.
t_0 is the age corresponding to zero length.
p is the power constant.

2.5 Reproductive biology

2.5.1 Females

Reproductive organs from 25 female *K. breviceps* and 26 female *K. sima* from South Africa were examined to determine the reproductive status of the individual animals.

Ovaries were weighed, sectioned at 1 mm intervals and examined macroscopically. The total number of *corpora lutea* (CLs) and *corpora albicantia* (Cas) per ovary as well as the overall number of *corpora* per animal was recorded. Since *corpora atretica* result from non-ovulatory events (Best, 1967; Perrin and Donovan, 1984) these were not included in the *corpora* count. The total *corpora* count was plotted versus the length and age of the animals to determine the onset of sexual maturity. Where possible, the total number of *corpora* in the left ovary versus the total number of *corpora* in the right ovary was also recorded. The length, height and width of the CLs and the largest CA were measured using vernier callipers and a *corpus* index (mm^3) was calculated for each (after Cockcroft and Ross, 1990).

The reproductive condition of the females (i.e. lactating and/or pregnant) at the time of stranding was recorded as was the total length, weight and sex of the foetuses. Lactating females and calves that stranded together were considered cow/calf pairs (sensu Cockcroft and Ross, 1990). If the larger female was not lactating, but both animals stranded in the same location on the same date or a few days apart, they were considered possible cow/calf pairs. The same was assumed for some refloated animals, where definite relationships could not be established.

To examine the seasonality of mating and calving in *K. breviceps,* three foetuses and 11 juveniles from Australia were included in the sample as they originate from the same hemisphere and should thus reflect the same seasonality. Although age estimates were only available for eight of the 11 juveniles, the other three individuals were included as their lengths fell within the range for animals up to and including two years of age as indicated by the growth curve (i.e. 210 cm). Similarly, four South African juveniles with no age estimate were included. For *K. sima,* age estimates were only available for three South African juveniles. However, the total lengths of the remaining four juveniles fell within the range for animals up to and including two years (i.e. 160 cm) and were thus included in the analysis.

2.5.2 Males

Reproductive organs from 19 *K. breviceps* and 19 *K. sima* were examined to determine the reproductive status of the individuals.

Testes were weighed (to the nearest 0.01 of a gram) and a piece of tissue (about 1 cm^3) was taken from the centre of the testis. The tissue was dehydrated in a standard alcohol series (30 % to 100 %), embedded in Paraffin

wax, sectioned at 5 μm and subsequently stained with Mayer's haematoxylin and eosin. Slides were examined to determine the reproductive status of each animal. Twenty randomly selected sections through seminiferous tubules were investigated and specimens were defined as either immature (spermatogonia and Sertoli cells in the seminiferous epithelium), in early spermatogenesis (spermatogonia and spermatocytes present in the seminiferous epithelium, but no spermatids), or in late spermatogenesis (spermatids present in the seminiferous epithelium; see Plön and Bernard, 2007). A specimen was categorized accordingly if more than 50 % of the tubules were in a particular condition. Individuals in late spermatogenesis were considered adults. Seminiferous tubule diameters were measured using an ocular micrometer. Mean diameters were taken as the average of 20 randomly chosen tubules. For two animals from each species these data could not be obtained due to extensive tissue damage, probably as a result of decay prior to sampling, or freezing subsequent to sampling. For three *K. sima* males, for which no testis tissue was available for histological examination, body length and testis weight were used as indicators of the stage of maturity.

An index of testis development was calculated as the mean testis weight (in g, excluding the epididymides) divided by the mean testis length (in mm) per testis pair (Hohn et al., 1985; Desportes et al., 1993).

2.5.3 Testis size and male mating strategy

The combined testis weight as a percentage of the total body weight was calculated for the animal with the largest testes for each species. In addition, photographs of stranded animals of both *Kogia* species were examined to determine the degree of intraspecific scarring.

3. Results

3.1 Sample

Strandings of *K. breviceps* along the Southern African coastline show a clear bias towards immature males and mature females (Fig. 2). Females measuring between 300–320 cm stranded most frequently, whereas males between 180 to 200 cm stranded most frequently. For *K. sima,* males measuring around 220 cm stranded most frequently, whereas for females this was around 240 cm (Fig. 3).

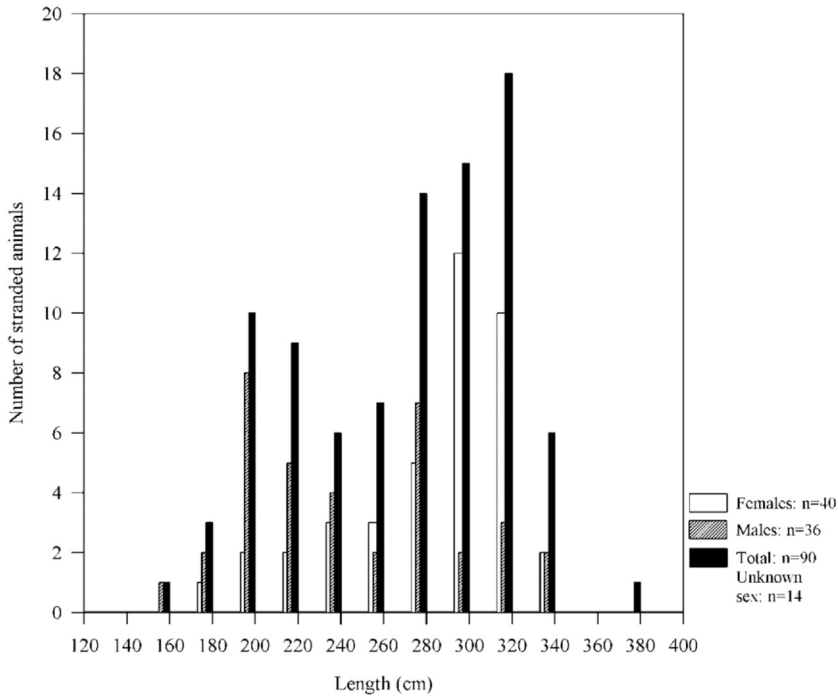

Fig. 2 Size-frequency of *Kogia breviceps* strandings.

3.2 Age determination

3.2.1 Tooth structure

In *Kogia* teeth, GLGs are arranged in a chevron pattern, similar to that found in the sperm whale *Physeter macrocephalus* (Fig. 4). The GLGs were composed of a broad opaque band and a narrow translucent band with numerous and conspicuous accessory layers as reported previously by Ross (1979). This differs from dolphin teeth, which have finer accessory layers.

The neonatal line and other laminae in the teeth of *K. sima* appeared fainter than in *K. breviceps*, which, together with their smaller size, made teeth of *K. sima* more difficult to read.

An enamel cap was found in some of the teeth of younger animals contrary to previous reports (Ross, 1979). However, this appeared to be more common in the Australian specimens, where it was found in two female *K. breviceps* specimens with 0.37 and 0.18 GLGs and a total length of 160 cm and 157 cm, respectively. In two Australian *K. breviceps* males, the enamel cap was partly worn away; these animals had 0.9 and 0. 7 GLGs present and measured 172 cm, while for the latter no length data were

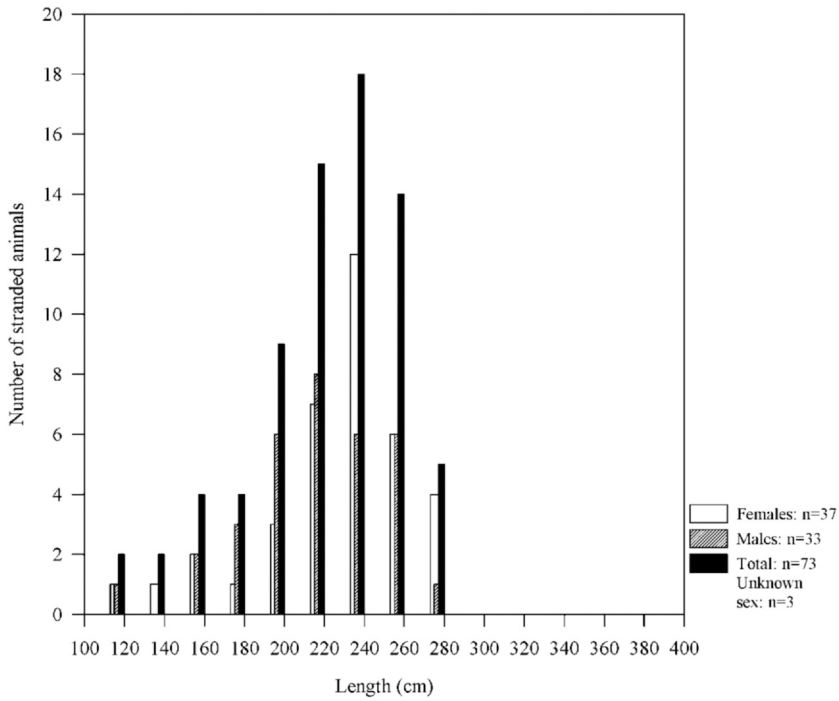

Fig. 3 Size-frequency of *Kogia sima* strandings.

available. Thus it appears that by approximately one year of age, the enamel cap is worn away in this species.

For *K. sima,* only one specimen from South Africa with two GLGs showed an enamel cap. Another *K. sima* from Australia showed an enamel cap and had a GLG reading of 8 and measured 216 cm; however, this appears to be an outlier.

In general, the tooth sections obtained from the Australian specimens were easier to read than those from the South African specimens as the GLGs appeared much clearer and more distinct.

The mean width of the first GLG for animals between one and two GLGs was determined and then used to calculate age estimates for animals, which had less than one GLG present in their dentine (Table 1).

3.3 Cemental versus dentinal GLGs

3.3.1 Kogia breviceps

Cemental readings were plotted against dentinal readings of complete GLGs only (Method 1) as well as complete GLGs plus increment (Method 2; Fig. 5).

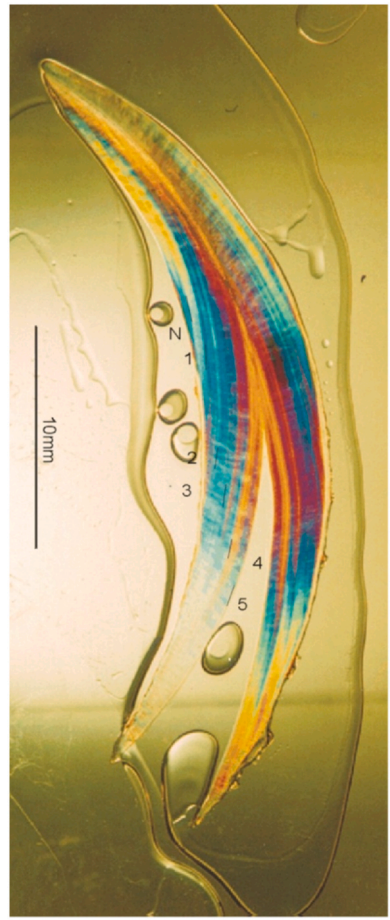

Fig. 4 Longitudinal section of a *Kogia breviceps* tooth viewed under translucent and polarized light (magnification: x12). The animal was estimated to be five years old; the bars on the photograph indicate the neonatal line (N) as well as the five GLGs (1 to 5, respectively).

Both methods showed a high correlation for both South African (method 1: $r^2 = 0.89$; method 2: $r^2 = 0.90$) and Australian specimens (method 1: $r^2 = 0.86$; method 2: $r^2 = 0.88$; Fig. 5). This indicates that age estimates from cemental layers may prove useful in cases where the pulp cavity is closed and osteodentine prevents reading of dentinal GLGs. As the correlation coefficients were higher for method 2, this method may be slightly better for age determination. Therefore, only the results from method 2 are subsequently used and hereafter only referred to as GLGs with a decimal number representing the increment.

Table 1 Width of the first GLG for *Kogia breviceps* and *Kogia sima* between one and two GLGs.

	PEM/SAM #	Estimated age	Width of first GLG (µm)
K. breviceps	N854	1.0	500
	76/17	1.2	666
	76/24	1.3	625
	N1863	1.3	666
	N177	1.3	583
	76/19	1.5	666
	86/22	1.6	666
	84/26	1.7	541
	93/14	1.7	500
			$\bar{x}$ = 601.44
K. sima	N228	1.4	541
	—	1.7	500
	N2041	1.7	541
	N236	1.9	500
			$\bar{x}$ = 520.5

PEM = Port Elizabeth Museum, Port Elizabeth Museum.
SAM = South African/ Iziko Museum, Cape Town.

Comparison of the age estimates from Ross' 1979 study and the ones from the present study showed no significant difference between the two sets of age estimates (Mann-Whitney-*U* test, p = 0.856; Table 2).

A lot of variation was seen in the closure of the pulp cavity (in %) in relation to body length and estimated age in *K. breviceps* (Fig. 6). The pulp cavity was 100 % closed in animals between 288 cm and 321 cm long in South African *K. breviceps*, which is in agreement with the data from an Australian specimen with a closed pulp cavity (323 cm long; Fig. 6A). The pulp cavity became occluded in *K. breviceps* as early as 14 GLGs in South African specimens, although other animals with occluded pulp cavities were

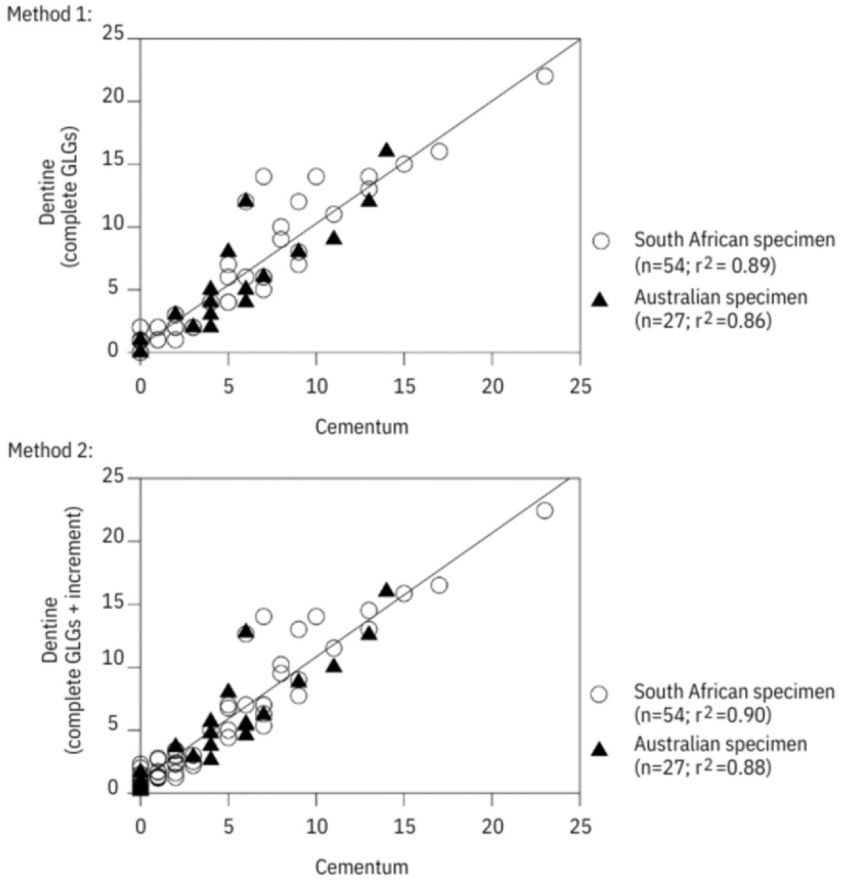

Fig. 5 Results for the two different reading methods of teeth for *Kogia breviceps*. Method 1: Correlation between cemental and dentinal readings consisting of only complete GLGs. Method 2: Correlation between cemental readings and dentinal readings consisting of complete GLGs plus an increment of the last incomplete layer.

19 and 22 years old (Fig. 6B). One Australian specimen had an occluded pulp cavity and a GLG reading of 12.56.

No seasonal pattern in the deposition of GLGs could be determined.

3.3.2 Kogia sima

In contrast to *K. breviceps*, the results for *K. sima* were slightly better for method 1 (r^2 = 0.74) than method 2 (r^2 = 73; Fig. 7). The lower correlation coefficient compared to *K. breviceps* indicates that cemental readings may not be as reliable in *K. sima* as they are for *K. breviceps*. Generally, there

Table 2 Comparison of Ross' (1979) results from age determination of *Kogia breviceps* with the results from the present study.

Old PEM/ELM/SAM # (current number)	Length of animal (cm)	Ross' estimate (GLGs + increment)	Present study (GLGs + increment)
SAM 35550 (68/13)	194.5	0.75	0.7
PEM 1517/92 (N179)	197	1	—
PEM 1517/90 (N177)	202	1.5	1.3
PEM 1511/10 (N40)	211	1	—
PEM 1519/12 (N225)	234	2.25	2.5
SAM 36980 (74/08)	236	2.75	2.75
SAM 35522 (66/08)	266.5	4.75	5
PEM 1511/13 (N42)	270	4	5
ELM 674 (N424)	275	12.75	12
PEM 1517/28 (N152)	289.5	9[a]	—
SAM 35795 (69/15)	305	7	7
PEM 1516/48 (N138)	305	8.5	9
PEM 1517/89 (N176)	305.5	11.5	9.7
PEM 1517/91 (N178)	309.5	17.75[a]	15.5
PEM 1516/08 (N132)	325	10+	—

NB: Ross gave a range for the completion of the last layer in %; only the lower point of the range is used here as decimal values.
ELM = East London Museum, East London.
ELM = East London Museum, East London.
SAM = South African Museum, Cape Town.
[a]= Ross indicated some doubt in these results in his 1979 publication.

appears to be little difference between method 1 and 2 for either *Kogia* species, thus for all following analyses age estimates from method 2 have been used.

Body length and age at occlusion of the pulp cavity were similarly variable in *K. sima* as in *K. breviceps* (Fig. 8). The shortest animal with an occluded pulp cavity measured 196 cm in length, while most other animals with closed pulp cavities ranged between 254 and 256 cm (Fig. 8A). While

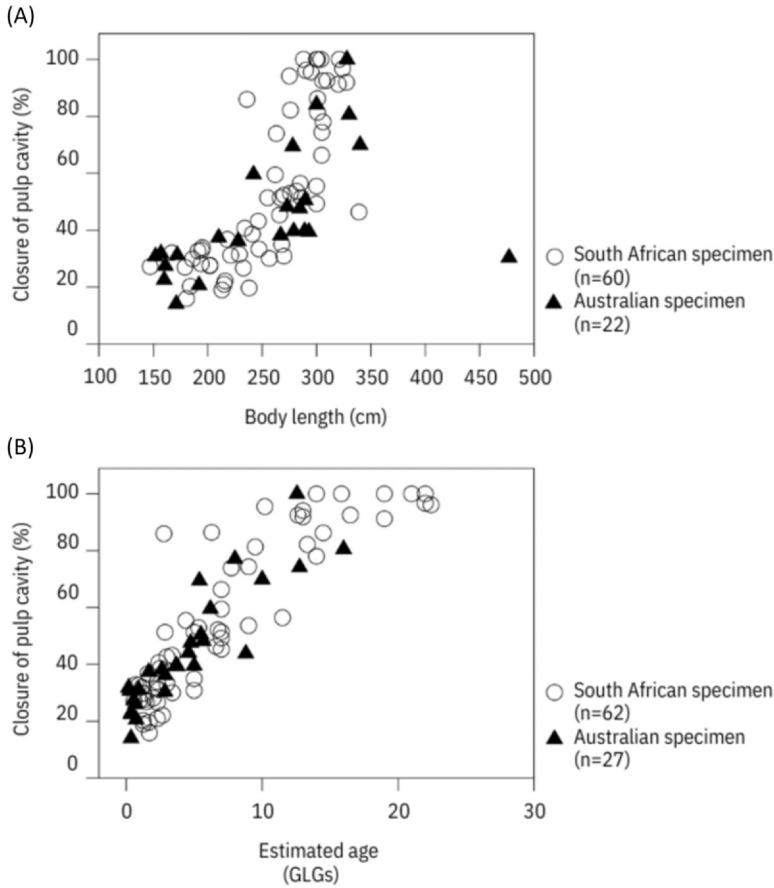

Fig. 6 Closure of pulp cavity in relation to body length (A) and estimated age (B) in *Kogia breviceps*.

there were three animals with occluded pulp cavities, which had estimated ages of three, five and seven years, respectively, the oldest animal in the sample, a 21.5 year old female, had a pulp cavity that was only 83.8 % closed (Fig. 8B). While this animal may represent an outlier, two other animals, a 14 year old female and a 13 year old male, had pulp cavities that were 96.7 % and 84.3 % occluded, respectively. Thus it appears that the pulp cavity closes between 11.8 and 17, which are the ages estimated for the remaining individuals with occluded pulp cavities (Fig. 8B).

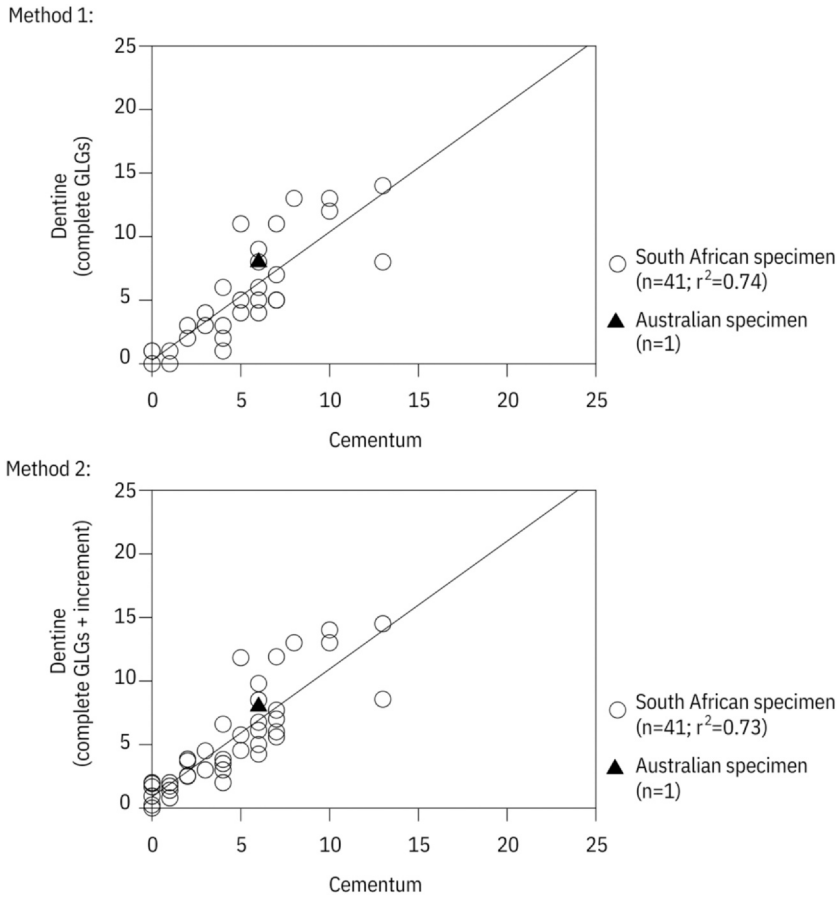

Fig. 7 Results for the two different reading methods of teeth for *Kogia sima*. Method 1: Correlation between cemental and dentinal readings consisting of only complete GLGs. Method 2: Correlation between cemental readings and dentinal readings consisting of complete GLGs plus an increment of the last incomplete layer.

3.3.3 Growth

Table 3 provides a summary of the main parameters obtained from the von Bertalanffy growth model for males and females of *K. breviceps* and *K. sima*, respectively.

