Abstract.–Age and reproductive parameters were determined for bottlenose dolphins *Tursiops truncatus* captured in shark nets off Natal, on the southeast coast of southern Africa. Calibration of dentinal and cemental growth-layer-group (GLG) readings, using a known-age captive-born dolphin, indicated that dentinal and cemental GLGs are deposited annually, at least up to an age of 6 years. Female growth in length and mass and male growth in length are best described by von Bertalanffy growth curves. Male growth in mass is characterized by a growth spurt at puberty. Most growth occurs during the suckling years. Both sexes reach physical maturity and their asymptotic size—243 cm and 176 kg for males, and 238 cm and 160 kg for females—between 12 and 15 years. Both males and females may reach ages in excess of 40 years, based on counts of GLGs in teeth. Females attain sexual maturity between 9 and 11 years of age, 2 or 3 years earlier than males. Mating and birth are seasonally diffuse, although there is a peak of births in summer. The calf is born at a mean length and mass of 103 cm and 13.8 kg, respectively, after a gestation period of about 1 year. Lactation lasts between 18 months and two years, although there is evidence of an extended mother and calf association of up to 3 years. Postpubertal female ovulation rate is 0.28/year, and the estimated calving interval is approximately 3 years. There is no evidence that females become reproductively senescent with increasing age. Estimates of population replacement suggest that man-induced mortality may equal or exceed the replacement rate.

Age, Growth, and Reproduction of Bottlenose Dolphins *Tursiops truncatus* from the East Coast of Southern Africa

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Many populations of small inshore delphinids are exploited either directly or indirectly (Mitchell 1975, Beddington et al. 1985, Northridge and Pilleri 1986), and their continued survival depends on adequate management based on knowledge of their life history. In this context, knowledge of the reproductive parameters of a species is important in formulating management and conservation proposals. In particular, the reproductive biology of females is crucial to an understanding of the likelihood of a species' survival.

An estimated 900 bottlenose dolphins *Tursiops truncatus* inhabit Natal, along a stretch of some 400 km of coastal waters, southeast of southern Africa (Ross et al. 1989). Between January 1980 and December 1987, a minimum of 212 of these animals were captured in noncommercial inshore nets set to catch and deplete the numbers of large sharks off bathing beaches (Cockcroft and Ross In press). The catch of dolphins in anti-shark nets is of concern in the continued survival of these animals off Natal (Ross et al. 1989, Cockcroft and Ross In press).

Feeding studies on the bottlenose dolphins off Natal have shown that groups are segregated by sex and size. Lactating females and their calves frequent and feed in the nearshore zone, adolescents feed slightly further offshore, while resting females and adult males feed still further offshore (Cockcroft and Ross 1990). Consequently, the catch of these animals in the shark nets is biased, with calves less than 2 years old and lactating females constituting almost 60% of the total (Cockcroft and Ross In press). Other age and sex classes, particularly pregnant females and adolescents, are, therefore, probably underrepresented.

This study was undertaken to establish the reproductive potential of bottlenose dolphins off Natal, as part of a more extensive investigation of the natural history of these animals and severity of the threat to the population through capture in shark nets. Where appropriate, recognition is given to the effects of biases in sex and size composition, noted above, which reduce the accuracy of deductions made from catch data (Perrin and Reilly 1984).

Materials and methods

Routine necropsies were performed on all bottlenose dolphins retrieved from the Natal shark nets. Biological and morphological parameters, including sex, total length, and mass were recorded for each animal, based on the recommendations of Norris (1961) and Mitchell (1975). Collected organs were preserved in 10% formalin and later transferred to 50% ethyl alcohol for storage.

Testes were excised, weighed after removal of the epididymis, and the dimensions (length × maximum height × width) measured. The epididymis was visually checked for the presence of sperm and scored as present or not; no microscopic evaluation was undertaken. Testes from young animals (combined testis mass ≲100 g) were preserved whole, while only a section removed from the bigger testis of older males was kept. Standard histological slides, approximately 5 μm thick and stained with haemotoxylin and eosin, were prepared from whole testes or from three locations (outer, middle, and inner) of sections of large testes. From each slide the diameter of a minimum of 10 circular seminiferous tubules was measured at a magnification of 125 using an ocular reticule, to assess testis development stage.