3.3.4 Kogia breviceps

For *K. breviceps*, von Bertalanffy growth curves were fitted to the length-at-age data for males and females separately (Fig. 9). Animals of unknown sex and Australian specimens were plotted onto the same graph, but excluded

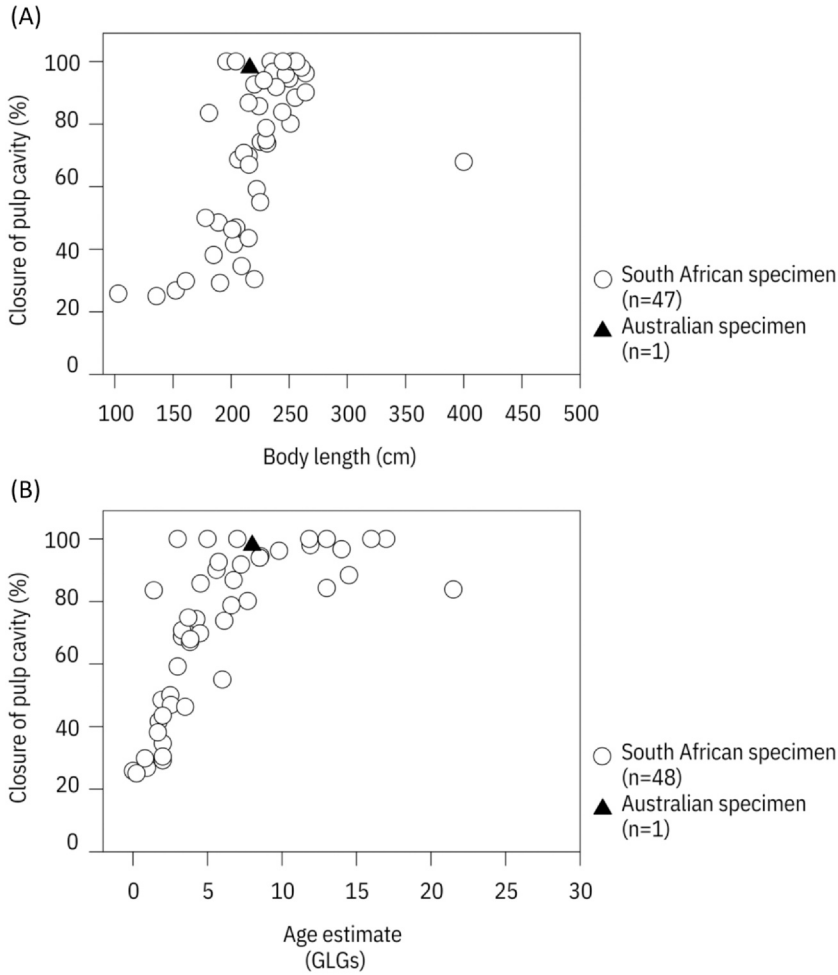

Fig. 8 Closure of pulp cavity in relation to body length (A) and estimated age (B) in *Kogia sima*.

from the calculations for the growth curves. Individuals were considered physically mature if they had a standard length equal to or greater than the asymptotic value generated by the von Bertalanffy model. Length at birth was estimated to be 120 cm for females and 142.6 cm for males by the model. The latter may be quite an overestimate, resulting from the fact that only larger male calves were available in the sample. The longest foetus measured 113 cm, whereas the shortest calf measured 147 cm with an estimated age of 0.57 GLGs (see also Fig. 16).

Table 3 Parameters derived from a von Bertalanffy growth equation for male and female *Kogia breviceps* and *Kogia sima*.

	Parameter	Males		Females	
		Length (cm)	Mass (kg)	Length (cm)	Mass (kg)
K. breviceps	L_1	147	69	184	158.8
	L_2	304	374.0	324	480
	t_0	−16.09	−0.76	0.33	1.56
	L_{inf}	286.0	412.1	306.0	536.3
	k	0.4	0.2	0.2	0.0
	Lt_0	142.6	52.8	120	52.8
	n	25	14	29	8
K. sima	L_1	103	14.5	181	31.5
	L_2	260.4	303	264	264
	t_0	−4.39	−30.31	−0.39	−1.4
	L_{inf}	263.8	294.9	249.1	208.7
	k	0.34	0.25	0.15	0.49
	Lt_0	106.51	57.41	103	30.71
	n	21	13	23	13

L_1 = Smallest length or mass in the sample
L_2 = Largest length or mass in the sample
t_0 = Age corresponding to zero length or weight
L_{inf} = Asymptotic length or mass
k = Constant of catabolism (or growth constant)
Lt_0 = Estimated length or mass at birth
n = Sample size

The data were too scanty to calculate foetal growth rates or conception dates using the Huggett and Widdas method (1951). However, using Scott's (1949) equation describing the relationship between the maximum body length of adult animals (x in cm; both males and females) and neonatal length (y in cm) for both mysticetes and odontocetes (y = 0.2411x + 44.3), a length at birth of 123.63 cm was calculated for *K. breviceps*, using a mean maximum body length of 329.05 cm for both sexes in this study (calculated as the mean

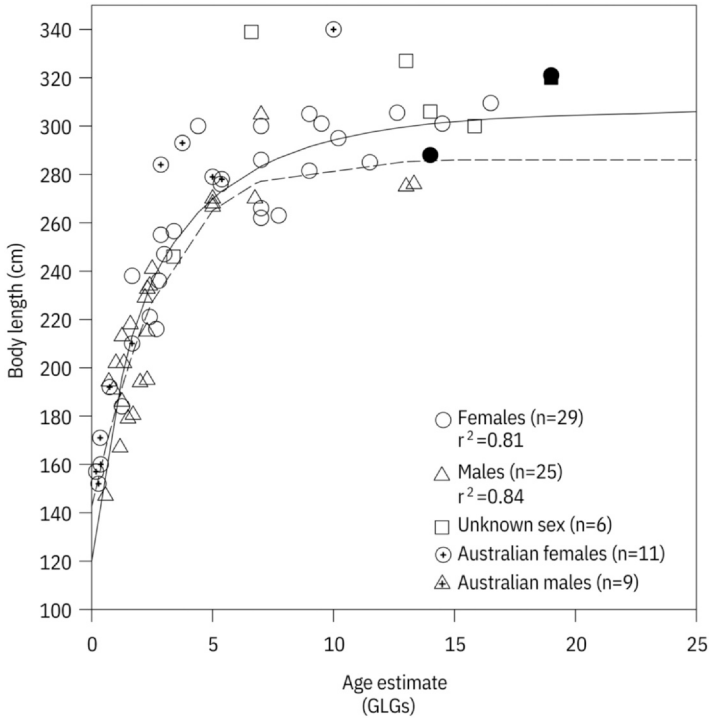

Fig. 9 Von Bertalanffy growth curve for *Kogia breviceps*. The solid line shows the fit for females, the dotted line for males. Australian specimens and animals of unknown sex were not included in these calculations, but plotted afterwards. Filled symbols represent specimen for which cemental readings were used as an age estimate.

of the maximum body length recorded for each sex). This agrees well with the estimated length at birth of 120 cm for the present study.

To determine foetal growth rates, Kasuya's (1977) equation describing the relationship between neonatal length (x in cm) and daily foetal growth rate for the linear part of the foetal growth phase (y in cm/day) for several Delphinid species was used. The formula is as follows: $y = 0.001462x + 0.1622$. Using 120 cm as length at birth in *K. breviceps*, the foetal growth rate is 0.338 cm per day.

The asymptotic length calculated by the von Bertalanffy growth model was 306.04 cm ($r^2 = 0.81$) for *K. breviceps* females and 286.08 cm ($r^2 = 0.84$) for males (Fig. 9). Both sexes reach physical maturity at about the same age of 15 years.

The longest female *K. breviceps* in the sample measured 327.6 cm and the longest male 330.5 cm. The oldest female *K. breviceps* in the sample was

estimated to be 22.4 years old. The oldest *K. breviceps* male from South Africa was estimated to be 13.3 years old and the oldest Australian male was 16 years old. However, an animal of unknown sex (a possible male) was estimated to be 19 years old. Thus the life expectancy may actually lie between 16 and 23 years in *K. breviceps*.

A regression of body length on body weight for the 19 males and 13 females, for which data were available, yielded a good correlation of 0.91 and 0.96, respectively (Fig. 10A). A von Bertalanffy growth model could only be fitted to the female data due to the distribution of the sample (Fig. 10B). The model estimated the weight at birth as 52.8 kg and the asymptotic weight at 536.3 kg (r^2 = 0.94), although the latter might be an overestimate as no clear asymptote was reached. For males the weight at birth was also estimated at 52.8 kg, but the asymptotic weight was estimated at 412.1 kg (r^2 = 0.83). The longest foetus weighed 23 kg, whereas the shortest calf weighed 69 kg and had an age estimate of 0.57 GLGs (see also Fig. 16). In this respect the birth weight estimate of around 53 kg for both sexes calculated by the model appears to agree well with the available data.

The heaviest females in the sample were 320 cm and 321 cm in length, with no age estimate and an estimate of 19 GLGs, respectively; both weighed 480 kg. For the males the heaviest animal had an age estimate of 13.33, measured 276 cm and weighed 374.03 kg.

3.3.5 *Kogia sima*

For *K. sima*, size at birth was estimated to be at 106.5 cm for females and 103 cm for males by the von Bertalanffy growth model (Fig. 11). Both estimates appear realistic as the longest foetus measured 108 cm, while the two shortest calves measured 103 cm and 103.5 cm (see also Fig. 20). The 103 cm long calf had a GLG reading of zero, indicating that birth occurs between 103 cm and 108 cm. The data were too scanty to calculate foetal growth rates or conception dates using the Huggett and Widdas method (1951). However, using Scott's (1949) equation and a mean maximum adult length of 267.35 cm for both sexes (calculated as the mean of the maximum body length recorded for each sex), a neonatal length of 108.8 cm can be calculated. This is somewhat longer than the 103 cm estimated from the lengths of foetuses and calves. In addition, Kasuya's (1977) formula gave a foetal growth rate of 0.313 cm/day, based on a length at birth of 103 cm in *K. sima*.

The asymptotic length calculated by the growth model is reached at 249.14 cm in females (r^2 = 0.9), while the males appear to reach physical

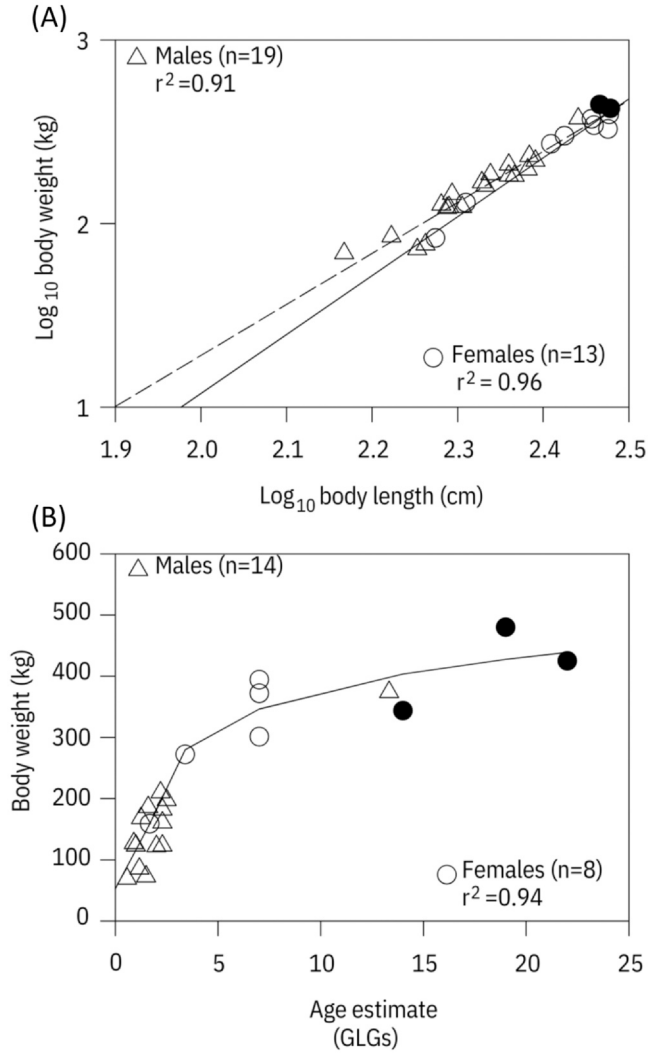

Fig. 10 Body length (A) and age (B) in relation to body weight in *Kogia breviceps*. Filled symbols represent specimens for which cemental readings were used as an age estimate. A von Bertalanffy growth curve could only be fitted to the female data (B).

maturity at a slightly larger body size of 263.75 cm (r^2 = 0.84; Fig. 11, Table 3). This corresponds to 13 and 16 years of age for females and males, respectively.

The longest animal in the sample was a 274.3 cm long female; no age estimate was available for this individual. The longest female for which the

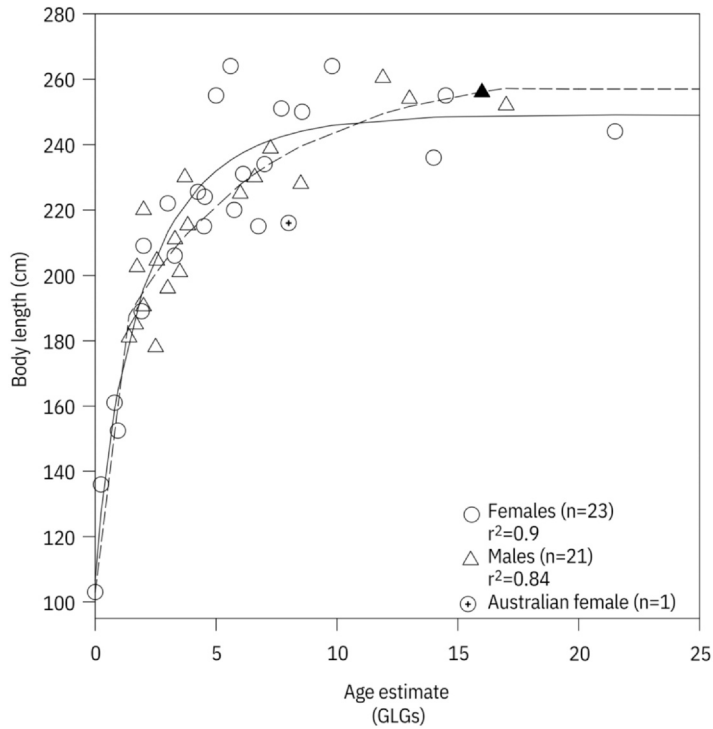

Fig. 11 Von Bertalanffy growth curve for *Kogia sima*. The solid line shows the fit for females, the dotted for males. The Australian female was not included in these calculations. The filled symbol represents a specimen for which cemental readings were used as an age estimate.

age could be determined measured 264 cm and for male *K. sima* the longest animal measured 260.4 cm. The oldest female was 21.5 years and the oldest male was estimated to be 17 years old. These data indicate a life expectancy of 17–22 years for *K. sima*.

The regression of body length on body weight gave a similarly good regression coefficient for both sexes (r^2 = 0.95 and 0.96 for males and females, respectively; Fig. 12A). The von Bertalanffy model calculated weight at birth at 30.7 kg for female *K. sima* and the asymptotic weight at 208.7 kg (r^2 = 0.92; Fig. 12B, Table 3). For males, the model calculated weight at birth at 57.4 kg and the asymptotic weight at 294.9 kg (r^2 = 0.88; Fig. 12B, Table 3). However, as the growth curve for males does not reach a plateau, this may be a substantial overestimate. The longest foetus present in the sample weighed 13 kg, while the two shortest calves weighed 31.5 kg and 14.5 kg (see also Fig. 20). Thus birth weight probably lies

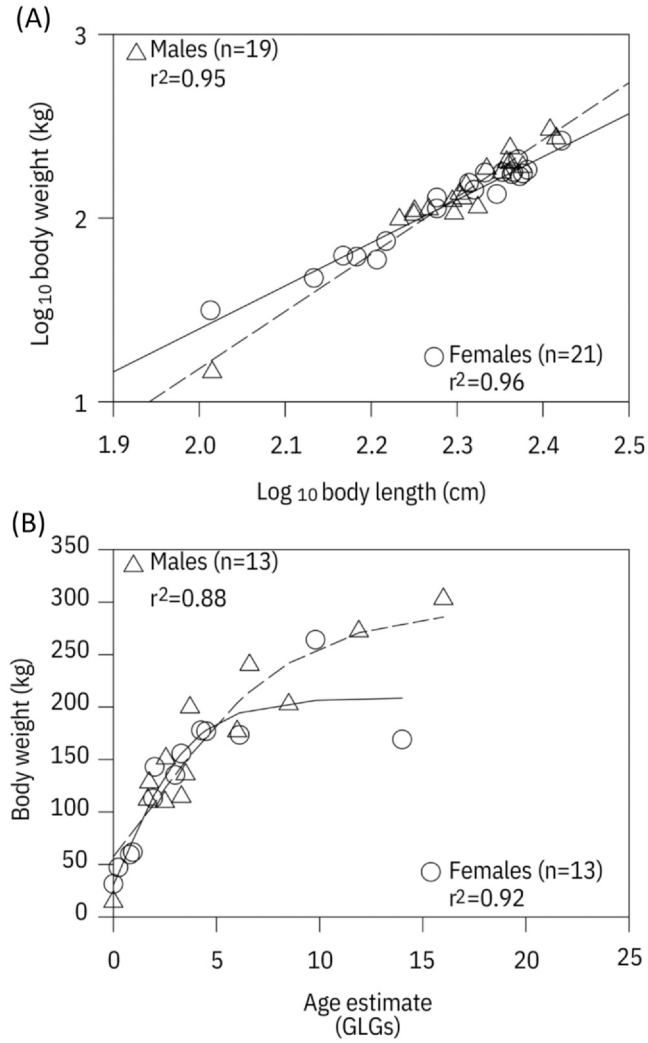

Fig. 12 Body length (A) and age (B) in relation to body weight in *Kogia sima*. The solid line shows the fit of the von Bertalanffy model for females, the dotted line for males.

between 13 kg and 15 kg in this species. The GLG reading of the calf weighing 31.5 kg was 0, indicating that it was a neonate.

The heaviest female in the sample was a 9.8 year old animal, measuring 264 cm with a weight of 264 kg (Fig. 12B, Table 3). The heaviest male was estimated to be 16 years old, measured 256 cm in body length and weighed 303 kg (Fig. 12B, Table 3).

3.4 Reproductive biology

3.4.1 Females

The colour of the ovaries of both species changed from beige or white for immature ovaries (i.e. ovaries without Graafian follicles or *corpora*) to dark grey, dark brown or black for mature ovaries (Fig. 13).

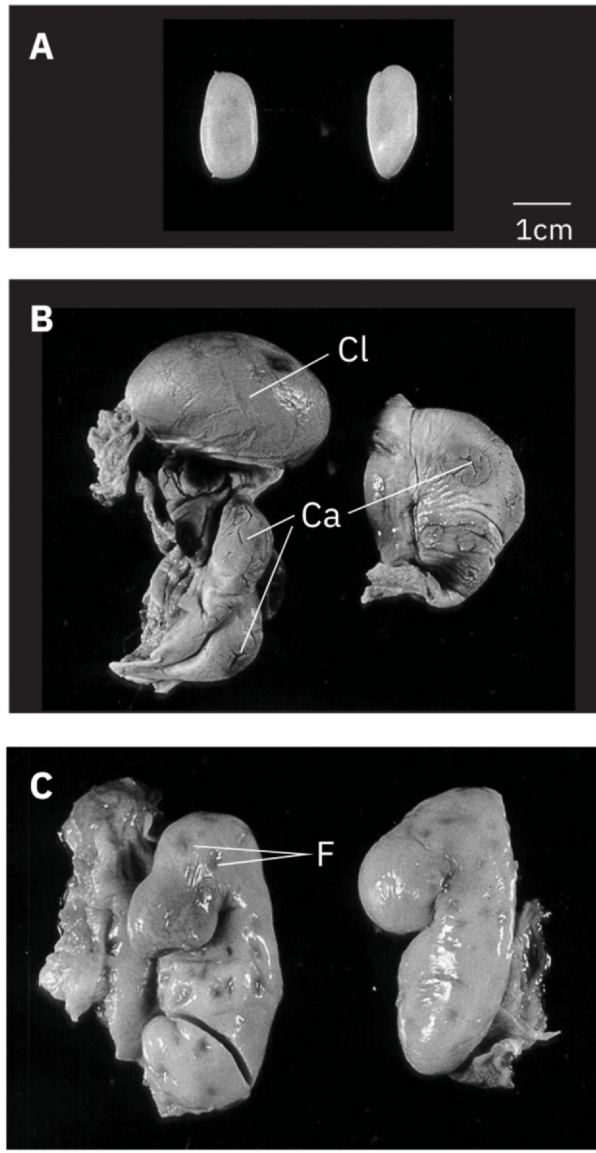

Fig. 13 Ovaries of *Kogia*. (A) Immature ovaries. (B) Mature ovaries. CL: *Corpus luteum*. CA: *Corpus albicans*. (C) Mature ovaries. F: Follicles.

3.4.2 *Kogia breviceps*

To test whether or not ovulations occurred equally in both ovaries, a paired *t*-test was carried out on data available for 13 *K. breviceps* females stranded along the South African coastline and for two taken from the literature (Harrison et al., 1972; Jenness and Odell, 1978; Table 4). No significant difference was found between the accumulation rate of the left (total: 79 *corpora*) and of the right (total: 66 *corpora*) ovary at the 5 % level ($p = 0.29$), indicating that ovulations occur equally in both ovaries.

Table 4 Accumulation of *corpora* in the left and the right ovary of female *Kogia breviceps*. No significant difference was found between the accumulation rate of the left and of the right ovary at the 5 % level ($p = 0.29$), indicating ovulations occur equally in both ovaries.

Animal No.	Number of *corpora* in the left ovary	Number of *corpora* in the right ovary
94/09	1	1
92/14	4	3
86/17	9	7
84/24	3	4
83/20	8	2
82/20	0	3
82/04	7	6
81/22	10	6
78/25	2	2
78/19	2	1
N1078	0	2
N178	8	3
N176	2	5
Jenness and Odell (1978)	16	13
Harrison et al. (1972)	7	8
n = 15	total = 79	total = 66
$\bar{x} \pm$ SE	5.3 (±4.5)	4.4 (±3.2)

On the basis of *corpora* present in the ovaries, 17 females out of 23 examined were mature and six females were immature (Fig. 14, Table 5). A marked increase in the number of *corpora* occurred at a body length of around 260 cm and about seven GLGs (Fig. 14). No female had only one

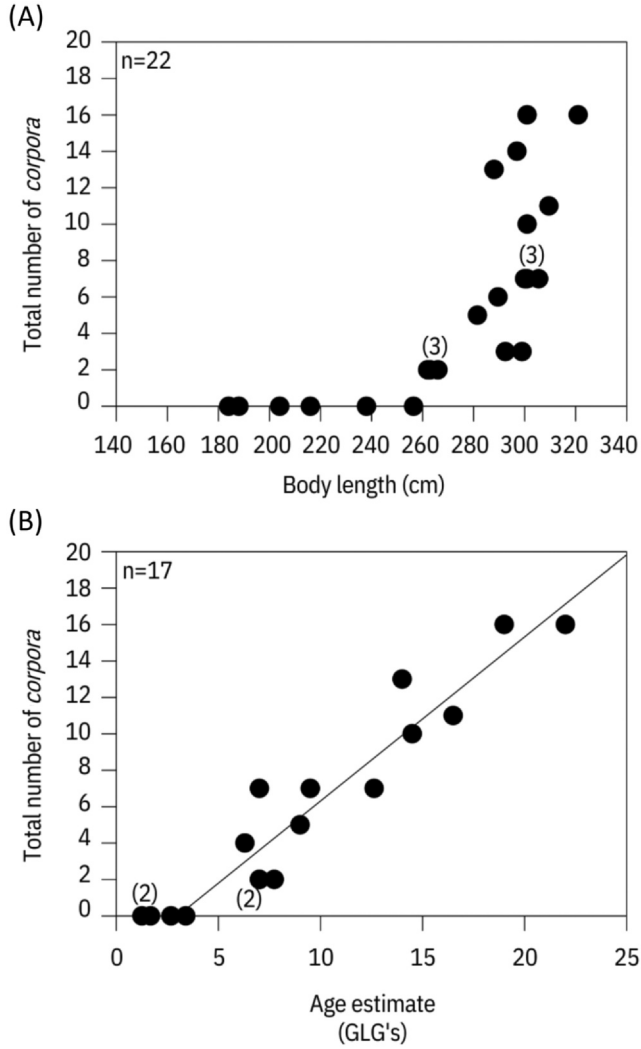

Fig. 14 Attainment of sexual maturity, in relation to (A) length and (B) estimated age, and ovulation rate in female *Kogia breviceps*. The solid line (B) represents the regression ($y = -2.7 + 0.9x$) between the number of *corpora* and the age for mature females ($r^2 = 0.86$).

Table 5 Summary of the size and ages for different maturity stages for *Kogia breviceps* females. Determination of maturity was based on histological examination of the reproductive organs and only specimens for which the state of maturity could be confirmed histologically were included here (i.e. calves were excluded).

	Immature		Mature	
	n	Range	n	Range
Age (GLGs)	4	1.3–3.4	13	6.3–22.0
Length (cm)	6	184.0–256.6	17	262.0–321.0
Mass (kg)	4	83.5–272.2	7	301.0–480.0

corpus present in her ovaries, but three females measuring 262 cm, 263 cm and 266 cm with 7 GLGs, 7.7 GLGs and 7 GLGs, respectively, all had two *corpora* (Fig. 14). The onset of sexual maturity in female *K. breviceps* is therefore estimated to be at about 262 cm and 7 GLGs. However, considering that the ovulation rate is one per year in this species (see below) and both females already had two *corpora* present in the ovaries, sexual maturity occurs most likely at around 5 years. The youngest female with *corpora* in her ovaries was estimated to be 6.3 years and had 4 *corpora* present. The maximum number of *corpora* recorded was 16 for two females, which measured 301 cm and 321 cm and had GLG counts of 22 and 19, respectively.

A concurrent increase in combined ovarian weight was observed at a total body length of about 260 cm and at about 6 GLGs (Fig. 15). The highest combined ovary weight in an immature female was 12.2 g (L: 256.5 cm, GLGs: 3.4) and the lowest combined ovary weight for a mature female with seven *corpora* was 17.4 g (L: 305.5 cm, GLGs: 12.6), which indicates that sexual maturity occurs between 12 g and 17 g of combined ovary weight. One female (SAM 82/20), although mature (with three *corpora* in her ovaries), had a combined ovary weight of only 13.8 g, but one of the ovaries was much smaller than the other one.

The heaviest immature *K. breviceps* female weighed 272.16 kg (L: 256.5 cm, GLGs: 3.4; Table 5). The lightest mature female was 301 kg (L: 266 cm, GLGs: 7; Table 5). Therefore the weight at the onset of sexual maturity was between 272.2 kg and 301 kg for female *K. breviceps* (Table 5).

A regression of estimated age against total number of *corpora* for all mature females is described by the regression equation $y = -2.7 + 0.9x$ (where y is the total number of *corpora* and x is the age estimate (GLGs)) and yields an ovulation rate of 0.9 per year (Fig. 14). This indicates that, on average, ovulations occur about every 13.3 months.

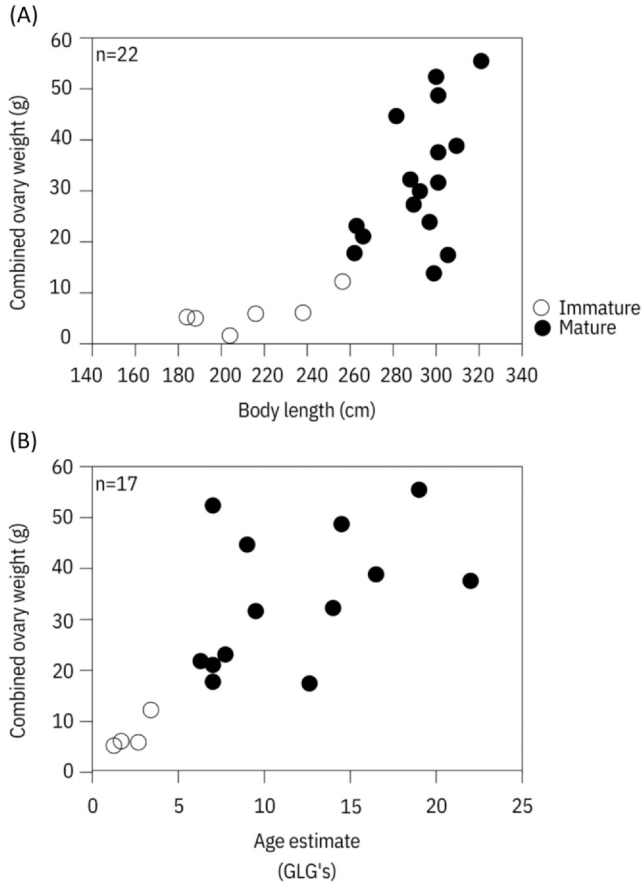

Fig. 15 Increase of combined ovary weight with (A) body length and (B) estimated age in female *Kogia breviceps*.

No post-reproductive females were observed based on macroscopic examination of the ovaries. The two oldest females both had 16 *corpora* in their ovaries and were 19 and 22 years old, respectively (Fig. 14B), indicating that both females probably ovulated annually after reaching sexual maturity. The oldest female that was pregnant (PEM N178) had an estimated age of 16.5 GLGs (Table 6).

Using Kasuya's (1977) formula ($t_g - t_0 = x/(0.001802x + 0.1234)$; where x = mean neonatal length in cm, and $t_g - t_0$: the linear foetal growth period i.e. a minimum estimate of gestation), the gestation length (based on a neonate length of 120 cm) is 353.3 days or 11.8 months.

Table 6 Records of female *Kogia breviceps* stranded along the Southern African coastline accompanied by a foetus or calf. Information on the animals' length, age and sex was included whenever available.

No. of cow/calf	Length of cow/calf (cm)	Age of cow/calf	Sex of calf	Length of foetus (cm)	Sex of foetus	Comments
(A) Assumed cow/calf pairs						
N41 N40	269.5 211	— —	—	19.5	F	Cow lactating
N138 —	305 —	9 —	—	113.5	M	—
N277 N278	266 204	7 —	F	31	—	—
78/25 —	— —	6.3 —	—	27	F	—
82/04[a]	288 ca 150	14 —	—	49	F	Cow lactating
N853 N854	297 202	— —	M	—	—	Cow lactating

Table 6 Records of female *Kogia breviceps* stranded along the Southern African coastline accompanied by a foetus or calf. Information on the animals' length, age and sex was included whenever available.

No. of cow/calf	Length of cow/calf (cm)	Age of cow/calf	Sex of calf	Length of foetus (cm)	Sex of foetus	Comments
82/27 —	300 —	4.4 —	—	65		—
83/20 83/21	301 191	14.5 —	M	21	F	Traces of milk
N1078 N1079	262 194	7 —	M	48	M	Cow lactating
N1707 —	286 —	— —	—	27.5	M?	—
92/14[a]	300 —	7 —	—	38	F	Cow lact., with 2 smaller indiv.
(B) Possible cow/calf pairs						
−68/13	194.3[a]	−0.71	M	—	—	With much larger indiv. (cow?)

(continued)

Table 6 Records of female *Kogia breviceps* stranded along the Southern African coastline accompanied by a foetus or calf. Information on the animals' length, age and sex was included whenever available.

No. of cow/calf	Length of cow/calf (cm)	Age of cow/calf	Sex of calf	Length of foetus (cm)	Sex of foetus	Comments
N178 N179	309.5 197	16.5 —	M	17.9	M	—
N176 177	305.5 202	12.6 1.3	M	23	M	—
82/20 82/21	299 215 +	— 2.3	M	—	—	—
N1174[a]	290−	—	—	—	—	—
N1862 N1863	320 213	−1.3	M	—	—	—
94/09[a]	263 180	7.7−	—	28.6	M	—
96/16 96/17	281.5 184	9 1.3	F	23	M	—

[a]= Animal refloated; age of calf= complete GLGs plus increment.

The monthly occurrence of foetuses and juveniles up to and including the age of two GLGs suggests a reproductive season with conceptions occurring from April to September and births possibly occurring from March to August (Fig. 16). The Australian specimens included in this analysis showed the same trend. These results would suggest a gestation period of approximately 11 months. This in combination with a high percentage of simultaneously pregnant and lactating females (24.1 %) and the ovulation rate suggests annual reproduction for *K. breviceps*.

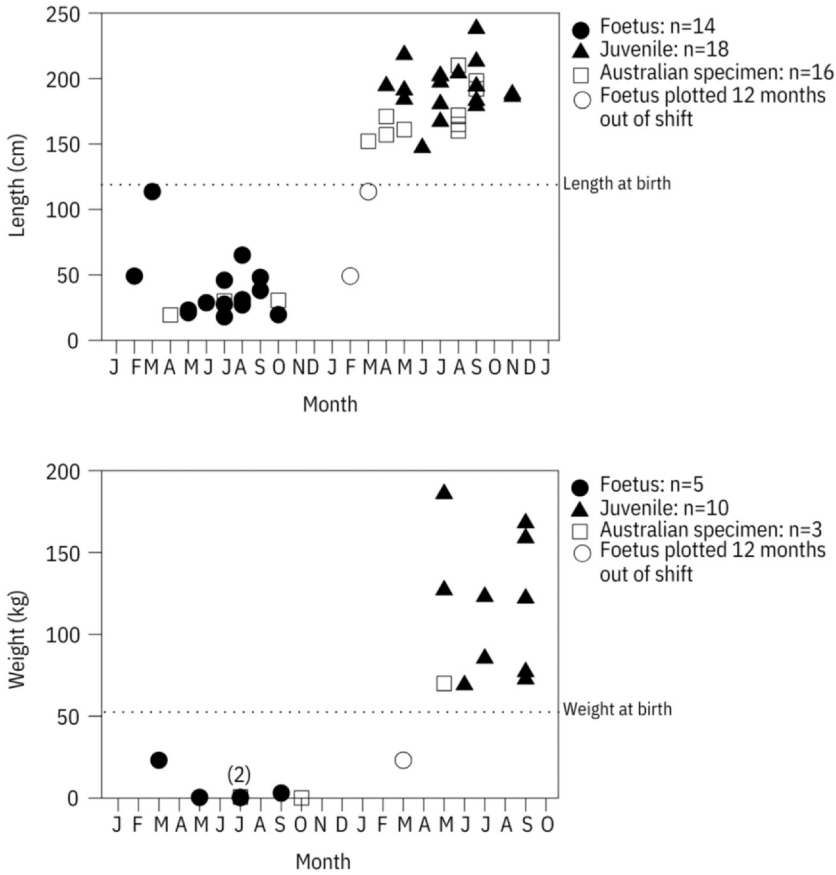

Fig. 16 Occurrence of *Kogia breviceps* foetuses (filled circles) and juveniles (up to and including the age of two; filled triangles) throughout the year. Open circles are original data plotted 12 months out of shift. All juveniles were plotted 12 months out of shift. Three of the Australian specimens included (indicated as squares) were foetuses and 11 were juveniles, although weights were only available for two Australian foetuses and one juvenile.

The results for the largest *corpus* (CL or CA) plotted versus month did not support the trend in seasonality seen in Fig. 16, although the largest *corpus* still fell into the mating season (September; Fig. 17A). When the CL index was plotted against the length of the foetus or calf, it appeared to decrease with increasing length of the offspring. However, a range of CL indices was observed for foetuses between 17.9 cm and 49 cm (Fig. 17B).

The longest calf that stranded with a lactating cow measured 211 cm (Table 6), which would coincide with about two GLGs if extrapolated from the growth curve (Fig. 9). A 202 cm long calf, which also stranded

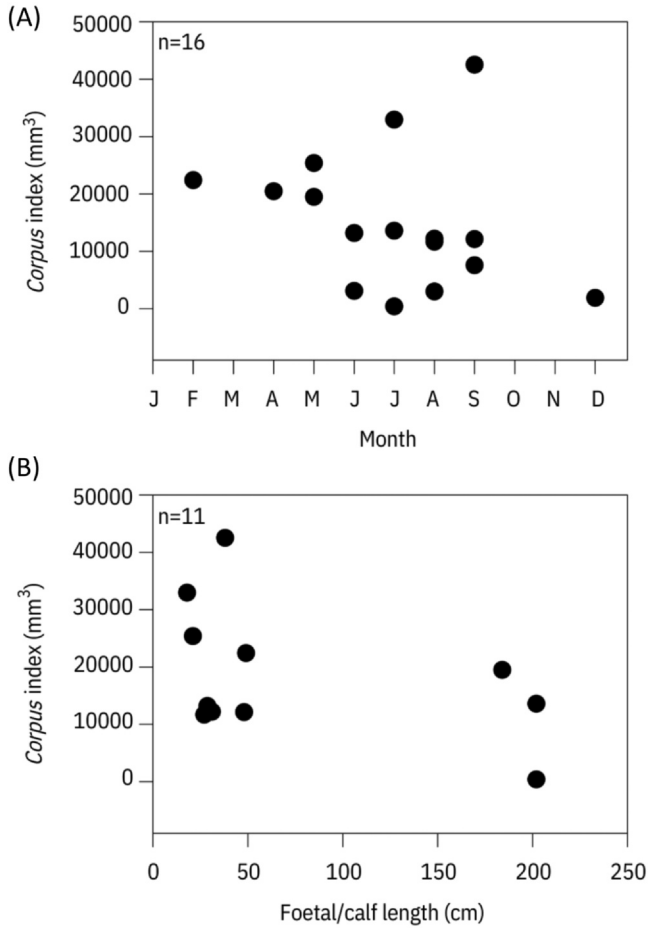

Fig. 17 *Corpus* index (in mm^3) of the largest *corpus* (CL or CA) in relation to month (A) and foetal or calf length (B) in *Kogia breviceps*.

with a lactating female, had an age estimate of two GLGs (Table 6), which indicates that lactation can last up to two years. However, the shortest calf that stranded with a cow that was not lactating measured 180 cm (Table 6). This would indicate that it was around one year old (extrapolated from the growth curve; Fig. 9). Another cow, which only showed traces of milk, was accompanied by a 191 cm long calf that had an age estimate of just under 1 GLG (Table 6). These data indicate that weaning may start after a year of lactation, but that lactation may continue for up to two years.

The foetal sex ratio of the 12 *K. breviceps* foetuses present was 1:1.4 for females (n = 5) to males (n = 7), respectively. The juvenile sex ratio for 19 calves up to and including two years of age (≤210 cm) was 1:2.2 for females (n = 6) to males (n = 13), respectively. However, neither the foetal nor the juvenile sex ratio were significantly different from parity (χ^2 = 0.33 and 2.58, respectively; $p > 0.05$).

3.4.3 *Kogia sima*

There was a significant difference at the 5 % level in the rate at which *corpora* accumulated in the ovaries of nine female *K. sima* from South Africa ($p = 0.0159$), with the left ovary (total: 22 *corpora*) being significantly more active than the right one (total: 9 *corpora*; Table 7).

Table 7 Accumulation of *corpora* in the left and the right ovary in female *Kogia sima*.

Animal No.	Number of *corpora* in the left ovary	Number of *corpora* in the right ovary
88/20	1	0
88/02	1	2
81/03	1	0
76/03	4	1
N832	3	0
N829	3	3
N678	4	1
N243	2	1
N145	3	1
n = 9	Total = 22	Total = 9
$\bar{x} \pm$ SE	2.4 (±1.2)	1.0 (±1.0)

Based on examination of the ovaries, 15 females were mature and 10 immature (Fig. 18, Table 8). The onset of sexual maturity in *K. sima* females is somewhat clearer than in *K. breviceps*. A marked increase in the total number of *corpora* occurred just below a total body length of 220 cm and around 5 GLGs (Fig. 18). The shortest female with only one *corpus* was

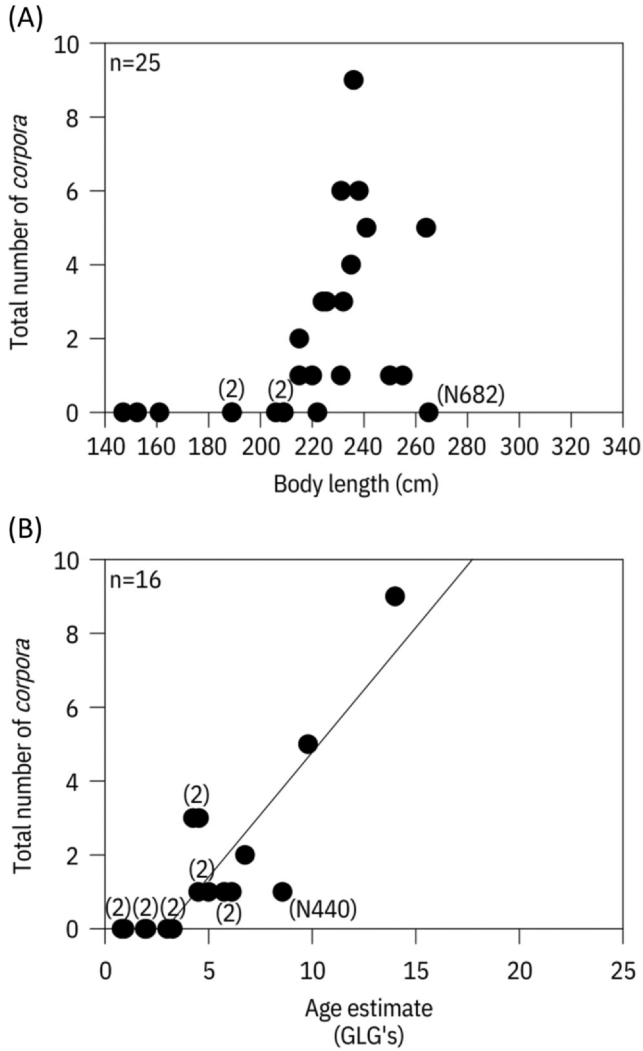

Fig. 18 Attainment of sexual maturity, in relation to (A) length and (B) estimated age, and ovulation rate in female *Kogia sima*. The solid line (B) represents the regression ($y = -2.0 + 0.7x$) between the number of *corpora* and the age for mature females ($r^2 = 0.65$).

Table 8 Summary of the size and ages for different maturity stages for *Kogia sima* females. Determination of maturity was based on histological examination of the reproductive organs and only specimens for which the state of maturity could be confirmed were included (i.e. calves were excluded).

	Immature		Mature	
	n	Range	n	Range
Age (GLGs)	6	0.8–3.3	10	4.3–14.0
Length (cm)	10	147.0–222.0[a]	15	215.0–264.0
Mass (kg)	8	59.4–155.6	9	169.0–264.0

[a]One outlier, a 265 cm long female, was omitted here as she appeared to be reproductively abnormal.

215 cm long (GLGs: 4.5; Fig. 18). Two other females with one *corpus* in the ovaries measured 231 cm and 255 cm and had 6.12 and 5 GLGs, respectively. No age estimate was available for a 220 cm long female with one *corpus*. Therefore the onset of sexual maturity for *K. sima* females seems to occur at about 215 cm and around 5 GLGs (Fig. 18). The youngest mature female had a GLG reading of 4.25, but already three *corpora* present in her ovaries. The highest number of *corpora* recorded for *K. sima* was nine in a 236 cm long female (PEM N1322, GLGs: 14).

Two outliers were observed: a 265 cm long female (PEM N682) with no *corpora* in her ovaries, for which no age estimate was available, and a 250 cm long female (PEM N440) with one *corpus* and an age estimate of 8.6 GLGs (Fig. 18A and B, respectively). As these two females seem to have an unusually low *corpora* count for their length and age, it is suggested that they possibly suffered from some impairment of reproductive ability.

The increase in combined ovarian weight with the onset of maturity was not as clear as previously observed for *K. breviceps*, although there was a general trend of increasing combined ovary weight with increasing length and age (Fig. 19). The highest combined ovary weight for an immature female was 11.6 g (L: 189 cm, no age estimate available) and the lowest combined ovary weight for a mature female with one *corpus* was 3.5 g (L: 255 cm, GLGs: 5), although in the latter case one ovary appeared extremely small and was possibly infertile. There were a number of outliers that should be mentioned. Two mature females, based on the presence of *corpora* in their ovaries, showed very low combined ovary weights of 3.5 g and 4.6 g, respectively for their length (L: 255 cm and 238 cm, GLGs: 5 and no age estimate available, respectively). In contrast, one immature female (PEM N207) had a remarkably high combined ovary weight of 11.6 g for

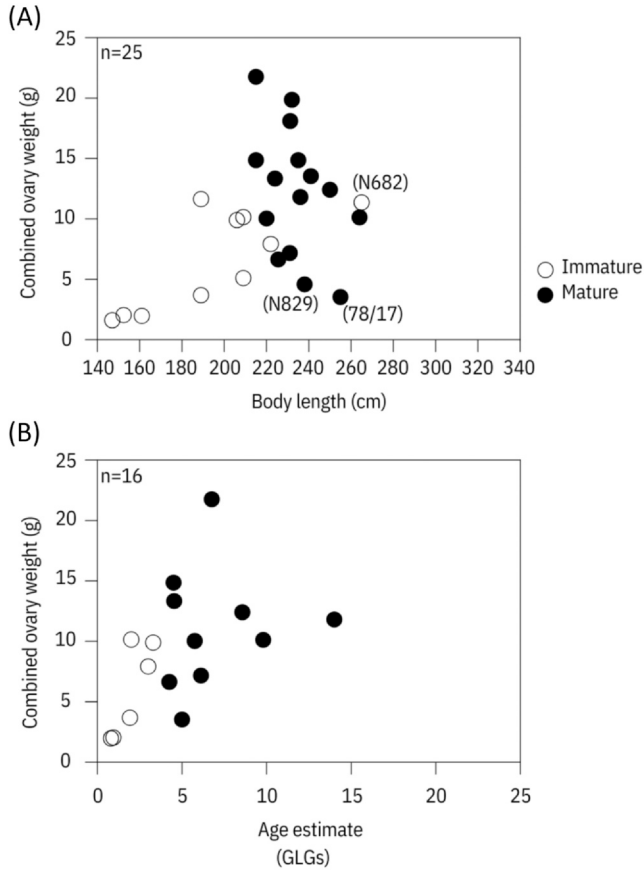

Fig. 19 Increase of combined ovary weight with (A) body length and (B) estimated age in female *Kogia sima*.

her length (L: 189 cm, GLG: no age estimate available; Fig. 19A). Another female (PEM N682), which was immature based on ovarian examination, should have been mature according to her combined ovary weight of 11.4 g and length of 265 cm; no age estimate was available for this female (Fig. 19A). Furthermore, a range of combined ovary weights was observed for four animals aged around 5 GLGs (Fig. 19B). These ranged from 6.6 g to 14.9 g for animals between 4.25 and 5 GLGs. However, the two higher combined ovary weights can be attributed to a large CL present in each case, which resulted in the ovary with the CL being about twice as heavy as the ovary without the CL. The mature female already mentioned as having a relatively low combined ovary weight (3.5 g) for her length also had a

relatively low combined ovary weight for her age (GLGs: 5; Fig. 19B). From Figs. 18 and 19 it appears that at least two females may have had a somewhat impaired reproductive ability.

The heaviest immature *K. sima* female weighed 155.6 kg (L: 206 cm, GLGs: 3.3), whereas the lightest mature female weighed 176.9 kg (L: 215 cm, GLGs: 4.5; Table 8). There were, however, two mature females for which no age estimate was available, which wighed 169 kg and 175 kg and measured 236 cm and 238 cm, respectively. Thus maturity probably occurs between 155.6 kg and 169 kg in female *K. sima* (Table 8).

A regression of estimated age against total number of *corpora* described by the equation $y = -2.0 + 0.7x$ (where y: total number of *corpora* and x: age estimate (GLGs)) was fitted to all mature *K. sima* females and yielded an ovulation rate of 0.7 per year, which means that ovulations occur about every 17.1 months (or roughly one and a half years; Fig. 18).

As in *K. breviceps,* no post-reproductive females were observed. The oldest pregnant female was also the oldest female in the sample and had an age estimate of 14 GLGs (Table 8). This may indicate that, in *K. sima*, females usually do not enter a long post-reproductive period but reproduce throughout their lives.

Using Kasuya's (1977) formula, the estimated gestation length, based on a neonate length of 103 cm is 333.3 days or 11.1 months.

For *K. sima,* a clearer picture of the reproductive seasonality emerged as both conceptions and births occurred between December and March (Fig. 20A), although the sample size is smaller than for *K. breviceps*. This would indicate a gestation length of 12 months. Although the ovulation rate suggests that ovulations occur roughly every one and a half years, 11.5 % of mature females that stranded along the Southern African coast were found to be simultaneously lactating and pregnant. These data indicate that *K. sima* may also show annual reproduction, if the conditions are right, although that may be facultative and some animals may only reproduce every two years. This is further supported by one foetus, which was apparently conceived in December, suggesting that in *K. sima* a post-partum oestrus may occur in some animals, some of the time.

As with *K. breviceps,* the results for the largest *corpus* plotted versus month did not support the trend in seasonality seen in Fig. 20, and the largest *corpus* just fell outside the mating season (April; Fig. 21A). Similarly, when the *corpus* index was plotted against the length of the foetus or calf no real trend could be determined (Fig. 21B).

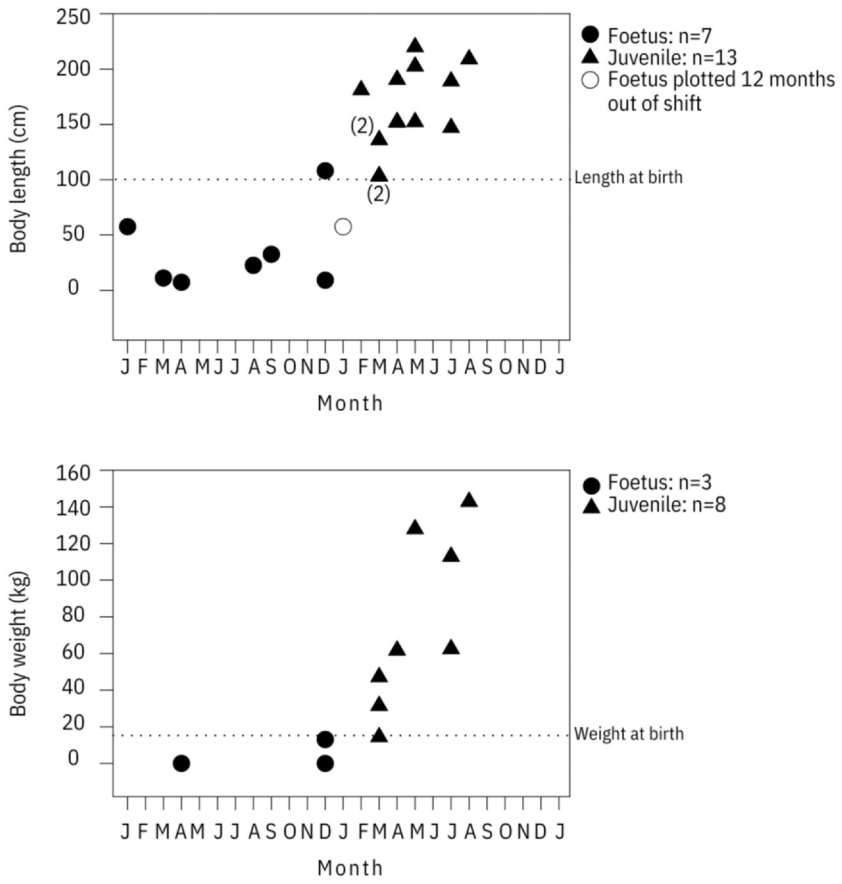

Fig. 20 Occurrence of *Kogia sima* foetuses (filled circles) and juveniles (up to and including the age of one; filled triangles) throughout the year. Open circles are original data plotted 12 months out of shift. All juveniles were plotted 12 months out of shift.