Lactating females and calves caught together were considered mother and calf pairs. Both left and right ovaries were routinely collected and preserved from all females. These were sectioned serially at about 1-mm intervals, and the number and dimensions of corpora albicantia in each ovary and the presence and dimensions of any corpus luteum were recorded. The length and mass of any fetus present in the uterus was recorded before preservation. Mammary glands were assessed for the presence of milk and, for most lactating females, the width, length, and depth measured.

The state of physical maturity of animals was assessed from the degree of fusion of the epiphyses to the centra of midthoracic vertebrae (immature = unfused, maturing = fusing, and mature = fused). The brain mass of neonates and calves was measured directly. That of adults was estimated by filling the skull with coarse dry sand, after first sealing all apertures with adhesive tape, measuring the volume of sand in a measuring cylinder, and assuming this to represent the brain mass.

Age was determined from the number of growth-layer groups (GLGs; *sensu* Perrin and Myrick 1980) counted in the dentine and cement of longitudinal thin sections of teeth. The largest mandibular or maxillary teeth were used. Numerous methods of obtaining thin sections were employed, including hand grinding on 1200-grade abrasive paper or between glass sheets using jewelers rouge, or obtaining thin (~20 μm) ground sections using a geological abrasive wheel. However, the best results were achieved with a custom-built, slow speed saw and diamond lapidary blade that cut thin (120 μm) sections. These were etched in 5% formic acid for 5 minutes, washed in running water for 1 hour and dried and mounted on perspex slides using cyanoacrylate glue. Sections were then viewed, at 8× magnification, through a binocular microscope using both transmitted polarized light and reflected light on the pencil-rubbed etched surface of the tooth.

Dentinal GLGs in all teeth were counted three times by each of two independent observers. Additionally, one observer (VGC) made a minimum of three cemental GLG counts in all teeth where the pulp was occluded, but only in a selection of teeth in which it was not. Initially, dentinal and cemental GLG counts were assessed separately, and the mean of any three counts (dentinal or cemental) that were within 15% of one another was accepted as the age of the animal. However, in teeth where counts varied by more than 15%, further counts were done until any three were within 15% of one another. Finally, for teeth where the pulp cavity was open, the mean of a combination of GLG counts in both cement and dentine was accepted as an estimate of age. Where occlusion of the pulp had occurred, only mean cemental counts were used to estimate age.

The number of dentinal and cemental GLGs in the teeth of one known-age animal ("Dolfie," PEM N6, born 30 December 1972 and died 9 August 1979) were also counted as above. In addition, because of the importance of the age estimate of this animal, a third observer (GJBR) counted GLGs in the dentine.

Results

Age and growth

More than 6½ but less than 7 dentinal GLGs were counted in teeth of the known-age animal "Dolfie" (Fig. 1). This corresponded well with the actual age of 6 years and 8 months and indicated an annual deposition of GLGs in the dentine. However, only six GLGs were counted in the cement of this animal, indicating that cemental GLGs probably reflect whole years only and may underestimate age by 1 year. Despite this, cemental and dentinal GLG counts were taken to represent age in years.

Age estimates from dentinal and cemental GLG counts of the teeth of 174 male and female *Tursiops* were well correlated ($r = 0.95$ and $r = 0.96$, respectively) up to approximately 12 GLGs; thereafter, counts diverged with increasing age due to the closure of the pulp (Fig. 2). The smallest individual from the nets was 29 kg and 125 cm, and had about 15% of the first GLG formed (2 months old). The heaviest male was 204 kg, the longest was 257 cm, and the oldest 42 years. The corresponding parameters for females were 182 kg, 249 cm, and 43 years, respectively.