The longest calf that stranded with a lactating female measured 152.4 cm and had a GLG reading of 0.94 (Table 9), which suggests that lactation can last at least one year. Another calf, measuring approximately 130 cm (no age estimate was available) stranded with a non-lactating female (Table 9), suggesting that weaning can start as early as six months, as extrapolated from the growth curve (Fig. 11).

The sex ratio for the five *K. sima* foetuses present was 1:1.5 for females (n = 2) to males (n = 3), respectively. For seven juveniles up to and including two years of age (≤160) the ratio was 1.33:1 for females (n = 4) to

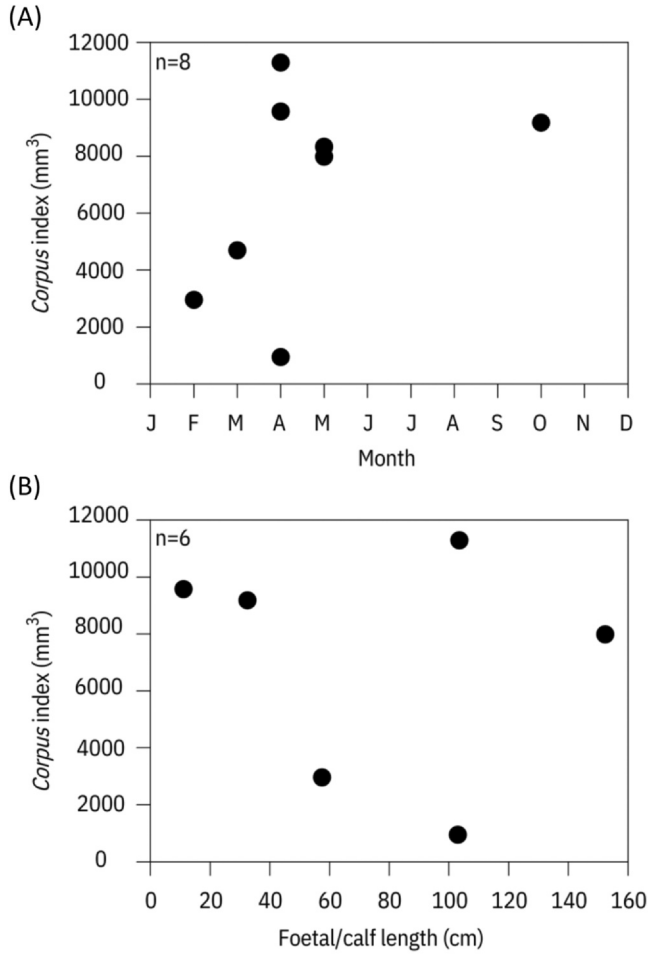

Fig. 21 *Corpus* index (in mm^3) of the largest *corpus* (CL or CA) in relation to month (A) and foetal or calf length (B) in *Kogia sima*.

males (n = 3), respectively. However, neither the foetal nor the juvenile sex ratio were significantly different from parity (χ^2 = 0.2 and 0.14, respectively; $p > 0.05$).

3.4.4 Males

A dependent paired *t*-test showed no significant difference in either length or weight between the left and the right testis in both *K. breviceps* (testis length: p = 0.27302; testis weight: p = 0.2717) and *K. sima* (testis length: p = 0.155025; testis weight: p = 0.499991). Thus it was concluded that either testis may be examined to establish the stage of maturity of an animal.

Table 9 Records of female *Kogia sima* stranded along the Southern African coastline with a foetus or calf. Information on the animals' length, age and sex was included whenever available.

No. of cow/calf	Length of cow/calf (cm)	Age of cow/calf	Sex of calf	Sex of foetus	Length of foetus	Comments
(A) Assumed cow/calf pairs						
N101 N102	231.2 151.9	— —	M	—	—	Cow lactating
N103 N104	230.5 152.4	— —	M	—	—	Cow lactating
N139 N140	ca244 135.9	— 0.3	F	—	—	Cow lactating
N145 N146	235 152.4	— 0.9	F	F	7.2	Cow lactating
N440 —	250/ —	8.6 —	—	M	108	—
N317 N318	220/ 147 +	5.8 —	F	—	—	Cow lactating
81/03 —	215 —	4.5 —	—	M	11.1	—
			M	—	—	

Table 9 Records of female *Kogia sima* stranded along the Southern African coastline with a foetus or calf. Information on the animals' length, age and sex was included whenever available.

No. of cow/calf	Length of cow/calf (cm)	Age of cow/calf	Sex of calf	Sex of foetus	Length of foetus	Comments
N678 N679	241 103.5	— —				Cow lactating
N829 N830	238 103	— 0	F	—	—	Cow lactating
N832 [a]	232 —	— —	—	—	—	Cow lactating
N1322 —	236 —	14 —	—	—	9.1	—
88/02 —	225.5 —	4.3 —	—	M	57.5	—
(B) Possible cow/calf pairs						
N185 N185a	240 ca130	— —	—	—	22.5	—
N243 N244	224 161	4.5 0.8	F	F	32.5	—

[a] = refloated; age of calf= complete GLG's plus increment

3.4.5 *Kogia breviceps*

Immature testes were observed in 13 *K. breviceps* (Table 10) based on histological examination. Immaturity is characterised by tightly packed, narrow seminiferous tubules with no lumen, surrounded by abundant interstitial tissue (Fig. 22A). The seminiferous epithelium comprised one cell layer of Sertoli cells with interspersed spermatogonia (Fig. 22). Seminiferous tubule diameters of immature animals ranged from 39.2 μm to 67.2 μm ($\bar{x}$: 53.0 μm ± 9.13; Table 10; Fig. 23). Early spermatogenesis was characterized by two to four cell layers of spermatogonia and spermatocytes in the seminiferous epithelium (Fig. 22B). No spermatids were present and very little interstitial tissue was present between the seminiferous tubules (Fig. 22B). Two individuals were found to be in early spermatogenesis, with seminiferous tubule diameters of 72.2 μm to 77.6 μm (Table 10, Fig. 23).

Table 10 Gonadal characteristics for different maturity stages in *Kogia breviceps*.

Maturity stage	Mean (SD)	Range	Sample size
Single testis weight (g)			
Immature*	42.34 (24.5)	13.8–83.6	13
Early spermatogenesis*	148.7 (69.9)	99.3–198.1	2
Late spermatogenesis	1000.7 (826.6)	457.5–1952.0	3
Mean testis length (mm)			
Immature*	123.8 (25.61	79.0–158.0	13
Early spermatogenesis*	155.5 (35.7)	130.5–181.0	2
Late spermatogenesis	310.0 (130.8)	220.0–460.0	3
Index of testis development (g/mm)[a]			
Immature*	0.33 (0.1)	0.16–0.57	13
Early spermatogenesis*	1.04 (0.7)	0.55–1.52	2
Late spermatogenesis	2.90 (1.2)	2.08–4.24	3
Seminiferous tubule diameter (μm)			
Immature*	53.0 (9.1)	39.2–67.2	12
Early spermatogenesis*	75.2 (3.5)	72.2–77.6	2
Late spermatogenesis	135.5 (64)	89.0–208.5	3

[a]=Mean testis weight/mean testis length per testis pair. Rows with an asterisk (*) are not significantly different from each other ($p \geq 0.0001$).

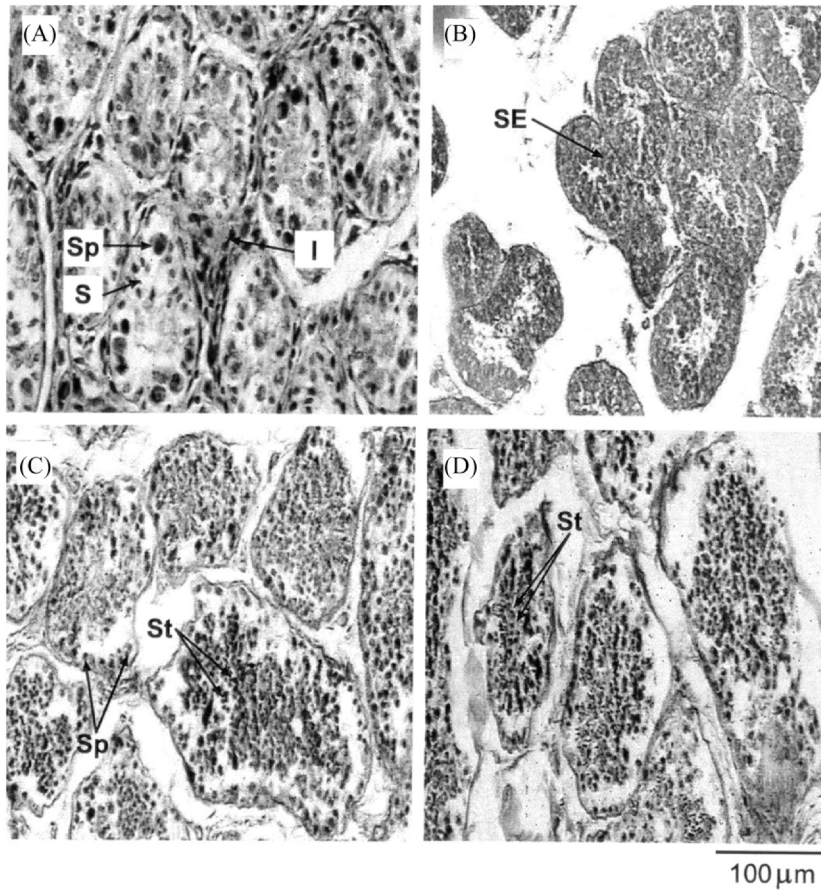

Fig. 22 Histological preparations of different maturity stages of the testes in *Kogia*. (A): Immature testis, characterised by tightly packed, narrow seminiferous tubules with no lumen and abundant surrounding interstitial tissue (I). Sp: Spermatogonia, S: Sertoli cells. (B): Early spermatogenesis is characterised by two to four cell layers of spermatogonia and spermatocytes in the seminiferous epithelium (SE). No spermatids are present and only little interstitial tissue is found between the seminiferous tubules. (C,D): Late spermatogenesis as indicated by large seminiferous tubules with an open lumen and a complex seminiferous epithelium with spermatogonia, spermatocytes and spermatids (St) present.

Three individuals (Table 10) were in late spermatogenesis, which was characterised by large seminiferous tubules with an open lumen (Fig. 22C and D). A complex seminiferous epithelium was present, which comprised three or more cell layers of spermatogonia, spermatocytes and spermatids, and little interstitial tissue was present (Fig. 22C and D). The seminiferous tubule diameters ranged

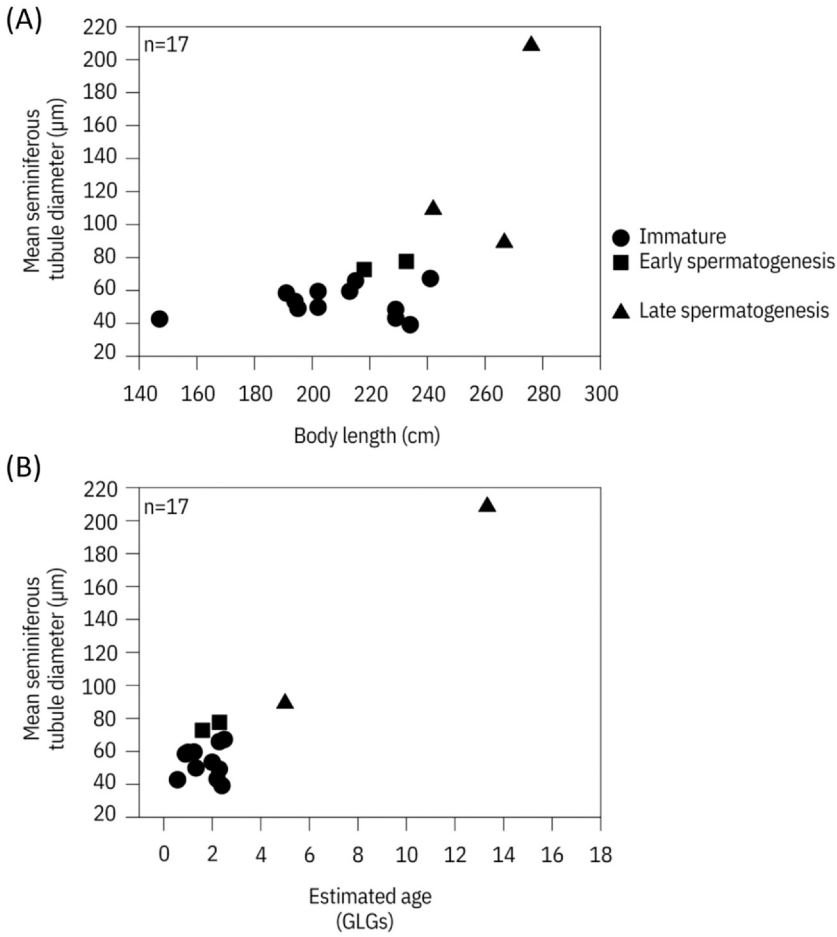

Fig. 23 Mean seminiferous tubule diameters for male *Kogia breviceps* of different maturity stages in relation to body length (cm) (A) and age (complete GLGs + increment) (B).

from 89.0 µm to 208.5 µm ($\bar{x}$: 135.5 µm ± 63.99) (Table 10, Fig. 23). No animal with testes in a mature but inactive or resting stage was observed and there was no evidence for a seasonal cessation of spermatogenesis.

3.5 Attainment of sexual maturity (ASM)

As expected from the length-frequency distribution of the sample, the majority of animals for which a tissue sample of the testes could be examined histologically were immature (Table 10).

Early spermatogenesis in male *K. breviceps* occurred at a mean testis weight of 148.7 g (n = 2) and a mean testis length of 155.5 mm (n = 2; Table 10, Fig. 24), which corresponds to ages between 1.6 and 2.3 years (Table 11, Fig. 24B), respectively. The three animals in late spermatogenesis had a mean testis weight of 1000.7 g (±826.6) and a mean testis length of 310 mm (±130.8; Table 10, Fig. 24). The age range for these animals was 5 to 13.3 years (Table 11, Fig. 24). The mean index of testis development was 1.04 for animals in early spermatogenesis and 2.9 for those in late spermatogenesis (Table 10). Some overlap of mean testis length occurred between immature animals and animals in early spermatogenesis (Table 10).

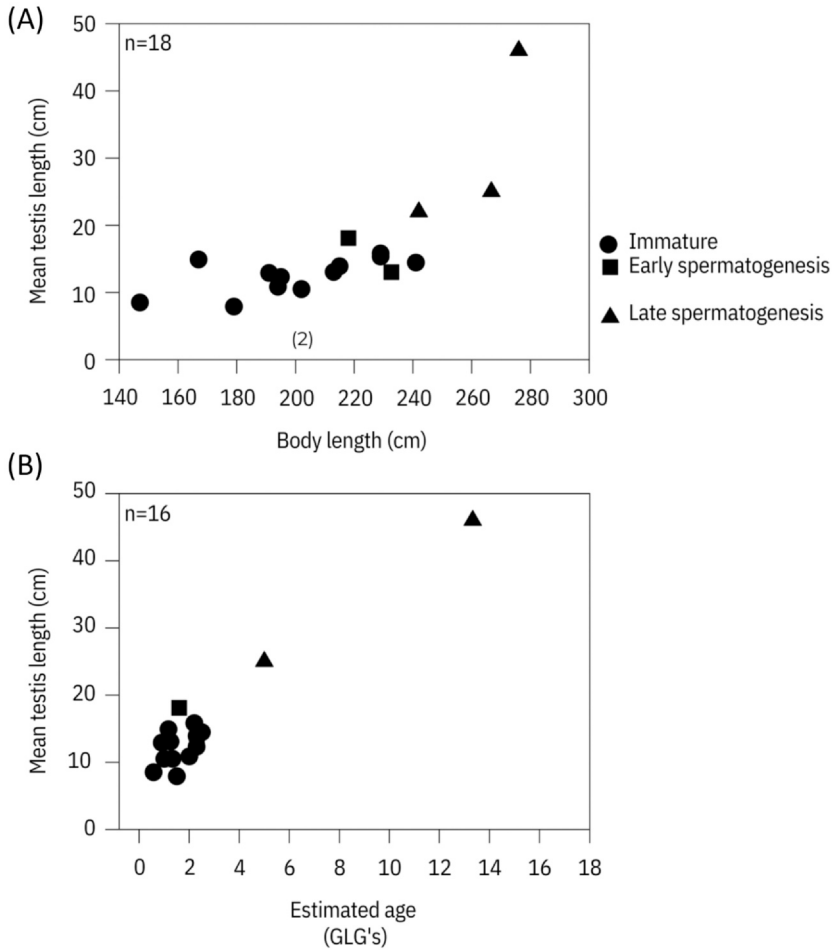

Fig. 24 Mean testis length (cm) as a function of body length (cm) (A) and estimated age (complete GLG's + increment) (B) in *Kogia breviceps*.

Table 11 Summary of the size and ages for different maturity stages for *Kogia breviceps* males. Determination of maturity was based on histological examination of the reproductive organs and subsequently only specimens for which the state of maturity could be confirmed were included (i.e. calves were excluded).

	Immature		Early spermatogenesis		Mature	
	n	Range	n	Range	n	Range
Age (GLGs)	13	0.6–2.5	2	1.6–2.3	2	5.0–13.3
Length (cm)	14	147.0–241.0	2	218–232.7	3	242.0–276.0
Mass (kg)	12	69.0–210.0	2	182.0–186	2	233.6–374.0

One-way ANOVA tables showed that there were significant differences between the mean testis weight ($p = 0.0007$), mean testis length ($p = 0.0003$), mean testis index ($p < 0.0001$), and mean seminiferous tubule diameter ($p = 0.0001$) of specimens that were immature, in early or in late spermatogenesis. A Tukey's multiple range test yielded significant differences between early and late spermatogenesis, as well as between late spermatogenesis and immature for all four categories, but not between immature and early spermatogenesis (Fig. 22).

The two male *K. breviceps* that were in early spermatogenesis measured 218 cm and 232 cm in length with combined testis weights of 198.6 g and 396.2 g, respectively (Table 11, Fig. 25). The shortest male in late spermatogenesis measured 242 cm and had a combined testis weight of 915 g (Fig. 25). Unfortunately, no age estimate was available for this animal. The youngest male in a late spermatogenic state was estimated to be 5 years old, measured 266.7 cm and had a combined testis weight of 1185 g (Table 11, Fig. 25). As the sample was too small to calculate a meaningful statistical estimate for the age and length at ASM a range between the oldest/longest immature animal and the youngest/shortest mature animal had to be taken as the onset of sexual maturity. In this sense a summary of the size and age ranges of immature and mature *K. breviceps* shows that ASM occurs between 2.5 and 5 years and 241–242 cm in *K. breviceps* (Table 11). However, the oldest male in early spermatogenesis was estimated to be 2.3 years old. If one takes the conservative approach and defines sexual maturity as the onset of late spermatogenesis, this would correspond to 5 years in male *K. breviceps*.

Compared to age, both body length and body weight appear to better define ASM (Table 11). Thus sexual maturity in males was reached between 241–242 cm and 210.0–233.6 kg (Table 11).

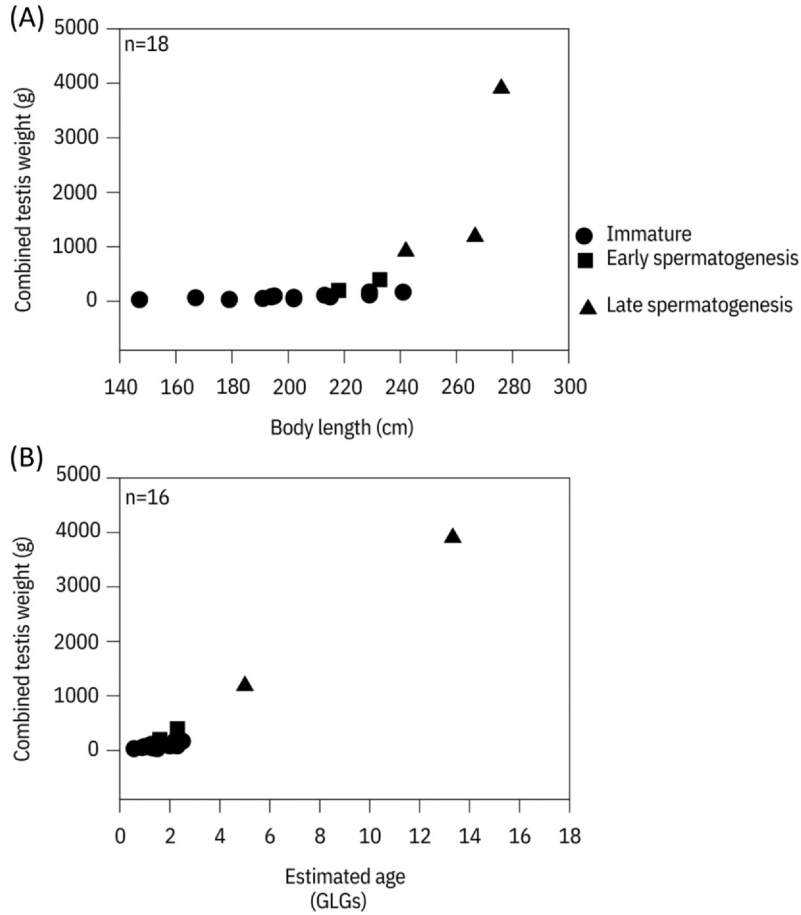

Fig. 25 Attainment of sexual maturity with body length (cm) (A) and age (complete GLGs + increment) (B) in male *Kogia breviceps*.

3.6 Testis weight as a percentage of body weight

The longest mature male *K. breviceps* had a combined testis weight of 3904 g or 1.04 % of its total body weight. It measured 276 cm and the estimated age for this animal was 13.3 GLGs, which indicated that it had reached physical maturity (see Fig. 9).

3.6.1 Seasonality

Unfortunately the small sample, which was biased towards immature males in *K. breviceps*, prevented a detailed examination of seasonality of spermatogenesis (Fig. 26). All stranded adult *K. breviceps* males were spermatogenically active.

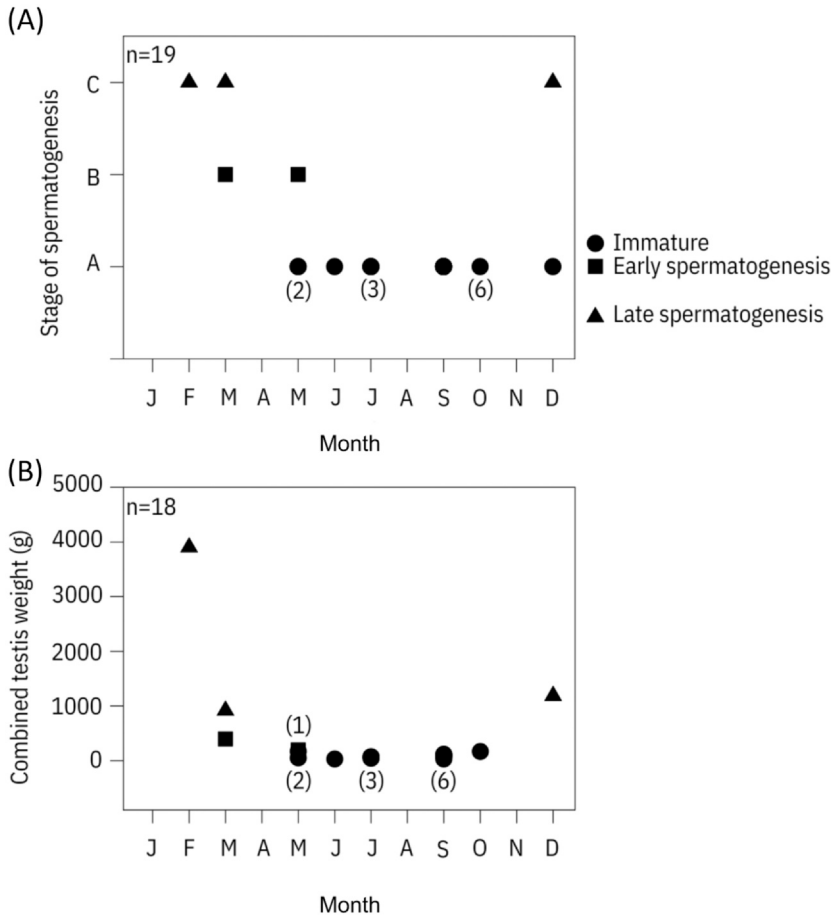

Fig. 26 Reproductive condition (A) and combined testis weight (B) over the year in male *Kogia breviceps*. Stage of spermatogenesis A: immature; B: early spermatogenesis; C: late spermatogenesis. Numbers in brackets are sample sizes when n > 1.

3.6.2 K. sima

Immature testes were observed in six *K. sima* (Table 12) and seminiferous tubule diameters of immature animals ranged from 34.6 μm to 52.0 μm ($\bar{x}$: 42.9 μm ± 7.0; Table 12; Fig. 27). One individual was found to be in early spermatogenesis, with a seminiferous tubule diameter of 65.0 μm (Table 12, Fig. 27).

Ten individuals were in late spermatogenesis (Table 12), which was characterised by large seminiferous tubules with an open lumen (Fig. 22C and D). A complex seminiferous epithelium was present, which comprised three or more

Table 12 Gonadal characteristics for different maturity stages in *Kogia sima*.

Maturity stage	Mean (SD)	Range	Sample size
Single testis weight (g)			
Immature	55.08	33.0–87.5	6
Early spermatogenesis	(21.7)	172.5	1
Late spermatogenesis	172.5	210.0–2461.5	12
	1317		
	(693.8)		
Mean testis length (mm)			
Immature	145.07	126.0–160.0	7
Early spermatogenesis	(12.9)	225.0	1
Late spermatogenesis	225.0	255.0–560.0	10
	395.15		
	(92.6)		
Index of testis development (g/mm)[a]			
Immature	0.41 (0.2)	0.3−0.6	7
Early spermatogenesis	0.77	0.8	1
Late spermatogenesis	2.61 (1.2)	0.8−4.2	10
Seminiferous tubule diameter (μm)			
Immature	42.9 (7.0)	34.6−52.0	6
Early spermatogenesis	65.0	65.0	1
Late spermatogenesis	100.2	87.1−123.2	10
	(12.2)		

[a]Mean testis weight/mean testis length per testes pair.

cell layers of spermatogonia, spermatocytes and spermatids, and little interstitial tissue (Fig. 22C and D). The seminiferous tubule diameters ranged from 87.1 μm to 123.2 μm ($\bar{x}$: 100.2 μm ± 12.16; Table 12, Fig. 27). No animal with testes in a mature but inactive or resting stage was observed and there was no evidence for a seasonal cessation of spermatogenesis.

The results previously reported for the length-frequency distribution of the sample were reflected in the samples available for histological examination of the testes: immature and mature animals were present in almost equal numbers (Table 12).

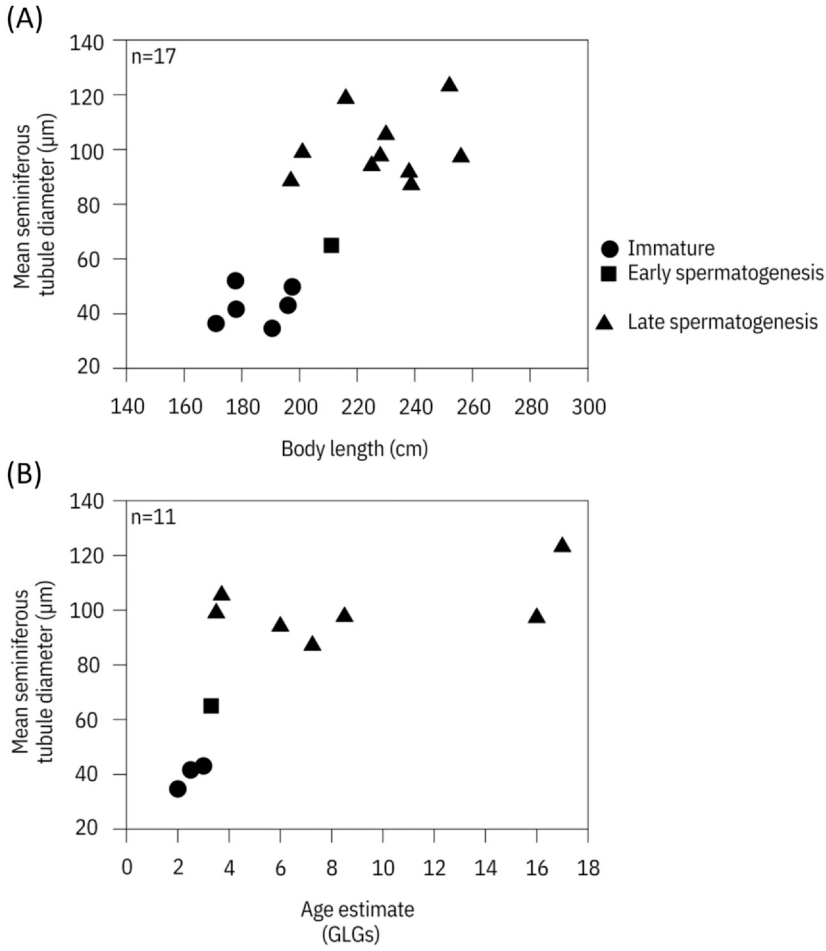

Fig. 27 Mean seminiferous tubule diameters for male *Kogia sima* of different maturity stages in relation to body length (cm) (A) and age (complete GLGs + increment) (B).

Only one animal was found to be in early spermatogenesis. It had a mean testis weight of 172.5 g and a mean testis length of 225.0 mm and an estimated age of 3.3 years (Tables 12 and 13, Fig. 28). Late spermatogenesis occurred at a mean testis weight of 1317 g and a mean testis length of 395.2 mm (Table 12, Fig. 28). Animals belonging to this maturity stage ranged from 2.6 to 17 years of age (Table 13). The testis development index was 0.8 for the animal in early spermatogenesis and the mean for animals in late spermatogenesis was 2.6 (±1.2; Table 12). No overlap between the different stages of maturity was found for any category.

Table 13 Summary of the size and ages for different maturity stages for *Kogia sima* males. Determination of maturity was based on histological examination of the reproductive organs and subsequently only specimens for which the state of maturity could be confirmed were included (i.e. calves were excluded).

	Immature		Early spermatogenesis		Mature	
	n	Range	n	Range	n	Range
Age (GLGs)	4	1.7–3.0	1	3.3	8	2.6–17.0
Length (cm)	7	171.0–197.5	1	211	11	197.0–256.0
Mass (kg)	4	98.5–111.8	1	114.5	9	124.0–303.0

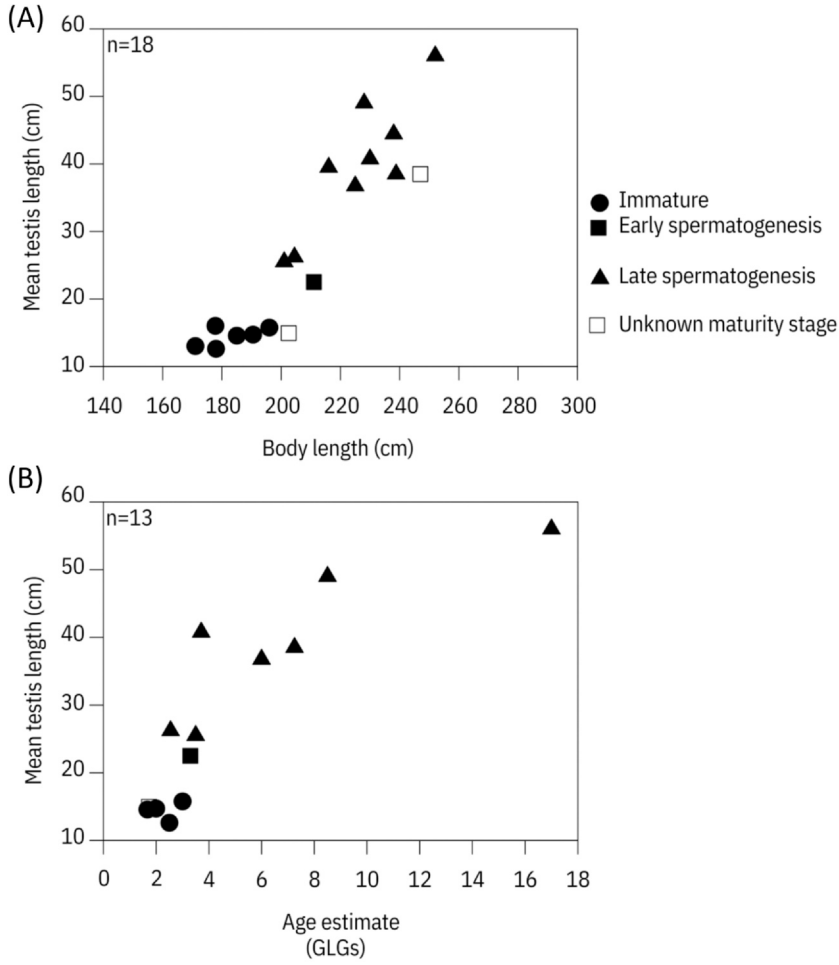

Fig. 28 Mean testis length (cm) as a function of body length (cm) (A) and estimated age (complete GLGs + increment) (B) in *Kogia sima*.

Whether or not the data obtained for the different stages of maturity were significantly different could not be tested, because of the low sample size of one animal in early spermatogenesis.

The oldest immature male was estimated to be three years old (Table 13) with a body length of 196 cm and combined testis weight of 190.9 g (Fig. 29). The youngest male in late spermatogenesis was 2.6 GLGs old (Table 13), measuring 204.5 cm with a combined testis weight of 556 g (Fig. 29). The animal in early spermatogenesis measured 211 cm, had an age estimate of 3.3 years and a combined testis weight of 345 g (Fig. 29).

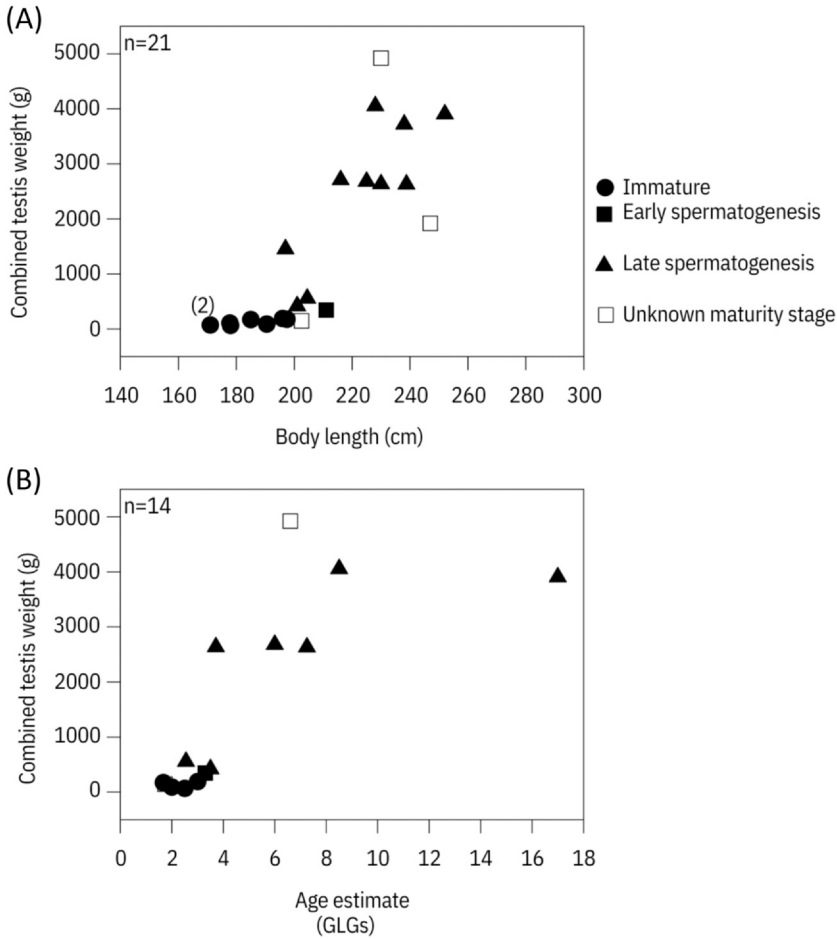

Fig. 29 Attainment of sexual maturity with body length (cm) (A) and age (complete GLGs + increment) (B) in male *Kogia sima*.

The shortest animal in late spermatogenesis measured 197 cm and had a combined testis weight of 1454 g (Fig. 29); no age estimate was available. Thus it appears that ASM occurred between 2.6 and 3 years of age in male *K. sima*.

The body length at ASM can be defined more accurately than in *K. breviceps* at 197 cm as the longest immature and the shortest mature male measured 197.5 cm and 197 cm, respectively (Table 13). Furthermore, sexual maturity was reached between body weights of 111.8 kg and 124.0 kg (Table 13).

3.7 Testis weight as a percentage of body weight

The maximum combined testis weight available for *K. sima* was 4923 g for a 230 cm long specimen weighing 240 kg (GLGs: 9). The combined testis weight made up 2.05 % of the total body weight of this animal. However, no testis tissue was available for examination from this specimen to ensure that spermatogenesis was occurring. Another animal that had a combined testes weight of 4053 g and was producing sperm, measured 228 cm and weighed 202.5 kg. The combined testis weight made up 2 % of its total body weight. No age estimate was available for the latter specimen, but according to the body lengths of both animals they had reached physical maturity (see Fig. 11).

3.7.1 Seasonality

All stranded adult *K. sima* males were spermatogenically active and the year-round presence of *K. sima* males in late spermatogenesis suggested an absence of seasonal testicular activity in this species (Fig. 30).

4. Discussion

4.1 Age determination

4.1.1 Tooth structure

The general description of the histology of longitudinal sections of *K. breviceps* teeth is in agreement with Ross (1979). The prenatal dentine is easily distinguishable from the postnatal dentine by a clear, narrow neonatal line and the growth layers in the dentine can be distinguished into GLGs. However, it appears that the present technique may give a better resolution than the one employed by Ross (1979). His sections were of the same thickness or thinner (200 μm) than the ones in the present study (300 μm),

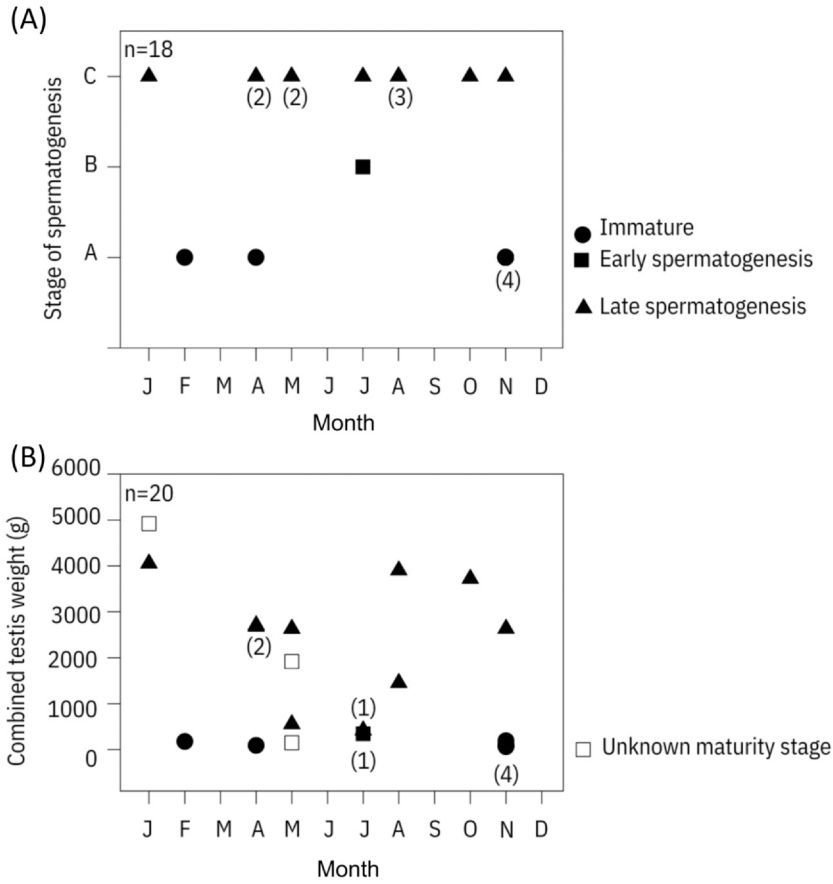

Fig. 30 Reproductive condition (A) and combined testis weight (B) over the year in male *Kogia sima*. Stage of spermatogenesis A: immature; B: early spermatogenesis; C: late spermatogenesis. Numbers in brackets are sample sizes when n > 1.

which may have resulted in loss of resolution and hence inability to distinguish between laminae. In addition, the use of polarized light in the present study appears to improve the resolution of the laminae significantly, which was also seen for Cape fur seal *A. pusillus pusillus* teeth (Oosthuizen, 1997). This technique uses the refractional properties of the apatite crystals in the teeth of these animals and thus enables distinction between layers, which would not be possible with normal light microscopy. Why stains such as haematoxylin (present study) or toluene blue (Ross (1979) did not yield satisfactory results for teeth of either *Kogia* species is unclear.

Contrary to Ross' findings (1979), an enamel cap was found in some young animals in the present study. All *K. breviceps* with an enamel cap were below one year of age and originated from Australia, indicating that the presence of an enamel cap may be more prevalent in Australian animals. For *K. sima,* an enamel cap was found for a South African specimen with two GLGs; the age estimate of 8 GLGs for the *K. sima* from Australia with an enamel cap is considered to be an overestimate. This indicates that something causes wear or grinding down of the teeth and thus loss of the enamel cap in older animals, which is supported by the worn tooth tips found in many adult animals of either *Kogia* species. In addition, the diet or environmental conditions to which the Australian animals were exposed to, may result not only in a clearer GLG pattern in the teeth, but also facilitate the formation of an enamel cap. The reason for GLGs appearing clearer and more distinct in Australian specimens may be a difference in overall condition between the Australian and South African population, possibly as a direct result from differences in diet. Another possibility may be different methods in the storage of the teeth.

The high degree of tooth wear found in the two *Kogia* species is puzzling. It is unlikely that this would result from feeding as cephalopods are relatively soft and would not cause increased abrasion of the teeth. Furthermore, the redundancy of teeth in teuthophagous odontocetes and subsequent reduction in the number of teeth would suggest that they are not used excessively (Heyning and Mead, 1996; MacLeod, 1998). Thus the extensive wear of teeth in the two *Kogia* species may have an alternative, as yet unknown origin. Tooth wear may vary between individuals, especially between sexes due to differences in diet, as well as between populations.

4.1.2 Age determination

The lack of significant difference between the age estimates from the present study and the ones made by Ross (1979) indicates that the interpretation of the GLGs was the same by both observers. The greatest source of error in age determination of *T. truncatus* is the misinterpretation of GLGs (Hohn et al., 1989). Errors are predominantly due to accessory layers and poorly prepared sections (Hohn et al., 1989). Any guide or "model" for estimating age from odontocete teeth must take into account that accessory layers are often a part of the GLG pattern (Hohn et al., 1989) and this is particularly the case with *Kogia* teeth as the number of accessory layers is high in the two species. This highlights the need to standardise age estimation techniques for *Kogia* in order to compare results from different studies.

Age estimation in *K. sima* seems less reliable than in *K. breviceps*. Ross (1979) indicates that the number of accessory layers present in the teeth in addition to the smaller tooth size and the resulting compression of GLGs make age estimation in this species exceedingly difficult. Although Klevezal' and Kleinenberg (1967) report that the method of preservation of the teeth does not appear to make a difference to the visualisation of the GLGs, there is some evidence that it might (pers. obs.; Peter Best, pers. com.). In addition, the readability of the teeth varies with the species examined (Kasuya et al., 1988) and inter-species variability in the genus *Stenella* shows that postnatal dentine in spinner dolphins *S. longirostris* has a better readability than in spotted dolphins *S. attenuata (*Perrin et al. (1977). Similarly, Bloch et al. (1993) state that the teeth of long-finned pilot whales *G. melas* originating from one school are easier to read than those from other schools. Genetic similarity, post-mortem changes in tissues, predisposition to disease, and environmental stress, such as malnutrition, are all possible reasons for this variation (Bloch et al., 1993). As mammalian teeth from species inhabiting colder areas show a clearer definition of laminae than those from animals inhabiting warmer areas (Grue and Jensen, 1979 in: Lockyer, 1995a; Langvatn, 1995), the differences in distribution patterns between the two *Kogia* species, with *K. breviceps* inhabiting cooler waters than *K. sima* may be reflected in the teeth. These factors combined with the high number of accessory layers, smaller tooth size and resulting compression of GLGs in *K. sima,* would explain the differences in readability between the teeth of *K. breviceps* and *K. sima.*

It should be kept in mind that for both *Kogia* species the present results on age determination can only be viewed as an estimate. Estimates of age are imprecise for most cetacean species as the definite rate of dentine and cementum deposition is not known for the majority of them. Furthermore, the age estimation is subjective and based on the observers' interpretation of GLGs. This imprecision tends to increase with the age of the animals. Although the present study presents the first age estimates for a comparatively large sample of *Kogia* and thus a good start into exploring the life history strategy of both species, the technique may be refined and perfected once teeth and age estimates from more animals become available. In particular, reading teeth from animals originating from different geographical locations may aid in defining the GLG patterns in the teeth of the two *Kogia* species as was found with the Australian samples in the present study.

The high correlation between dentinal and cemental layers for both *K. breviceps* and *K. sima* leads to the conclusion that both are deposited at

the same rate in both species, but after the closure of the pulp cavity, only cemental layers continue to be deposited. Similar results have been observed in other odontocetes (Sergeant, 1962; Kasuya and Marsh, 1984; Cockcroft and Ross, 1990a; Bloch et al., 1993). Furthermore, in most odontocetes, age estimation from dentinal layers alone has been hindered by the occlusion of the pulp cavity at some stage during the life of the animal (Sergeant, 1962). In general, dentinal counts are considered to be more reliable, with cemental counts only being used after occlusion of the pulp cavity (Cockcroft and Ross, 1990a; Bloch et al., 1993). Without direct evidence, it is assumed that the cemental deposition is homogenous throughout life (Kasuya et al., 1988).

On average, about 12 layers are laid down in the dentine of long-finned pilot whales *G. melas* before occlusion of the pulp cavity (Sergeant, 1962) and in bottlenose dolphins *T. truncatus* the pulp cavity closes at about 12 years, which almost coincides with the age at attainment of sexual maturity (Cockcroft and Ross, 1990a). Thus the start of the occlusion of the pulp cavity in *K. breviceps* at 14 years and in *K. sima* at 11 years appears to agree well with data for other odontocetes.

Similarly, cemental layers are used as an age estimate when osteodentine formation prevents age estimates to be made from dentinal layers (Miyazaki, 1984). Teeth of the two *Kogia* species appear to have an unusually high percentage of osteodentine compared to other odontocetes (Sergeant, 1962; Bloch et al., 1993). As expected, the occurrence of osteodentine increases with age in long-finned pilot whales *G. melas*, albeit in an irregular manner (Lockyer, 1995a). This is due to the fact that it may form at an early age, but not embed in the dentine until later, if at all (Lockyer, 1995a). The cause of osteodentine formation is not understood (Lockyer, 1995a). It has, however, been suggested for terrestrial mammals that a big mechanical load results in intensive deposition of secondary dentine and as a result many accessory bands form in the dentine (Klevezal' and Kleinenberg, 1967).

5. Length at birth and foetal growth rate

Based on the data from the present study, the length at birth for *K. breviceps* lies around 120 cm and the weight around 53 kg, compared to 103 cm and 14 kg for *K. sima*. These results agree well with Ross' (1979) estimate of the length at birth of 120 cm for *K. breviceps* and 100 cm for *K. sima*.

These data indicate that *K. breviceps* neonates are born at 40.5 % of mean adult asymptotic length (296 cm), whereas it is 40.2 % in *K. sima* (mean adult asymptotic length: 256.5 cm). This is in agreement with Scott's (1949) estimate that the length of neonates ranges between 20–50 % of maximum adult length depending on the species, with 25–30 % for the mysticetes. A more recent estimate for mysticetes is 25 % (Evans, 1987) and 40–48 % for odontocetes (Chivers, 2001).

However, the largest foetus ever reported for a *K. breviceps* was 125 cm from a stranded female in California, USA (Eliason and Houck, 1986), while the shortest neonate reported for a *K. sima* in the literature is 95 cm for an animal, which was thought to be less than a week old (Caldwell and Caldwell, 1989). Some variation of birth length is expected within a species, especially when comparing animals from different geographical locations.

The data calculated here for length at birth for the two *Kogia* species using Scott's (1949) equation (*K. breviceps*: 123.6 cm, *K. sima*: 120 cm) differ somewhat from the estimated length at birth based on actual calf and foetus lengths (*K. breviceps*: 120 cm; *K. sima*: 103 cm). As Scott based his equation on both mysticetes and odontocetes combined, some inaccuracies are to be expected. In addition, he used maximum recorded body length in his formula rather than average or mean adult body length. However, if only considered as a rough estimate of length at birth the data are not too far off from the observed length at birth for either species of *Kogia* in the present study.

The results for the foetal growth rate in cm/day during the linear part of the growth curve using Kasuya's (1977) formula indicate that growth is marginally faster in *K. breviceps* (0.34 cm/day) than *K. sima* (0.31 cm/day). Although Kasuya derived his equation from data on delphinids, this is to be expected as it was found that those species of cetaceans that produce a larger full-term foetus also exhibit a higher foetal growth rate rather than a prolonged gestation period (Huggett and Widdas, 1951; Laws, 1959; Frazer and Huggett, 1974). In comparison, the Ganges dolphin *Platanista gangetica*, the harbour porpoise *Phocoena phocoena* and the bottlenose dolphin *Tursiops truncatus* all have lower specific foetal growth rates of 0.23, 0.28 and 0.28 cm/day, respectively (Frazer and Huggett, 1974). Larger odontocetes, such as the beluga *D. leucas* and Baird's beaked whale *Berardius bairdii,* have specific foetal growth rates of 0.56 and 0.95 cm/day (Frazer and Huggett, 1974; Kasuya, 1977). A similar foetal growth rate to *Kogia* was seen in the long-finned pilot whale *G. melas* with 0.33 cm/day

(Frazer and Huggett, 1974). Interestingly, data presented on *K. breviceps* indicate a specific foetal growth rate of 0.8 cm/day (Frazer and Huggett, 1974), which does not conform with those of the present study. The main reason for this appears to be that the estimated gestation period was only 270 days or nine months (Frazer and Huggett, 1974), which is in contrast to 12 months in the present study. Considering the trend of increased foetal growth rate with increased length at birth (and thus increased adult length), the data from the present study are in better agreement than those presented by Frazer and Huggett (1974).

6. Growth

The growth curves generated for both *K. breviceps* and *K. sima* show a rapid increase of length with age. Cetaceans generally show rapid growth subsequent to birth, especially with regards to mass, and growth rate decreases gradually with age (Hohn, 1980; Cockcroft and Ross, 1990a). The growth rate of bottlenose dolphins *T. truncatus* off South Africa is greatest during the first year of life (Cockcroft and Ross, 1990a). Mass increases by 255 % in the first year, but only by 49 %, 13.5 % 10.6 % and 3.8 % in the following years (Cockcroft and Ross, 1990a). In contrast, length increases less rapidly by 57 %, 15.2 %, 3.7 %, 4 % and 5.5 % (Cockcroft and Ross, 1990a). Similarly, the growth rate of bottlenose dolphins *T. truncatus* from the western North Atlantic is high in the first year, with an increase in length of 53 %, an average of 10 % during the second year, and a considerable slowing down of the growth rate after 3 GLGs (Hohn, 1980).

The data for either *Kogia* species from the present study also show some variation of length with age, which, considering the above data for other odontocetes, appears common among cetaceans. High variability in total lengths of individuals in any age class is also observed for *T. truncatus* from the western North Atlantic, which indicates that total length alone is not a reliable indicator of the age of the animals (Hohn, 1980). Juvenile *T. truncatus* from Sarasota, Florida, also show considerable variation in size-at-age (Read et al., 1993); for example, a 200 cm long female could be either one, two, or three years old. As these data are derived from known age animals, error due to age estimation from GLGs in the teeth can be excluded.

Both sexes of both species of *Kogia* continued growing past their ASM, which is not necessarily common among odontocetes of similar size. Among larger mammals, females usually start breeding before they have

reached adult body weight (Clutton-Brock and Iason, 1986); however, in bottlenose dolphins *T. truncatus* sexual maturity in the females coincides with physical maturity (Read et al., 1993). Males continue to grow past their attainment of sexual maturity, at which stage they have attained only 70 % of their asymptotic mass (Read et al., 1993). In captive populations, older males are known to sire more offspring than do young males, and genetic evidence suggests that this is also true for the Sarasota population (Duffield and Wells, 2002). This continued growth in males suggests that size may be an important factor in the mating system. Size at ASM is discussed in more detail below (see section on sexual dimorphism).

7. Length and age at physical maturity

In the present study, physical maturity could be calculated separately for females and males using the von Bertalanffy growth equation. While Ross estimates physical maturity based on the fusion of epiphyses to occur between 305 cm and 330 cm for both sexes of *K. breviceps* (Ross, 1979), the results from the present study indicate that physical maturity occurs at a shorter body length in males (286 cm). However, the estimate of the occurrence of physical maturity at 306 cm for female *K. breviceps* is in agreement with results from the previous study. An increased sample size may be accountable for these differences between the two studies and the skewed samples towards immature males may contribute towards the shorter asymptotic length in males. The age at physical maturity appeared to be similar in both sexes of *K. breviceps* and occurred around 15 years.

For *K. sima,* the asymptotic length was calculated as 249.1 cm for females and 263.8 cm for males. In contrast, Ross (1979) could only calculate the onset of physical maturity for the two sexes combined. The shortest physically mature animal measured 247 cm and was a male (Ross, 1979). The data obtained here for *K. sima* may be best compared to those for a similar sized odontocete like the bottlenose dolphin *T. truncatus*. Asymptotic length for these animals off South Africa occurs at 238 cm for females and 243 cm for males (Cockcroft and Ross, 1990). The age at physical maturity occurred around 13 years in female *K. sima*, while it appeared to be slightly later in males, corresponding to 16 years. Again, these data are comparable to data obtained from bottlenose dolphins off South Africa, where both males and females reach physical maturity between 12 and 15 years (Cockcroft and Ross, 1990).

8. Maximum length and age

Data from the present study on the maximum length recorded for female and male *K. breviceps* (327.6 cm and 330.5 cm, respectively) exceed the previous records of 309.5 cm and 325 cm reported for South African animals (Ross, 1979), presenting a substantially greater maximum length for female *K. breviceps* than previous studies. In comparison, Odell et al. (1984) report the mean adult length of females as 303 cm and that of males as 307 cm based on strandings along the Florida coastline. These data differ somewhat from South Africa and geographical variation in body length is observed quite frequently among odontocetes (Cockcroft and Ross, 1990).

In the present study, the longest female *K. sima* measured 274.3 cm and the longest male 260.4 cm. This is a slight increase from the longest specimen reported for South Africa, which was a 264 cm long female (Ross, 1979).

The maximum age estimates obtained for *K. breviceps* of 22 years for females and 13 years for males (16 for a male animal from Australia) are in agreement with previous work on the species. For specimens from New Zealand, the maximum age estimates are 12.5 and 16 + for females and males, respectively (Tuohy et al., 2001), while a female from New Caledonia was estimated to be 19 years of age (Bustamante et al., 2003). The shorter life expectancy of *K. breviceps* males in comparison with females is possibly a reflection of the biased sample towards immature males and mature females. However, it may also be a true reflection of differential life spans in this species and should be taken into consideration in future studies on its life history and social system.

Maximum age estimates in *K. sima* are also higher for females than for males (21.5 and 17, respectively), with a difference of five years. As the sample for this species is normally distributed, this difference may be a true indication of different life expectancies in this species. Male long-finned pilot whales *G. melas* off Newfoundland have a higher mortality throughout life than females and subsequently females attain higher maximum ages than males (Sergeant, 1962; Bloch et al., 1993). However, additional samples for either *Kogia* species would provide more insight into this aspect.

The maximum life span of 16–23 years for *K. breviceps* and 17–22 years for *K. sima* is surprisingly low for odontocetes the size of *Kogia*. Similar life expectancies have, to date, only been reported from some of the smallest odontocetes, such as the vaquita *P. sinus* (21 years; Hohn et al., 1996). In Hector's dolphins *C. hectori,* the maximum age recorded is 19 GLGs for females and 20 for males (Slooten, 1991). For harbour porpoises *P. phocoena*,

maximum age estimates of 24 were reported from the population off California and from British waters (Hohn and Brownell, 1990; Lockyer, 1995b). In contrast, odontocetes the size of *Kogia* reach maximum ages around 50 to 60 years (Perrin and Reilly, 1984). The bottlenose dolphin *T. truncatus*, for example, which has a similar body length to *K. sima,* reaches maximum ages in excess of 40 years (Cockcroft and Ross, 1990).

9. Body weight

Data on body weights for medium to large odontocetes, including the two *Kogia* species, are scarce in the literature, probably due to the logistical difficulties involved. Thus, the present sample represents the first comprehensive collection of body weight data for the two *Kogia* species. Ross (1979) presents data for three animals, one of which was a foetus and the other rather emaciated. Weights of another cow stranded with its female calf were added in his 1984 publication (Ross, 1984). In his summary of published data on weights of another six animals from the literature, the maximum weight is 417 kg for an animal of 298.6 cm of unknown sex (Tomilin, 1957 in: Ross, 1979). This is exceeded in the present study by two females each weighing 480 kg. Data published by Marten (2000) on a 179 cm long male *K. breviceps* weighing 79 kg and by Price et al. (1984) on a 173 cm long female *K. breviceps* weighing 84 kg appear to fit in well with the present data. However, the weight of 450 kg reported for a 317 cm long male stranded in New Brunswick, Canada, exceeds the maximum weight recorded for a male *K. breviceps* in the present study (374 kg) and appears to be the maximum reported for a male *K. breviceps* (McAlpine and Murison, 1997).

Weight at birth was estimated to be around 53 kg in *K. breviceps* in the present study. As there appear to be no published data in the literature, this is the first estimate of birth weight of this species. In addition, birth weights of odontocetes are scarce in the literature, making a comparison with other species difficult. However, Best (2007) produced a length/ weight formula for the species based on 18 animals from South Africa.

For *K. sima,* published data on body weights for 11 animals range from 47.3 kg for a 136 cm long female to 209.1 kg for a 235 cm long female from South Africa (Ross, 1979). Previously published data ranged from 61.5 kg to 156 kg (Ross, 1984). Thus, the data from the present study present new record weights for the species. In addition, Best (2007) produced a length/ weight formula for the species based on 25 animals from South Africa.

Weight at birth was estimated to be between 13 kg and 15 kg in the present study, with length at birth being around 103 cm. This supports previous data on a 105 cm long *K. sima* calf, which weighed 20 kg (Carvan, 1988).

9.1 Female reproduction

9.1.1 Reproductive anatomy

The morphological characteristics of the ovaries and *corpora* of the two *Kogia* species as described by Beckmen (1986) and Ross (1979) were in agreement with the findings for the present study. In addition, the ovaries of both *K. breviceps* and *K. sima* get darker in colour with age from a beige-pink over dark-brown to black as reported by Beckmen (1986). There are conflicting results in the literature whether the CLs of the two *Kogia* species are pedunculate (Harrison et al., 1972; Ross, 1979) or not (Beckmen, 1986). Re-examination of Ross' (1979) material with additional material revealed that, although the CLs protrude from the surface of the ovary, they are not truly pedunculate.

In general, the CL of pregnancy does not change size throughout gestation (Matthews, 1938; Kasuya et al., 1974; Harrison et al., 1981; Marsh and Kasuya, 1984; Perrin and Donovan, 1984; Dans et al., 1997), but may increase slightly in early pregnancy until the foetus has reached a certain length and then regresses again slightly (Sergeant, 1962; Best, 1967; Miyazaki, 1984). However, Harrison et al. (1981) observe wide individual variation in the CL volume (or index) against foetal length and similar results are reported in the present study for both species of *Kogia*.

10. Ovarian symmetry

Both ovaries are equally functional in *K. breviceps*, but in *K. sima* the left ovary is more active than the right one. Ohsumi (1964) suggests that one criterion for the classification of Cetacea could be the type of accumulation of *corpora* in the ovaries. Accordingly, the results from the present study show that *K. breviceps* would be classed as having a Type I accumulation rate like the sperm whale *P. macrocephalus* and the mysticetes, which is in agreement with previous findings (Ohsumi, 1964; Harrison et al., 1972). However, *K. sima*, although ovulating from both ovaries, would be classed as having a Type II or III accumulation rate. An equal accumulation pattern between the two ovaries is generally regarded as more "primitive" and accumulation predominantly in one ovary as more

derived (Heyning, 1984, pers. com.). A similar trend was found in the evolution of the nasal passages of cetaceans from the primitive condition in mysticetes (double nares, nasal passage not confluent) to the intermediate condition in Physeteridae and Kogiidae (single blowhole, nasal passages not confluent; Schenkkan and Purves, 1973; Heyning and Mead, 1990) to the most derived state in all other odontocetes (single blowhole, nasal passages confluent; Heyning, 1997). Thus, the results for ovarian symmetry in the two species of *Kogia* may reflect a possible evolutionary history from the mysticetes to the odontocetes, as mysticetes, *Physeter* and *K. breviceps* ovulate from both ovaries equally and *K. sima* and delphinids ovulate predominantly from the left ovary (Ohsumi, 1964). In addition, it is interesting to note that the Ziphiids also show a Type I accumulation rate like the mysticetes, and *K. breviceps* and Physeter (Ohsumi, 1964). However, sample sizes in the present study are still small and additional samples would help clarify this point.

11. Attainment of sexual maturity (ASM)

11.1 Ovarian weight

The onset of sexual maturity in *K. breviceps* occurred between combined ovary weights of 12.2 g and 17.4 g. Ovarian weight was not a good indicator of ASM in *K. sima* as it varied substantially depending on the condition of the latest CL. It is unlikely that inaccuracies in age estimation played a role here since a good relationship between increasing age and increasing number of *corpora* was found and the age determination proved to be reliable. The lowest combined ovary weight of 3.52 g for a female with one seemingly infertile ovary or 4.57 g for a mature female with two functional ovaries and six CAs in *K. sima* is surprising. However, combined ovary weights as low as 2.0 g, 3.0 g, 3.3 g and 4.2 g for mature females of spotted dolphin *S. attenuata*, Hector's dolphin *C. hectorii* (Slooten, 1991), Tucuxi *Sotalia fluviatilis* (Harrison and Brownell, 1971), and the vaquita *P. sinus* (Hohn et al., 1996) have been reported. The abovementioned species are all smaller in body size than *K. sima* and scaling almost certainly has an effect on ovary weight as well. Marsh and Kasuya (1984) found an overall increase of ovarian weights with increasing length and age in short-finned pilot whales *G. macrorhynchus*, but observed a considerable variation of ovary weights for animals of the same age or length. A large overlap in ovarian weights between immature and mature animals was also reported

for sperm whales *P. macrocephalus* (Best, 1967), although the effects a large CL may have on the weight of the ovary were removed by placing pregnant females in a different category. The macroscopic (or histological) examination of the ovaries for *corpora* remains the most reliable indicator for the onset of sexual maturity in cetaceans.

11.2 Body length

The length at ASM of 262 cm for *K. breviceps* and 215 cm for *K. sima* agrees well with the results of 270–280 cm and 210–220 cm, respectively, reported previously for the South African population (Ross, 1979). Furthermore, they indicate that sexual maturity occurs at 85.62 % and 86 % of asymptotic body length in *K. breviceps* and *K. sima*, respectively, which is in good agreement with the mean of 85.1 % proposed by Laws (1956) for all female cetaceans. Odell et al. (1984) report that the smallest adult *K. breviceps* female examined measured 260 cm, but subsequent data presented by Credle (1988) include a 252 cm long lactating female. The shortest mature *K. sima* female in her dataset was a 218 cm long lactating female. The fact that both these females were lactating suggests that the actual length at first ovulation for animals from the south-eastern United States may be somewhat shorter than that from South Africa. Similarly, Reyes and van Waerebeek (1992) report on a 260.5 cm long female *K. breviceps* from Peru, which was sexually mature. For striped dolphins *S. coeruleoalba* factors affecting size differences between parts of the population inhabiting different areas of the Mediterranean include stronger seasonality and lower population density, leading to larger individuals (Calzada and Aguilar, 1995). Differences in body sizes between different populations of the same species have also been attributed to food quality and quantity (Bryden, 1972; Read and Gaskin, 1990; Bloch et al., 1993; Di-Méglio et al., 1996; Read and Tolley, 1997).

11.3 Age

The estimate of age at ASM from the present study may be somewhat imprecise due to the small number of first time ovulators available (DeMaster, 1984; Read, 1990a). However, estimates for age at ASM have not been attempted before for any population of either species of *Kogia*. The relatively low age estimate at ASM of 5 GLGs for both *K. breviceps* and *K. sima* is somewhat surprising for odontocetes of a comparatively large body size. Subsequent studies on a small sample of *K. breviceps* females stranded in New Zealand, however, determined that animals between 5 and 7 GLGs were mature (Tuohy et al., 2001), which supports the present

results. Among the odontocetes, similarly low ages at sexual maturity are usually only found in the porpoises (Perrin and Reilly, 1984). Mean age at sexual maturity in female harbour porpoises *P. phocoena* was estimated to be between 3.15–3.44 years depending on the method used (Read, 1990a). In the vaquita *P. sinus,* sexual maturity occurs between three and six years (Hohn et al., 1996). But even among the mysticetes, which reach sexual maturity on average around eight to ten years (Lockyer, 1984), there are some exceptions to be found. The average age at which the humpback whale *M. novaengliae* reaches sexual maturity is estimated to be five years (Clapham and Mayo, 1990; Clapham, 1992). The implications of these relatively low ages at ASM in both *Kogia* species in relation to other odontocetes will be discussed in detail below.

11.4 Body weight

Similarly to male *Kogia*, there are no previous records for body weights at ASM for females of either species. Thus the present data of ASM between 272.16 kg and 301 kg for female *K. breviceps* and 155.58 kg and 169 kg for female *K. sima* present the first record for the two species. In addition, these data indicate that sexual maturity occurs at higher body weights in females than in males for both species.

11.5 Ovulation rate and reproductive cycle

11.5.1 Ovulation rate

The high correlations (r^2 = 0.86 for *K. breviceps* and 0.65 for *K. sima*, respectively) between *corpora* counts and age estimates suggest that in both *Kogia* species *corpora albicantia* persist throughout life as they do in most other cetaceans (Perrin and Reilly, 1984; Read, 1990a); this supports previous findings for *Kogia* (Harrison et al., 1972; Ross, 1979).

The annual ovulation rate of 0.9 calculated for mature *K. breviceps* in combination with the observed seasonal birth and mating season shows that females ovulate annually. The deviation from parity is probably due to some females failing to conceive in one year and subsequently having to wait until the following year's mating season. Although the majority of cetaceans have a reproductive cycle of two to three years (Best et al., 1984; Brownell, 1984; Gaskin et al., 1984; Lockyer, 1984; Perrin and Reilly, 1984), annual reproductive cycles have been reported for some species, like the harbour porpoise *P. phocoena* (Gaskin et al., 1984; Read and Gaskin, 1990; Sørensen and Kinze, 1994; Read and Hohn, 1995), Dall's porpoise *P. dalli* (Kasuya, 1978; Ferrero and Walker, 1999), minke whale *B. acutorostrata* (Masaki, 1979; Lockyer, 1984),

and in some humpback whales *M. novaeangliae* (Clapham and Mayo, 1990; Straley et al., 1994). There is also some evidence, although scanty, that the franciscana *P. blainvillei* shows annual reproductive cycles, with a possible post-partum oestrus (Brownell, 1984). A post-partum oestrus and pre-implantation pregnancy has also been suggested for the harbour porpoise *P. phocoena* (Gaskin et al., 1984; Read, 1990b; Sørensen and Kinze, 1994). Most adult harbour porpoise females spend much of the year simultaneously pregnant and lactating, nursing the current calf and carrying next years' offspring (Read and Hohn, 1995). Annual ovulation rates reported for other cetaceans with annual reproduction are close to the one reported here for *K. breviceps* and include 0.91 for Dall's porpoise *P. dalli* (Ferrero and Walker, 1999) and 0.96 (Masaki, 1979) and 0.81 (Best, 1982) for the minke whale *B. acutorostrata*. But even in species that usually exhibit a two-year reproductive cycle, like the fin whale *B. physalus* and the common dolphin *Delphinus delphis*, some females have been reported to be simultaneously lactating and pregnant (Lockyer, 1987; Mendolia, 1989). Studies of the humpback whale *M. novaengliae* have shown that, although the average reproductive interval is two years, there is considerable individual variability, ranging from one to five years (Clapham and Mayo, 1990) and often individuals show successful annual reproduction (Straley et al., 1994). Although it is likely that postpartum ovulation is common in humpback whales, possibly only a certain percentage of mature females can maintain a pregnancy every year as sufficient prey must be found to sustain it (Wiley and Clapham, 1993; Straley et al., 1994).

The annual ovulation rate for *K. sima* females would indicate that the reproductive cycle lasts roughly one and a half years. However, the data on birth and mating season indicate that reproduction is annual in most females. The annual ovulation rates of 0.66 (Read, 1990a) and 0.68 (Read and Hohn, 1995) reported for harbour porpoises are close to the one reported here for *K. sima* (0.7) and is typical of the annual reproduction of *P. phocoena* (Read, 1990a). As a number of *K. sima* in the present study were also found to be simultaneously pregnant and lactating, *K. sima* may also exhibit annual ovulation. However, depending on environmental conditions as well as the constitution of the female, some females may probably only reproduce every other year at least some of the time. This would explain the deviation from an annual ovulation rate. The deviation from unity in the harbour porpoise data may have resulted from younger females ovulating more than once a year (Read, 1990a), but no evidence for that was found for *K. sima* in the present study.

The individual variation of the accumulation rate of *corpora* in the present study is common in cetaceans and is a reflection of differences in the annual ovulation rate between individuals as well as variation in the attainment of sexual maturity (Perrin et al., 1976; Kasuya and Marsh, 1984; Read and Hohn, 1995). Unfortunately the present sample was too small to attempt to fit a non-linear curve to the data or correct for individual variation in age at ASM (Read and Hohn, 1995).

The two *K. breviceps* females with the highest *corpora* count of 16 CA had age estimates of 19 and 22 GLGs. The highest number of *corpora* reported for a female *K. breviceps* in the literature was 29 for an animal stranded in Florida; the animal (L: 315 cm) was lactating and accompanied by a calf (Jenness and Odell, 1978). As ASM is reached at about five years of age, this female could have been at least 34 years old as there is no evidence for a number of spontaneous, infertile ovulations at the onset of sexual maturity and assuming an annual ovulation rate. Since no post-reproductive females were observed in the present study, it appears that females remain reproductively active throughout their entire life. If a post-reproductive phase should occur, it is unlikely to last very long.

In *K. sima* the oldest female examined (with 14 GLG) was also pregnant and no post-reproductive females were observed in the sample. This would also indicate the absence of a long post-reproductive period and may in turn reflect certain social structures. Stranding data and observations at sea suggest that females are almost invariably solitary or accompanied by a calf. This would indicate that female *Kogia* do not have cohesive, stable kinship female groups as are observed in species with a high life expectancy for post-reproductive females, like the short-finned pilot whale *G. macrorhynchus* and the sperm whale *P. macrocephalus* (Marsh and Kasuya, 1986). An increased duration of lactation with maternal age and a simultaneous drop in pregnancy rate in these two species (Best, 1968; Kasuya and Marsh, 1984) reflects an increasing investment in calf-rearing and a decreasing investment in calf-bearing with age (Marsh and Kasuya, 1986). A long post-reproductive period in females is thought to have evolved to ensure survival of offspring, which is probably closely related to the post-reproductive female (Marsh and Kasuya, 1986). Although no communal nursing has yet been observed in any cetacean species, which would provide definite evidence of an important role for older females that spend an increasing proportion of their lives lactating (Marsh and Kasuya, 1986), alloparental care in the form of babysitting has been observed in sperm whales *P. macrocephalus* (Whitehead, 1996). Thus the absence of post-

reproductive females supports the notion that *Kogia* females do not live in stable, closely related female groups. Harbour porpoises *P. phocoena* also show an absence of a long post-reproductive period in old females (Sørensen and Kinze, 1994) and the group size suggests no stable, cohesive female groups in this species (Carwardine, 1995).

The maximum reported ages for a *K. breviceps* and *K. sima* female in the present sample were 22.4 GLGs and 21.5 GLGs, respectively. With age at ASM estimated at around 5 GLGs for both *K. breviceps* and *K. sima*, the maximum reproductive lifespan would be 17.4 years and 16.5 years, respectively, resulting in 16 and 12 offspring per lifetime using the annual ovulation rates calculated above. However, it is unlikely that each of the ovulations results in a successful pregnancy and rearing of the calf. Even harbour porpoises *P. phocoena* with an annual ovulation have probably not more than a few offspring per lifetime (Read, 1990a). Data for the species from the western North Atlantic indicated a reproductive lifespan of around 13 years and a maximum number of offspring of four to seven (Gaskin et al., 1984; Read, 1990a; 1990b; Read and Hohn, 1995). However, care should be taken when comparing these species, since they have different ovulation rates. The different ovulation rates of *K. breviceps* and *K. sima* reflect the different reproductive strategies employed by the two species, which will be discussed in detail below.

11.5.2 Gestation

Although the two estimates for length of gestation based on Kasuya's (1977) formula and foetal and calf lengths throughout the year give slightly different results, gestation lengths for both *Kogia* species lie between 11 and 12 months. More data, especially on neonatal length, are needed to define the gestation period more accurately. An estimated gestation length of 11 months for *K. breviceps* based on foetal and calf lengths throughout the year is in agreement with one of Ross' (1979) estimates (using the same method) for the population off South Africa and suggests that his alternative estimate of seven months is not realistic. No previous estimates of gestation length were available for *K. sima*, but the estimate of 11 to 12 months is in agreement with the general length of gestation in odontocetes (Perrin and Reilly, 1984).

11.5.3 Lactation and weaning

Evidence from the present study indicates that weaning may start after one year of lactation in *K. breviceps*, but as early as six months in *K. sima*. Data for a 136 cm long *K. sima* from South Africa (Ross, 1979) and a 131.5 cm

and 140 cm long *K. sima* from Peru (Reyes and Van Waerebeek, 1992) and Sri Lanka (Chantrapornsyl et al., 1991), respectively, all with evidence of solid food in their stomachs, support these findings. However, the present data also suggest that lactation can last up to two years in either species, which supports the suggestion that, although both *Kogia* species may be able to conceive in successive years (Ross, 1979), this may not be the norm (Fig. 31).

The few estimates available suggest that great energetic demands are placed on the mother during lactation (Evans, 1987; Lockyer, 1987; 1995b). Cockcroft and Ross (1990b) estimated that a female bottlenose dolphin *T. truncatus* required 8.3 % of her body mass in food per day (the equivalent of 37,000 kJ) during lactation, while only needing 5.2 % after weaning of the calf. Thus, a lactating female needs sufficient fat reserves and must decrease her own energy requirements or increase food consumption to meet these demands (Cockcroft and Ross, 1990). Lockyer's results (1987) from a study on fin whales *B. physalus* support the idea that fat deposits play an important role as lactating females are the leanest females, while pregnant females are very fat. Similarly, body fat decreases in lactating harbour porpoises (Lockyer, 1995b). Thus body condition, food abundance, and fertility are intimately linked. It is possible that the prevailing food conditions from consecutive seasons combined could ensure

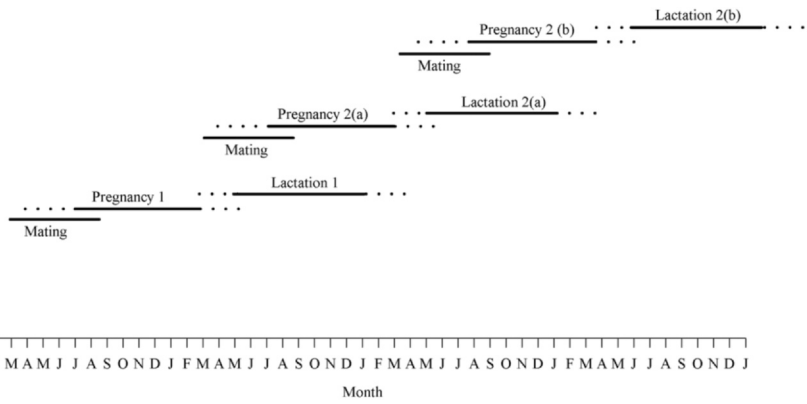

Fig. 31 Proposed reproductive chronology in *Kogia*. In pregnancy 2a mating occurs in the month post-partum. Some animals may miss this pregnancy and only mate in the next season (=pregnancy 2b). The seasonality of the reproductive events is modelled on the data for *Kogia breviceps*. While *Kogia breviceps* may enter more often into pregnancy 2a, *Kogia simus* may enter more often into pregnancy 2b.

successful reproduction even in a year when food abundance is low (Lockyer, 1987). The energetic requirements resulting from annual reproduction and thus simultaneous lactation and pregnancy will be discussed in more detail as part of the reproductive strategy of the two *Kogia* species below.

Slijper (1966) remarks that the milk of belugas *D. leucas* is unusually high in water content (66 %) and low in fat (22 %), which he put down to experimental error as both the fat and water content in other species ranged between 40–50 %. Jenness and Odell (1978) present data for the composition of *K. breviceps* milk, which is also unusually low in fat (almost 50 % that of other cetacean species). Although individual variation of milk composition is large (Jenness and Odell, 1978), another possible explanation in view of the annual ovulation rate may be that these differences are real and were selected for to compensate for the energetic demands of simultaneous pregnancy and lactation. Further comparative investigation, especially with other odontocetes with an annual ovulation rate, like the harbour porpoise *P. phocoena*, is needed to clarify this. Different diets almost certainly account for some of the differences seen in the fat content of cetacean milk as another teuthophagous species, the sperm whale *P. macrocephalus*, also showed a lower milk fat content than other cetaceans (Best et al., 1984). Cockcroft and Ross (1990b) also report an unusually low fat content in bottlenose dolphin *T. truncatus* milk of 14 to 19 % compared to over 29 % for other dolphin species and suggest that this may be a result of the longer lactation time of 18 to 24 months (Cockcroft and Ross, 1990).

In contrast to the two *Kogia* species, the closest relative, the sperm whale *P. macrocephalus*, has a long lactation period that takes up about 40 % of the females' reproductive cycle (Gaskin, 1982). Consequently, the annual number of receptive females is low and males have to compete for access to females (Gaskin, 1982). Again this is almost the opposite scenario to *K. breviceps*, where lactation seems surprisingly short and most females appear to ovulate every year.

The separation of a calf from its mother is not necessarily triggered by the onset of a new pregnancy. In bottlenose dolphins *T. truncatus*, the siblings even remain with the mother after the birth of the new calf in some instances (Wells et al., 1987). There is also some evidence from sightings of mother/calf/juvenile groups that the young of harbour porpoises *P. phocoena* stay with the mother until the next calf is born, and possibly for another month or so after that (Gaskin et al., 1984). However, based on the stranding record there is no evidence of that in either species of *Kogia*,

which may be a result of the sufficient independence of the calf to not follow a stranding cow inshore. Alternatively, it may indicate that calves leave the mother when the next offspring is born.

12. Simultaneous lactation and pregnancy

The high percentage of mature females of *K. breviceps* (24.1 %) and *K. sima* (11.5 %) simultaneously lactating and pregnant indicates that a large percentage of females may fall pregnant in consecutive years. However, the lower percentage of this condition for *K. sima* suggests that it may not present the normal reproductive strategy employed by this species (Fig. 31) and is supported by the ovulation rate. Simultaneous lactation and pregnancy is commonly found only in a small percentage of the total sample of adult females. For example, out of all adult females examined (n = 536) of Eastern Tropical Pacific (ETP) spinner dolphins *S. longirostris*, 0.75 % were simultaneously lactating and pregnant (calculated from Perrin et al., 1977), while in striped dolphins *S. coeruleoalba* the percentage was 1.9 (n = 699) (Miyazaki, 1984), in ETP spotted dolphins *S. attenuata* the percentage was 4.13 (n = 1114) (calculated from Perrin et al., 1976), in dusky dolphins *L. obscurus* the percentage was 9.8 (calculated from van Waerebeek and Read, 1994), and in the northern form of short-finned pilot whales *G. macrorhynchus* the percentage was 9.6 (Kasuya and Tai, 1993). In contrast, only three mature females of the southern form were found simultaneously lactating and pregnant (Kasuya and Marsh, 1984) and only one female showed that condition in bottlenose dolphins *T. truncatus* from South Africa (Cockcroft and Ross, 1990). No simultaneously lactating and pregnant females were reported for Hector's dolphins *C. hectori* (Slooten, 1991) or for the vaquita *P. sinus* (Hohn et al., 1996), while the relatively high percentage of 15.5 (n = 57; calculated from Sørensen and Kinze, 1994) of simultaneously lactating and pregnant female harbour porpoises *P. phocoena* reflects the annual reproduction found in this species (Read, 1990b; Read and Hohn, 1995). Simultaneous lactation and pregnancy, suggesting reproduction in successive years, has been reported before for *Kogia* (Hale, 1947; 1962; Ross, 1979; 1984; Odell et al., 1984; Beckmen, 1986). Although this is unusual for marine mammals, it has also been suggested for the harbour porpoise *P. phocoena* (Gaskin et al., 1984; Read, 1990b), Dall's porpoise *P. dalli* (Kasuya et al., 1974; Ferrero and Walker, 1999) and the harp seal *Pagophilus groenlandicus* (Sergeant, 1966; Bowen et al., 1981). It implies that a

post-partum oestrus may occur (Gaskin et al., 1984; Read, 1990b), although no supporting evidence for that was found in either species of *Kogia*. Most adult female harbour porpoises spend much of the year simultaneously lactating and pregnant (Read, 1990b) and as a response to these elevated energy requirements consume larger amounts of prey (Recchia and Read, 1989).

The percentages of *Kogia* females simultaneously lactating and pregnant may not be a true representation of the whole population, as females accompanied by a calf may come closer inshore to feed and thus may be more likely to strand (Ross, 1979). However, the percentage of *K. breviceps* that stranded on the south-eastern coast of the United States simultaneously lactating and pregnant was only 8.05 % and no *K. sima* females were found in this condition (data from (Credle, 1988)). The different oceanographic conditions experienced by the two populations could explain the observed differences in reproduction.

In the present study, 6.9 % of mature *K. breviceps* females were lactating and 24 % were pregnant, in comparison to 39.1 % and 16.1 % females, respectively, stranded along the south-eastern United States. For *K. sima*, 23 % of South African animals were in either condition, compared to adult females stranded on the south-eastern United States coast, of which 40 % were lactating and 30 % were pregnant. These data suggest a longer period of lactation and possibly a longer reproductive cycle for the *Kogia* populations off the south-eastern United States and would support the earlier statement that different oceanographic conditions could result in different *Kogia* populations exhibiting differing reproductive strategies.

The occurrence of mother/calf pair strandings is similar in South Africa and the south-eastern United States: for *K. breviceps* it was 51.7 % and 41.6 %, respectively, and for *K. sima* it was 38.5 % and 50 %, respectively. In these calculations, both assumed cow/calf pairs (the animals stranded together and the cow was lactating) and possible cow/calf pairs (the animals stranded together, but no definite relationship could be established as the mother was not reported to be lactating and no uteri were available for examination) were included. In the latter case, researchers commonly assume that the stranded couples have a cow-calf relationship and these data were therefore included in the calculation.

12.1 Resting phase

The fact that a high percentage of females of both *Kogia* species were found simultaneously pregnant and lactating suggests that a resting period, which is part of the reproductive cycle of many cetaceans (Best, 1968; Lockyer, 1984; Perrin and Reilly, 1984), may be rare. However, females that fail to

fall pregnant in the mating season of one year will have to wait 12 months for the next mating season as will females that fail to maintain a foetus. Consequently, if conditions are such that females cannot maintain pregnancies in successive years, an interval of up to 12 months will occur and it is then likely that the female will be in good condition for the following mating season (Fig. 31). This interval may be regarded as equal to the resting period of other cetaceans, although somewhat more flexible. Similar data have been reported for the harbour porpoise *P. phocoena* (Read and Gaskin, 1990). Based on the data on ovulation rate from either *Kogia* species, this scenario is more often observed in *K. sima* than in *K. breviceps*.

12.2 Seasonality

Seasonality is the most obvious effect of the environment on reproduction (Bronson, 1989) and the mating season and gestation time of mammals have probably evolved to place parturition in a season that maximises the survival of the offspring (Kasuya, 1995). All physiological processes in mammals, including reproduction, are limited by the amount of food available (Bronson, 1989), and in an environment that is characterised by seasonal variation in climate and food availability, natural selection will favour reproduction during the season that maximises the potential for success (Barlow, 1984; Bronson, 1989; Kasuya, 1995). Early and late lactation are the energetically most demanding periods for the cow and thus should coincide with a time when levels of resources are optimal (Bronson, 1989; Urian et al., 1996).

The only available reference to seasonal reproduction in *Kogia* stems from Sylvestre (1983), who concludes that calving and mating off Florida may take place in winter to early spring for *K. breviceps* based on one cow-calf pair stranded in mid-March. Additional unpublished data of neonates and calves of the two *Kogia* species stranded in the south-eastern United States (Credle, 1988) suggest that the seasonality of births may be different in the Florida populations of *K. breviceps* and *K. sima* than in the populations off South Africa, but further investigations are needed in this respect. Ross (1979) suggests a mating and calving season of seven months each for *K. breviceps* off South Africa, both lasting from autumn to spring. This is supported by the results from the present study.

The gestation period of *K. breviceps* was estimated at about 11 months in the present study and the data indicate that the mating season would follow immediately after the calving season. In contrast, both the mating and calving period occur at the same time in *K. sima*. The calving seasons of the

two species show a small overlap in March. While *K. breviceps* gives birth in autumn and winter and over a longer period of six months, *K. sima* appears to be restricted to a shorter period of four months during summer, although the data for the latter are rather scanty. The shorter, more restricted mating and calving period, which occurs at a time when water temperatures are the highest, may indicate that *K. sima* needs higher water temperatures to meet the thermoregulatory requirements of the newborn calf, whereas *K. breviceps* may be able to cope with slightly lower temperatures, as reflected by the general temperature requirements of the two species. An annual peak of births appeared to be associated with high water temperatures in bottlenose dolphins *T. truncatus* (Wells et al., 1987). Although the two *Kogia* species appear to occupy a similar habitat over the continental shelf edge and slope (Ross, 1979; 1984; Davis et al., 1998) and feed on the same prey (Ross, 1979; Candela, 1987), the above results indicate that the mating seasons overlap only little. Furthermore, the diet of both species indicates that they may occupy the same ecological niche. If several populations use the same food resource, they should evolve mechanisms to reproduce at different times of the year and thus avoid high energetic demands of lactation when the main resource is being heavily utilised (Bronson, 1989; Urian et al., 1996). Food is not the only factor determining the breeding season of a species, but out of the many different environmental factors that interact in complex ways to influence a mammals' reproduction, food availability probably plays the most important role (Bronson, 1989). Therefore the different peaks in the calving season may have evolved to prevent direct competition between the two species at a time when energy requirements are the highest. This correlation of the timing of reproductive seasonality in cetaceans with water temperatures, food availability or other environmental factors has been widely discussed (Wells et al., 1987; Sørensen and Kinze, 1994; Hohn et al., 1996).

The occurrence of neonates of *K. breviceps* in March (124 cm), June (120–124 cm) and August (122 cm) off Florida suggests a calving season from spring to late summer for that population (data from Credle, 1988). Similarly neonates of *K. sima* reported in June (91 cm, possibly aborted or early birth), July (100 cm), August (105 cm) and October (105 cm) off Florida suggest a calving season in summer and autumn for this species (data from Credle, 1988). Although further analysis of the reproduction and seasonality of the Florida populations of *Kogia* is necessary, these data show that the calving season differs between species off South Africa and Australia (whose calf lengths revealed a similar seasonal pattern) on the one

hand and Florida on the other. Different reproductive seasonalities, as well as differing percentages of simultaneously lactating and pregnant females and foetal and calf sex ratios between the South African and Florida populations, suggest that the reproductive strategies may differ between different *Kogia* populations.

No clear correlation could be determined between the *corpus* index and either month or foetal/calf length and thus this analysis did not assist the examination of seasonality of reproduction in either species of *Kogia*. Wide individual variation in the volume of the largest *corpus* has been reported before (Harrison et al., 1981), although Cockcroft and Ross (1990a) found a correlation between *corpus* volume index and calf length for bottlenose dolphins *T. truncatus* from South Africa. However, the relatively small sample sizes available for either species of *Kogia* for this analysis may explain the lack of any obvious trend.

12.3 Reproductive strategy

The gestation period of *K. breviceps* and *K. sima* was estimated at 11 and 12 months, respectively. Lactation lasts about one year in both species, but may extend to two years. A relatively high percentage of females is simultaneously lactating and pregnant in both species, but the accumulation rate of *corpora* indicates that although *K. breviceps* may generally have an annual reproduction, at least some *K. sima* females may only reproduce every two years. Both species exhibit seasonal reproduction, but while *K. breviceps* appears to have a protracted mating and calving season of six months each, *K. sima* exhibits a shorter mating and calving season over the period of three months, with births occurring during the warmest part of the year. The mating and calving seasons were found to overlap slightly between the two *Kogia* species off South Africa.

Close similarities in life history strategies have been observed between two species of the same genus before (Hohn et al., 1996). The life history of the vaquita *P. sinus* is very similar to that of the harbour porpoise *P. phocoena* with the exception of an annual ovulation found in the latter (Hohn et al., 1996).

Researchers have had difficulties in explaining how the energetic requirements of annual reproduction in cetaceans could be met (Gaskin, 1982; Straley et al., 1994; Read and Hohn, 1995). As an indicator of body condition, blubber mass is thought to be a reflection of a cetacean's energy reserves and thus provide information about an individual's probability of future survival and reproduction (Read, 1990). Although differing results

were obtained, two independent studies that assessed body condition of harbour porpoises *P. phocoena* (Read, 1990; Lockyer, 1995b) revealed that the variation of blubber parameters (such as thickness, mass and lipid content), and therefore body condition, among different reproductive classes reflect the relative energetic costs of reproduction (Read, 1990). Accordingly, lactating harbour porpoises had less blubber mass or lipid content than pregnant females (Read, 1990; Lockyer, 1995b) and Chittleborough's (1965) data from humpback whale *M. novaeangliae* catches indicate that mature females with near-term foetuses yielded more oil than other mature females. The current thought is that, under good conditions (meaning abundant food resources), reproduction in successive years will be favoured, whereas in poor years the pregnancy will be missed and reproduction may only occur every other year (Gaskin, 1982; Lockyer, 1987; Straley et al., 1994). Furthermore, female harbour porpoises from the Bay of Fundy population may be able to compensate for the energetic requirements of lactation by an increased energy intake, as the annual variation between herring consumption and body condition was found to co-vary (Read, 1990). In this context the differences in reproductive rates between two populations of harbour porpoises from California and the Bay of Fundy were ascribed to differing prey availabilities (Read and Hohn, 1995). Considering that a truly annual strategy may endanger the survival of the female, Gaskin (1982) proposed that the mean number of calves produced per lifetime in this species is unlikely to exceed four. Apart from the harbour porpoise, annual reproduction has been reported in the Dall's porpoise *P. dalli* (Ferrero and Walker, 1999), the minke whale *B. acutorostrata* (Masaki, 1979; Best, 1982; Lockyer, 1984) and, occasionally, in the humpback whale *M. novaeangliae* (Clapham and Mayo, 1990; Straley et al., 1994).

A surprising fact in the reproductive strategy of both *Kogia* species is that sexual maturity is attained at a relatively early age. This is usually only found in phocoenids (Gaskin et al., 1984) and small dolphins (Perrin and Reilly, 1984), with a relatively short lifespan of around 15 to 20 years (Gaskin et al., 1984; Perrin and Reilly, 1984; Slooten, 1991; Sørensen and Kinze, 1994; Read and Hohn, 1995; Hohn et al., 1996). In both *Kogia* species the lifespan is similarly short (*K. breviceps*: 22.4 years; *K. sima*: 21.5 years). It was suggested that, although harbour porpoises can live up to 24 years, such a high age is rarely found in this species due to a combination of natural and incidental mortality (Hohn and Brownell, 1990; Read and Hohn, 1995; Lockyer, 1995a). The same may be true for either species of *Kogia*, as the low age at ASM may have evolved as a result of predation pressure. Similarly, a

decrease of age at ASM resulting from exploitation has been reported for a number of delphinids (Perrin and Henderson, 1984; Kasuya, 1985) and a higher number of simultaneously lactating and pregnant females was also reported in these populations (Perrin et al., 1976; Perrin et al., 1977). As no data of ovulation rates are available from any other populations of *K. breviceps* and no obvious exploitation of the animals themselves or of their main prey occurs, these data are thought to represent the norm rather than elevated ovulation rates in response to exploitation.

A high number of ovulations does not necessarily mean that a large number of offspring is produced per lifetime. Even harbour porpoises with an annual ovulation may only produce between four and seven offspring per lifetime (Gaskin et al., 1984; Read, 1990a). The highest number of *corpora* recorded for a *K. breviceps* female is 29 reported for a 315 cm long animal (Jenness and Odell, 1978). Assuming annual ovulation of 0.9 as observed for *K. breviceps* in the present study and given that the age at ASM is also five, this would indicate an estimated age of at least 31.1 years. However, the ovulation rate reported for *K. breviceps* here is not necessarily applicable to animals from the Florida population, as differences in the length of the reproductive cycle between two populations of the same species have been reported before for harbour porpoises from the Gulf of Maine (Read and Hohn, 1995) and from California (Hohn and Brownell, 1990). The differences in the length of the reproductive cycle between populations of harbour porpoises at least in part reflect variations in prey resource levels (Gaskin et al., 1984; Read and Hohn, 1995).

12.4 Mating system

As discussed earlier, either a roving male strategy or harem strategy may be employed by males of the two *Kogia* species. The difference between the two strategies is largely determined by the dispersal of the females (Best and Butterworth, 1980; Krebs and Davies, 1981; Whitehead, 1990; Sandell and Liberg, 1992; Magnusson and Kasuya, 1997; Whitehead, 1998). Where females range widely or live solitarily or in small groups, males may employ a roving strategy in search of receptive females (Connor et al., 2000). A harem strategy is expected when a male can defend resources (Clapham, 1996) or when females are more gregarious, thus inhabiting fewer, larger groups, which would result in longer travel times between groups for the males and in turn result in residence (Whitehead, 1998). Beckmen (1986) observed that both *Kogia* species show extensive *bursa ovarica* and well developed fimbriae in their reproductive tracts, which is unusual for

odontocetes. She theorised that since *Kogia* are solitary and thus may have the need for each mating to be successful, these structures may have evolved to ensure that no ova are lost into the body cavity. The small group size in both species would support such a theory and suggests that males employ a roving strategy rather than are able to defend a harem.

12.5 Foetal and juvenile sex ratio

Little research has been carried out on foetal and juvenile sex ratios in cetaceans, but differences in juvenile mortality between odontocetes and mysticetes may reflect differences in the length of the period of maternal care between the two groups (Ralls et al., 1980). Although the foetal sex ratio in *K. breviceps* is slightly skewed towards males and this trend is even stronger in the juvenile sex ratio, neither differed significantly from parity. Although a predominance of males in the juvenile sex ratio in *K. breviceps* has been mentioned previously (Ross, 1979; Brabyn, 1991; Baird et al., 1996), no further possible implications of this were discussed. Since both the foetal as well as the juvenile sex ratio in *K. breviceps* are slightly skewed towards males, this may be a reflection of a higher percentage of males in the population or may indicate that male calves and juveniles are more likely to strand. Possible explanations for this are differential juvenile mortality rates between the sexes as was suggested for the striped dolphin *S. coeruleoalba* (Aguilar, 1991), the sperm whale *P. macrocephalus* (Ralls et al., 1980), and the harbour porpoise *P. phocoena* (Lockyer, 1995b). Greater susceptibility of males to nutritional stress, greater tendencies of males to emigrate, and male-male competition may all contribute to higher mortality rates in males and more than one of these factors may apply to a single species (Ralls et al., 1980). The general mammalian pattern shows more male than female dispersal, and emigration exposes the individual to nutritional stress, high risks of predation, and risks from strange conspecifics (Ralls et al., 1980). Males are more susceptible to nutritional stress than females (Ralls et al., 1980; Clutton-Brock and Iason, 1986) and therefore the inexperience of calves in finding food after separation from the mother may result in increased male juvenile mortality (Read and Hohn, 1995; Lockyer, 1995a, b). Additionally, when home ranges overlap and offspring come into competition with the parents, the sex ratio should favour the sex that disperses (Clutton-Brock and Iason, 1986).

In contrast to the data from the present study, calves of *K. breviceps* stranded along the south-eastern United States showed a sex ratio of 1.3: 1 for females to males, respectively, while it was 1.5: 1 for females to males

for *K. sima* (data from Credle, 1988). This is in contrast to the South African data and seems to reflect a slight predominance of females. However, it is unclear how old these "calves" were, as no age determination was carried out on that sample and it appears that only animals that stranded with a mature female were classified as calves. Therefore, it is possible that a comparison of animals, for which age estimates are available, may give different results, as only older juvenile males may suffer higher mortality (due to fights or nutritional stress).

12.6 Male reproduction

12.6.1 Attainment of sexual maturity

The onset of sexual maturity, defined here as late spermatogenesis, has previously been determined to occur between body lengths of 270 cm and 300 cm for *K. breviceps* and between 210 cm and 220 cm for *K. sima*, with early spermatogenesis starting at a body length of 200 cm in the latter (based on examination of the epididymides; Ross, 1979, 1984). The present study, which was based on animals from the same geographical region, showed that the onset of sexual maturity occurred between 241 cm and 242 cm and 2.5 and 5 years in *K. breviceps* (Table 11) and at about 197 cm and between 2.6 and 3 years in *K. sima* (Table 13). Thus, both *Kogia* species may actually attain sexual maturity at a somewhat shorter body length than previously reported. There are no previous records for body weight at ASM for either species and thus the present data of 210–233.6 kg for *K. breviceps* and 111.8–124 kg for *K. sima* present a first report on body weight at the onset of sexual maturity in the two species.

Few records of testis weights and dimensions (Scheffer and Slipp, 1948; Hubbs, 1951; Harrison et al., 1972; Caldwell and Caldwell, 1989) are available for either *Kogia* species. Roest (1970) concludes that a 224 cm long *K. sima* was mature based on the size of the testes (each about 40 cm long). The only histological studies of ASM in both *Kogia* species have been carried out in South Africa (Ross, 1979; 1984). The data obtained for testis weight and length for the different maturity stages for both species of *Kogia* in the present study concur well with those previously presented in the literature (Roest, 1970; Harrison et al., 1972; Caldwell and Caldwell, 1989). The only data that exceed the ranges presented here are 3090 g and 50 cm for the left testis and 2840 g and 48.5 cm for the right testis of a 305 cm long mature *K. breviceps* (Caldwell and Caldwell, 1989). Hubbs (1951) reports a 234.5 cm long animal with approximately 10.16 cm long testes and suggests that it was mature. Although the reported body length

could indicate a sexually mature animal, the data for testis length suggest that the animal was immature according to the data from the present study. Testes lengths of 47.5 cm and 50 cm and testes weights of 910 g and 1030 g, respectively, presented by Harrison et al. (1972) for a 229 cm long *K. sima* from Japan are intriguing, as body length, testis length, and testis weight indicate a mature animal, but no sperm were present. The only obvious interpretation of this is that the animal may have been producing sperm seasonally, but this would represent the only indication of a male seasonal cycle in the two *Kogia* species in the literature.

The results of the present study reveal that there was no overlap in testis size (both length and weight) in either *K. breviceps* or *K. sima* between early and late spermatogenesis. Thus either measure could be used to indicate the onset of sexual maturity. A small degree of overlap was observed between the mean testis length of immature animals and those in early spermatogenesis in *K. breviceps*; all other categories showed no overlap. Some overlap has been reported for all categories in spotted dolphins *S. attenuata* (Hohn et al., 1985) and in long finned pilot whales *G. melas* (Desportes et al., 1993), with the exception of testis length in the latter. Thus the little or no overlap in testis size between different maturity stages found for both *Kogia* species in this study may be an artefact of the relatively small sample size and it is difficult to determine which parameter would be the best indicator for sexual maturity in the genus.

As expected, the diameter of the seminiferous tubules increased in both species as the testes matured. The seminiferous tubule diameters from the present study as well as the different stages of maturity are in close agreement with the only data available in the literature from a *K. breviceps* from the Californian coast and *K. sima* from Japan (Harrison et al., 1972). The mean seminiferous tubule diameter of adult, spermatogenically active animals is greater in *K. breviceps* ($135.5 \pm 63.99\,\mu m$) than in *K. sima* ($100.2 \pm 12.16\,\mu m$) and similar results have been reported for the two species of *Globicephala* (Kasuya and Marsh, 1984). Since seminiferous tubule diameter is larger in large cetaceans, like the sperm whale *P. macrocephalus* (Best, 1969; Mitchell and Kozicki, 1984) and the humpback whale *M. novaeangliae* (Chittleborough, 1954), it is likely that the differences seen here in the two species of *Kogia* are due to scaling.

An index of testis development was calculated by Collet and Saint Girons (1984), Hohn et al. (1985), and Desportes et al. (1993) to allow comparison of maturity between stocks and species. But as the above authors have all calculated the testis index in different ways, such a

comparison is not possible. The mean testis index values obtained for both *K. breviceps* and *K. sima* were roughly half those of Desportes et al. (1993) for long-finned pilot whales *G. melas*, using the same formula; the biological significance of these results is unknown.

Attainment of sexual maturity between 2.5 and 5 years in *K. breviceps* and 2.55 and 3 years in *K. sima* was surprising, because most other odontocetes of similar size mature at a greater age (Perrin and Reilly, 1984; Evans, 1987). Studies on a small number of *K. breviceps* stranded in New Zealand indicate that mature males range in age between 3 and 16 GLGs (Tuohy et al., 2001), which supports the findings of the present study. In general, body length and weight are better correlated with the onset of sexual maturity in male *Kogia* than age, as different animals which would fall in the same length class showed quite different age estimates (Tables 11 and 13 and Figs. 24 and 29). This may partly be a result of the problems encountered with tooth wear and the age determination technique, or individually differing growth rates.

In both *Kogia* species, males attained sexual maturity at a shorter body length and lower body weight than females. However, age at sexual maturity was similar for both sexes in both *K. breviceps* and *K. sima*, as is commonly found in a number of phocoeinid and delphinid species (Miyazaki, 1984; Perrin and Reilly, 1984; Slooten, 1991; Hohn et al., 1996).

12.6.2 Seasonality

The results for both *K. breviceps* and *K. sima* did not show any conclusive evidence for a seasonal cycle of testicular activity. However, these data must be interpreted with caution due to the small sample size and the bias of samples towards immature males in *K. breviceps*. Since the majority of odontocetes appear to exhibit seasonal testicular activity (Sergeant, 1962; Gaskin et al., 1984; Hohn et al., 1985; van Waerebeek and Read, 1994), a similar result would be expected for the two *Kogia* species, especially as the data from the present study indicated that mating does not occur all year round.

12.6.3 Testis size and male mating strategy

Testis size usually increases as body size increases, regardless of the breeding system (Harcourt et al., 1981; Kenagy and Trombulak, 1986), but variation in relative testis size within and between species generally reflects variations in the requirements for sperm production (Setchell, 1978; Kenagy and Trombulak, 1986). Therefore testis weight as a percentage of body weight

is often used as an indicator of the mating system of a species (Harcourt et al., 1981; Kenagy and Trombulak, 1986; Rose et al., 1997). Large testes in relation to body weight are usually associated with a multimale breeding system (or polyandry), in which the males compete with each other in the form of sperm competition (Harcourt et al., 1981; Kenagy and Trombulak, 1986). Large testes are apparently a result of the selective pressures of multiple inseminations, sperm competition within the female reproductive tract, spontaneous ovulations, and seasonal reproduction (Harcourt et al., 1981; Kenagy and Trombulak, 1986). Sexual dimorphism is usually absent in these species (Aguilar and Monzon, 1992).

Small testes in relation to body weight are indicative of low copulatory frequency and thus of monogamous or extreme polygynous single-male mating systems, the latter involving one male mating with a number of females (i.e. harem; Harcourt et al., 1981; Kenagy and Trombulak, 1986). Sexual dimorphism is usually great in species where males have to fight over access to a number of females. In cetaceans, intraspecific fighting is thought to be reflected in the amount of scarring (MacLeod, 1998). Generally very little sexual dimorphism is found in monogamous species (Harcourt et al., 1981). Intermediate levels of sexual dimorphism, large testes, and thus assumed high copulatory frequency, and low degrees of scarring indicate a multimale breeding system, for example promiscuity or multimale polygyny (Harcourt et al., 1981; van Waerebeek and Read, 1994; Table 14).

Combined testis weights comprise less than 1 % of body mass in most terrestrial mammals and cetaceans have slightly, but significantly larger testes relative to body weight (Kenagy and Trombulak, 1986). In addition, there are large differences in testis size between mysticetes and odontocetes (Kenagy and Trombulak, 1986; Aguilar and Monzon, 1992). There are a number of possible explanations for cetaceans possessing larger testes than terrestrial mammals. An aquatic mode of life may facilitate larger testes due to the support of body weight in the aquatic medium or it may necessitate larger testes due to a possibly different reproductive physiology involved in internal fertilization in an aquatic medium (Kenagy and Trombulak, 1986). Furthermore, cetaceans as a group may show more frequent copulations than other mammals and thus exhibit larger testes (Kenagy and Trombulak, 1986; Connor et al., 2000). However, marsupials have significantly smaller testes than eutherian mammals, but within their range the testis sizes of the marsupials are still indicative of the different mating systems mentioned above (Rose et al., 1997). Thus relatively small testes in cetaceans probably

Table 14 Proposed male mating strategies for different species of odontocetes based on testis size, sexual dimorphism, degree of scarring and group size. Testis size is expressed as a percentage of the total body weight.

		Species examined											
		Dusky dolphin[a]	Vaquita[b]	Harbour porpoise[c]	Common dolphin[d]	Hector's dolphin[e]	Bottlenose dolphin[f]	Humpback dolphin[g]	Dwarf sperm whale[h]	Pygmy sperm whale[i]	Sperm whale[j]	Pilot whale[k]	Ziphiidae[l]
Criterion													
Testis size	Small testes in relation to body weight						1 %	0.7 %	2 %	1.7 %	0.01–0.05 %		√
	Medium sized testes in relation to body weight		5 %	3–4 %	4.2 %	2.9 %							
	Large testes in relation to body weight	8.5 %											
Sexual dimorphism	Males larger than females							√			√	√	√
	Little or no sexual dimorphism				√		√		√	√			
	Females larger than males		√	√									
Group size	Solitary or small groups		√	√		√		√	√	√			
	Medium sized schools	√					√					√	√
	Large schools				√								

Table 14 Proposed male mating strategies for different species of odontocetes based on testis size, sexual dimorphism, degree of scarring and group size. Testis size is expressed as a percentage of the total body weight.

		Species examined											
		Dusky dolphin[a]	Vaquita[b]	Harbour porpoise[c]	Common dolphin[d]	Hector's dolphin[e]	Bottlenose dolphin[f]	Humpback dolphin[g]	Dwarf sperm whale[h]	Pygmy sperm whale[i]	Sperm whale[j]	Pilot whale[k]	Ziphiidae[l]
Criterion													
Scarring	Little or no scarring	√	√	√	√	√	√	√	√	√		√	
	Extensive scarring										√		√
	Sp	S	S	S	R	R	?	R	R	R	J	H	
		p	p	p							H		
Proposed mating strategy													

Sp= sperm competition; R= roving males; JH= joint harem; H= harem.
[a]van Waerebeek and Read (1994), Carwardine (1995).
[b]Hohn et al. (1996).
[c]Gaskin et al. (1984), Carwardine (1995), Read and Hohn (1995), Hohn et al. (1996)
[d]Cockcroft (1993).
[e]Slooten (1991), Carwardine (1995), Dawson et al. (1993), Slooten and Dawson (1994), Dawson, pers.com
[f]Wells et al. (1987), Cockcroft (1993).
[g]Cockcroft (1993).
[h]Present study
[i]John Heyning, unpubl. data
[J]Best et al. (1984), Gaskin et al. (1984), Kato (1984), MacLeod (1998).
[k]Kasuya and Tai (1993), Magnusson and Kasuya (1997), MacLeod (1998), Kasuya, pers. com.
[l]Aguilar and Monzon (1992), MacLeod (1998).

still indicate a monogamous or extreme polygynous mating system, whereas relatively large testes are assumed to indicate frequent copulations and sperm competition.

In most mysticetes, the combined testis weight makes up less than 1 % of the total body mass, except in right whales (*Eubalaena* spp.), where it comprises up to 1.31 % of the body weight (Brownell and Ralls, 1986). Although a similar percentage has been reported for the humpback dolphin *Sousa chinensis* (0.7 %) and the bottlenose dolphin *T. truncatus* (1 %; Cockcroft, 1993), most odontocetes have a somewhat bigger testis weight to body weight ratio (Table 14). In Hector's dolphin *C. hectori* the testes make up 2.9 % of the total body weight (Slooten, 1991) (Table 14). Furthermore, values of 3.5 % and 3–4 % have been reported for the harbour porpoise *P. phocoena* (Gaskin et al., 1984; Read, 1990b), 4.2 % for the common dolphin *D. delphis* (Cockcroft, 1993), almost 5 % in the vaquita *P. sinus* (Hohn et al., 1996), and 5 % for the Tucuxi *Sotalia fluviatilis* (Best and da Silva, 1984), respectively (Table 14). The dusky dolphin *L. obscurus* has testes weighing up to 8.5 % of the total body weight, amongst the highest recorded for mammals (van Waerebeek and Read, 1994; Table 14). Based on testis size, it is suggested that the dusky dolphin may have a promiscuous mating system with sperm competition and this is supported by the fact that only little intraspecific scarring is observed in males (van Waerebeek and Read, 1994; Table 14). A similar scenario is found in the Hector's dolphin *C. hectori* (Slooten, 1991; Table 14). Due to the large testis size in the vaquita *P. sinus*, the small group size and reversed sexual dimorphism, sperm competition is suggested for this species (Hohn et al., 1996; Table 14). A multimale polygynous mating system (or joint harem) is reported for both the southern and northern form of the short-finned pilot whale *G. macrorhynchus* off Japan (Kasuya and Marsh, 1984; Kasuya and Tai, 1993; Magnusson and Kasuya, 1997; Table 14). While this would indicate that mating systems do not vary within a species, the mating systems of bottlenose dolphins *T. truncatus* may vary slightly between populations (Tolley et al., 1995; Connor et al., 2000). The above results support the suggestion that in mammals a polygynous mating system is the dominant strategy (Krebs and Davies, 1981). The one exception to the phenomenon that larger testes are found in cetaceans compared to terrestrial mammals (Aguilar and Monzon, 1992) appears to be the ziphiids, which also show some of the highest degree of intraspecific scarring (MacLeod, 1998). This suggests a mating system where males fight over access to females (Connor et al., 2000).

Although a number of researchers provide combined testes weights for either species of *Kogia* (Harrison et al., 1972; Caldwell and Caldwell, 1989), no body weights are provided for the animals concerned and thus the percentage that the combined testes weight contributes to the total body weight could not be determined. Caldwell and Caldwell (1989) remark on the large testis size of a 305 cm long *K. breviceps*, which had a combined testis weight of 5.93 kg. Similarly, Maigret and Robineau (1981) estimated the combined testis weight of a 222 cm long male *K. sima* stranded in Senegal at around 6 kg. Aguilar and Monzon (1992) provide relative testes weights for 54 cetacean species, including *K. breviceps* and *K. sima*, but unfortunately no reference to the original data is provided. The maximum combined testis weights of 1.04 % for *K. breviceps* and 2 % for *K. sima* obtained in this study suggest that both *Kogia* species have relatively small testes in comparison with other odontocete species (Table 14). Although it is frequently mentioned that both *Kogia* species have large testes (MacLeod, 1998), no indications of bigger testes in relation to body weight could be found in the literature. As yet unpublished data from the Los Angeles County Museum for a 300 cm long *K. breviceps* (LACM 88938) weighing 385k g showed a combined testis weight of 6049 g (John Heyning, pers. com.), which made up 1.69 % of the total body weight. No age estimate was available for the animal. However, none of the South African animals for which relative testis weight could be calculated had reached physical maturity and it is possible that larger specimens may have relatively larger testes.

There is a difference between sexual and social maturity in a number of cetacean species. Social maturity has been defined as the stage when males may gain access to receptive females and successfully fertilise them (*sensu* Best, 1969; Kasuya and Marsh, 1984; Desportes et al., 1993; Kasuya et al., 1997). In some species, like the long-finned pilot whale *G. melas*, sexually mature males may be capable of producing sperm, but may not reach social maturity until a later stage (Desportes et al., 1993). In the bottlenose dolphin *T. truncatus,* only males older than 21 years appear to sire calves (Duffield and Wells, 2002). An extreme example is the Baird's beaked whale *Berardius bairdii*, in which testis weight continues to increase for almost 20 years after ASM (Kasuya et al., 1997). In other species, such as the short-finned pilot whale *G. macrorhynchus*, full sexual maturity (determined by histology) and social maturity occur at the same time (Kasuya and Marsh, 1984). The substantial increase in testes size that occurred after ASM in both *K. breviceps* (4.3 fold) and *K. sima* (11.7 fold) may indicate that

social maturity is reached only at a later stage in life. A 7.62 fold increase of combined testis weight after ASM is reported for long-finned pilot whales *G. melas* (Desportes et al., 1993).

Sexual dimorphism is another important indicator for the mating system (Table 14). Cetaceans generally lack secondary sexual characters, with the exception of the narwhal *Monodon monoceros*, where only males possess an up to 2.6 m long tusk (Gerson and Hickie, 1985). Sexual dimorphism is most pronounced in the largest odontocete, the sperm whale *P. macrocephalus* (Best et al., 1984), with males being up to five metres longer than females (Leatherwood and Reeves, 1983). Sexual dimorphism in the shape and colour of the melon is reported for the northern bottlenose whale *Hyperoodon ampullatus* (Bloch et al., 1996) and in the colouration of the patch around the genital area for Hector's dolphins *C. hectori* and Commerson's dolphins *C. commersonii* (Slooten and Dawson, 1994). But in most medium-sized odontocetes sexual dimorphism may be expressed as differences in girth and weight rather than length (Hohn and Brownell, 1990; Cockcroft and Ross, 1990a; Cockcroft, 1993; Tolley et al., 1995; Ngqulana et al., 2017). Although only slight or no differences in asymptotic length are found between the sexes in bottlenose dolphins *T. truncatus* (Hohn and Brownell, 1990; Cockcroft and Ross, 1990a), males are about 30 % heavier (Cockcroft and Ross, 1990a; Cockcroft, 1993), more robust and possess larger appendages than females of the same length (Tolley et al., 1995). Thus it appears that robustness rather than length plays a role in male-female (Cockcroft and Ross, 1990) as well as male-male intraspecific interactions (Tolley et al., 1995). This may well be the case for a number of other cetacean species, for example common dolphin *D. delphis* males are about 10 % heavier than females (Cockcroft, 1993). In the smallest odontocetes, namely the phocoenids and the delphinid genus *Cephalorhynchus*, and in the large baleen whales, sexual dimorphism is reversed, with the females being larger than males (Brownell and Ralls, 1986; Read and Gaskin, 1990; Slooten, 1991; Connor et al., 2000; Table 14). However, sexual dimorphism in cetaceans has not been very well researched in the past and should be the subject of further investigation to shed more light on the mating system of the order. In the present study, reversed sexual size dimorphism was found for *K. breviceps*, while in *K. sima* males were larger than females in body length. Mammals in which females are larger than males have a variety of social systems ranging from monogamy to harems (Ralls, 1976; Brownell and Ralls, 1986; Clapham, 1996) and in this respect, the reversed sexual size dimorphism found in *K. breviceps* gives

no indication as to the mating system of the species. In *K. sima,* the fact that males were slightly larger than females may indicate that there is some male-male competition over access to females.

Knowledge about the degree of sexual dimorphism represents a starting point for the exploration of cetacean mating systems as it indicates the degree of male-male competition and the role it plays in determining male reproductive success (Connor et al., 2000). However, the extent of body scarring resulting from intrasexual fights is thought to present a further clue (Table 14). Depending on the type of scarring, they are indicators of intraspecific fighting in a number of odontocetes (Heyning, 1984; Kato, 1984; Gerson and Hickie, 1985; MacLeod, 1998; Table 14). In some instances, body scars are an indicator of the male maturity status (Kato, 1984) and "quality" (Gerson and Hickie, 1985; MacLeod, 1998) and thus indirectly add information about the breeding system of a species (Kato, 1984; MacLeod, 1998). A number of odontocete species show a clear reduction in the number of teeth (Gaskin, 1982; MacLeod, 1998) and this is especially obvious in teuthophagous species, such as *Physeter* (Kato, 1984) and both *Kogia* species, reaching an extreme in the ziphiids (Mead, 1984; Heyning and Mead, 1996; MacLeod, 1998). Studies suggest that the ziphiids employ suction-feeding in which the prey is sucked into the mouth in a hoover-like fashion without the need for teeth to chew or even grasp the prey (Heyning and Mead, 1996). A similar mechanism is considered likely in both genera of the sperm whales (Heyning and Mead, 1996) and a number of other odontocete species (Norris and Møhl, 1983). Thus, in species that feed by suction, the retained teeth might play a role in social interaction (Heyning, 1984; Kato, 1984; MacLeod, 1998), since in some species the remaining teeth show an adaptation for use as weapons (Gerson and Hickie, 1985). Body scarring is reported for a number of odontocete species (McCann, 1974; MacLeod, 1998) and even for one mysticete (Chu and Nieukirk, 1988).

Examination of photographs of stranded specimens of *Kogia* from South Africa did not show any tooth scars. This may be due to the bias in the stranding record since adult males may be underrepresented. However, no indications of intraspecific scarring were found on animals (both male and female) of both *Kogia* species stranded along the coast of Florida (Nelio Barros, pers. com.). Thus it appears that male animals of either *Kogia* species may not fight over females and this may be due to the small group size, averaging one to two animals for *K. breviceps* and one to six animals for *K. sima* (Ross, 1979; Barlow and Sexton, 1996; Table 14). Group size

influences the mating system of cetaceans (Evans, 1987; Cockcroft, 1993) as do social structure and association patterns (Evans, 1987; Wells et al., 1987). Large testes and little sexual dimorphism in conjunction with large schools, as found in the common dolphin *D. delphis*, are attributed to sperm competition, whereas small testes, great sexual dimorphism and small group sizes, as found in humpback dolphins *S. chinensis*, are thought to indicate that larger males dominate smaller males and deny access to females (Cockcroft, 1993; Plön et al., 2012; Table 14). The stranding data for *Kogia* specimens from South Africa suggest that groups are comprised of females with their calves, small groups of juveniles (up to four animals in *K. sima*) and solitary males (both immature and mature animals). Consequently, encounters between males would be rare and thus there may not be a need for intraspecific fights. However, Connor et al. (2000) point out that it is likely that most serious fighting in cetaceans may occur by means of strikes with the peduncle, flukes or other body parts. This would not result in any obvious wounds and thus, in the absence of any direct behavioural observations, the examination of body scars may lead to an underestimation of the frequency and severity of intra- and interspecific aggression (Connor et al., 2000). In this respect, one male *K. breviceps* (PEM N2115; L: 275 cm) was reported to have stranded with broken mandibles and ribs and specimens stranded in the Western Cape region are often found with broken mandibles (Peter Best, pers. com.). These occurrences are also reported in the literature (McAlpine and Murison, 1997) and may be indications of intraspecific aggression, but could just as easily result from the carcass being washed over rocks.

MacLeod (1998) states that the vast majority of 32 species of odontocetes, for which there was no evidence that intraspecific scarring acted as an indicator for male quality, were primarily non-teuthophagous. The four exceptions are the two *Kogia* species, the long-finned pilot whale *G. melas* and the Ginkgo-toothed beaked whale *Mesoplodon gingkodens*. He suggests sperm competition as an alternative to direct male-male aggressive competition in the genus *Kogia*, but gives no direct indication of testis weights for either *Kogia* species. As the length (Whitehead, 1990; Sandell and Liberg, 1992; Magnusson and Kasuya, 1997) and synchrony (Best and Butterworth, 1980) of female oestrus, as well as the group size, density and dispersion of the females (Best and Butterworth, 1980; Krebs and Davies, 1981; Whitehead, 1990; Sandell and Liberg, 1992; Magnusson and Kasuya, 1997; Connor et al., 2000) have a profound effect on the mating strategy of a species and as these data are lacking for both *Kogia* species, no definite

model for the mating strategy of either *Kogia* species can be established. However, based on the comparatively small testis size, indicating moderate copulation frequency (as opposed to high copulation frequency in sperm competition), reversed or small sexual size dimorphism, little scarring and small group size, a promiscuous or polygynous mating system, with more than one male gaining access to females, is suggested for either *Kogia* species (Table 14). The density and dispersion of the females largely determines the difference between a harem strategy and a roving male strategy (Best and Butterworth, 1980; Krebs and Davies, 1981; Whitehead, 1990; Sandell and Liberg, 1992; Magnusson and Kasuya, 1997). Where females range widely and are solitary or occur in small groups, as is the case in *Kogia,* males may employ a roving strategy in search of receptive females (Connor et al., 2000). However, observational data are needed to show whether females aggregate during the breeding season or not, but comparisons with other odontocetes favour the roving male theory (Table 14). The roving male strategy is also suggested for the sperm whale *P. macrocephalus* (Whitehead, 1990; Magnusson and Kasuya, 1997; Table 14), although there is evidence for male-male aggressive interaction in this species (Kato, 1984). Bottlenose dolphins *T. truncatus* also show little sexual dimorphism (Wells et al., 1987; Tolley et al., 1995) and have relatively small testes, which make up 1% of the total body weight (Cockcroft, 1993). Extensive studies on bottlenose dolphins in Sarasota, Florida, show that male pairs may adopt a roving strategy in which one male may dominate the other, but both mate with receptive females without showing any aggressive interaction (Wells et al., 1987; Table 14). Alliance formation between males is only observed in habitats where males encounter each other frequently (Connor et al., 2000). Thus if a male has a low probability of encountering a rival male while with a female, he would be better off alone (Connor et al., 2000). Although it appears unlikely that males of either *Kogia* species form pairs, as males seem to be solitary based on the stranding data, they may rove between females in order to maximize their reproductive opportunities rather than monopolize and fight over a number of females. Post-mortem examinations of stranded specimens of either *Kogia* species along the coast of the United States showed that the epididymis is almost always full of sperm (Nelio Barros, pers. com., John Heyning, pers. com., Dan Odell, pers. com.), which would further support an opportunistic mating strategy. By contrast, ziphiids have some of the smallest testes sizes recorded for odontocetes (Aguilar and Monzon, 1992) and this together with their extensive scarring may indicate a harem system (Table 14).

Although it has been assumed, based on morphology and field observations, that cetaceans in general have some form of polygynous or promiscuous mating system (Slooten, 1991; van Waerebeek and Read, 1994; Hohn et al., 1996; Connor et al., 2000) like most mammals (Krebs and Davies, 1981), the use of molecular analysis has, in recent years, provided data to support these observations (Amos et al., 1993; Clapham and Palsbøll, 1997; Debbie Duffield, pers. com.). Although the analysis of testes size, group size and sexual dimorphism may give a good first indication as to the mating system of a species, it remains widely speculative and only behavioural observations in the wild (Slooten et al., 1993) and genetic analyses will provide unequivocal evidence as to which males dominate the matings (Amos et al., 1993; Duffield and Wells, 2002).

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Cover image: Stranded dwarf sperm whale *Kogia sima* attended by two local assistants, somewhere on an Eastern Cape beach, South Africa.
Credit: Graham Ross/Port Elizabeth Museum, Port Elizabeth/Gqeberha, South Africa.

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