The relationships of both body length and mass to age, for captured *Tursiops* and stranded or captive born neonates, were fitted to a number of growth curves, including those of Gompertz, Richards, Putter, and Schnute. However, growth with age, for both
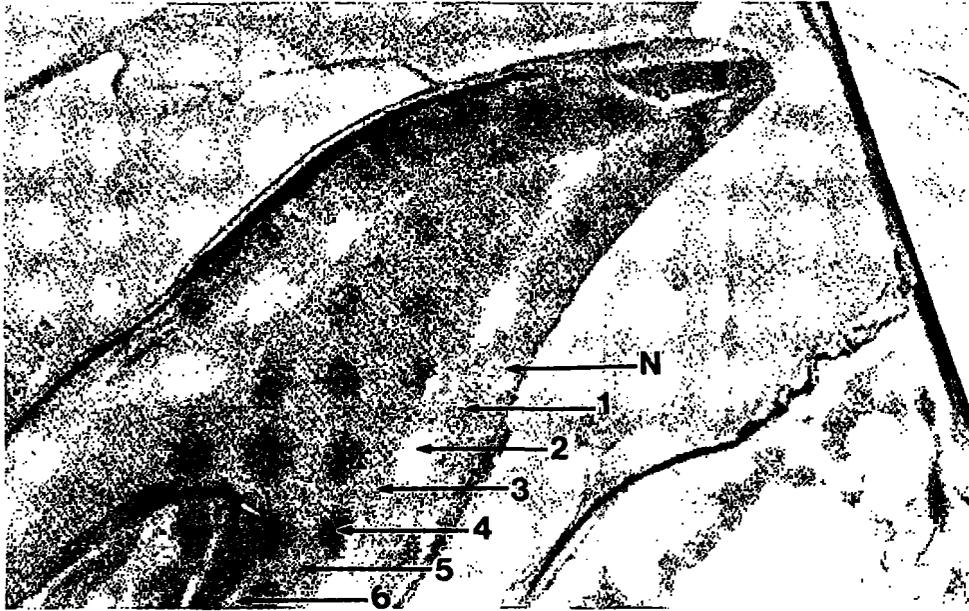
Figure 1
A thin-etched section of a tooth from "Dolfie", a captive-born bottlenose dolphin captured off southern Africa. The neonatal line (N) and the end of each of six growth-layer groups are marked.
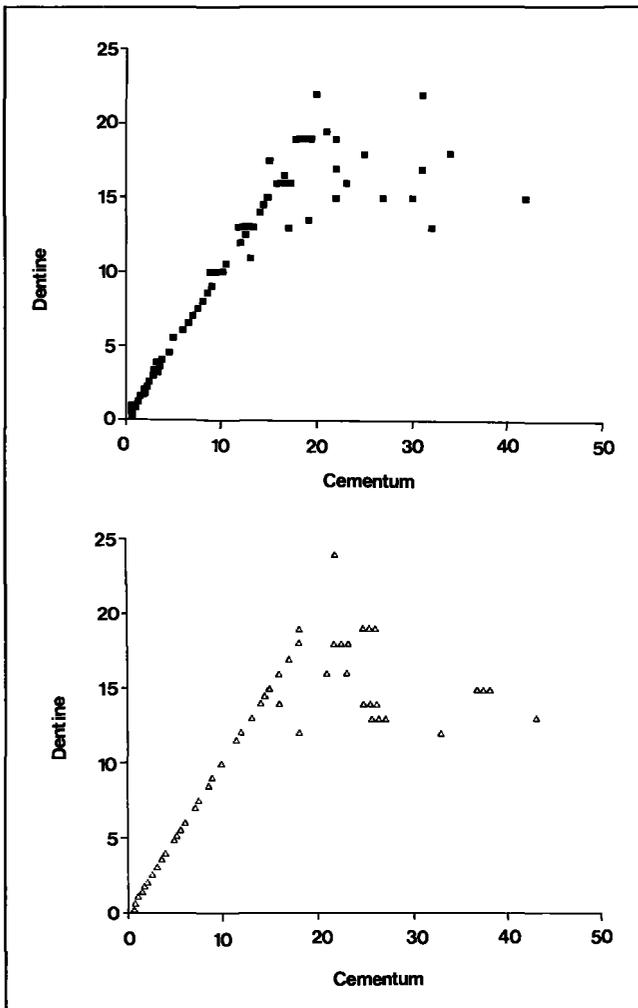
males and females, was best defined by derived von Bertalanffy growth curves (Figs. 3,4) of the form:

$$l(t) = l_{inf}(1 - e^{-k(t-t_0)})^p$$

Asymptotic length and mass, calculated from the mean length and mass of physically mature males (243 cm and 176 kg) and females (238 cm and 160 kg), were slightly overestimated by the derived curve (Table 1), but both show that the asymptotic length and mass of males are greater than of females. There was no significant difference between the mean mass of lactating and nonlactating mature females ($t = 0.236$, $P < 0.01$) which may have contributed to this sexual dimorphism.

Length and mass at birth L_{t0} predicted in Table 1 were almost identical to length and mass at birth (103 cm, range 86–115 cm, SD 7.6, $N = 26$; 13.8 kg, range 9.1–21 kg, SD 2.9, $N = 15$) calculated from the mean length and mass of captive-born or stranded neonates in which the umbilicus was unhealed.

In both males and females, most growth occurred during the first 10 to 12 years of life and thereafter reached a plateau (Figs. 3,4). In females, both mass and length increase in a smooth, continuous process with no evidence of any discontinuity. In males, length increase follows a similar pattern, whereas mass increase

Figure 2
Relationship between growth-layer-group counts in the dentine and cement of male (■) and female (△) bottlenose dolphins captured off southern Africa.
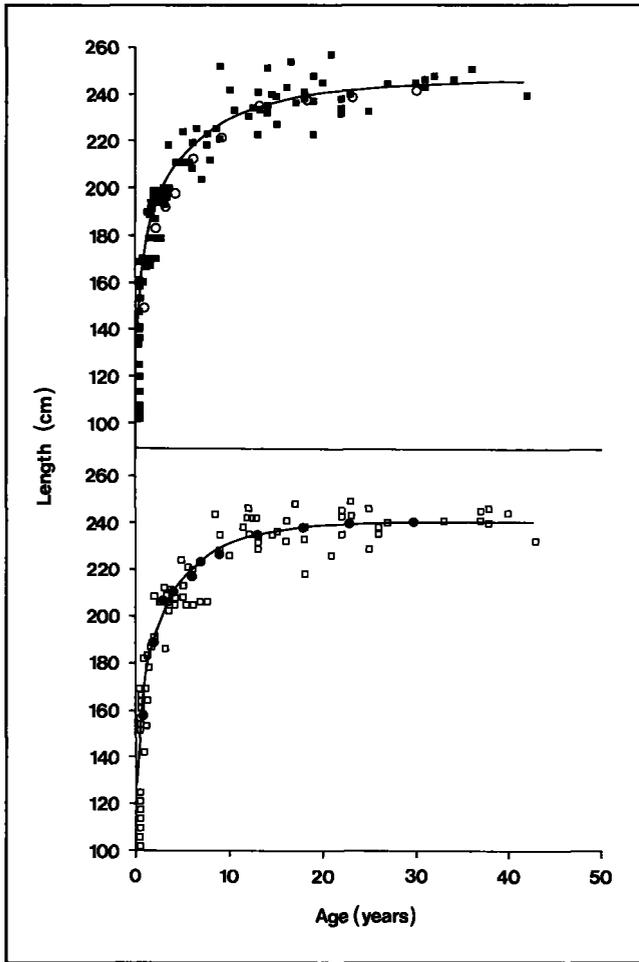
Figure 3

Increase in length with age (growth) of male (■) and female (□) bottlenose dolphins captured off southern Africa. A four-stage von Bertalanffy growth curve is fitted to these data. Mean lengths for various age classes of males (O) and females (●) are also shown.
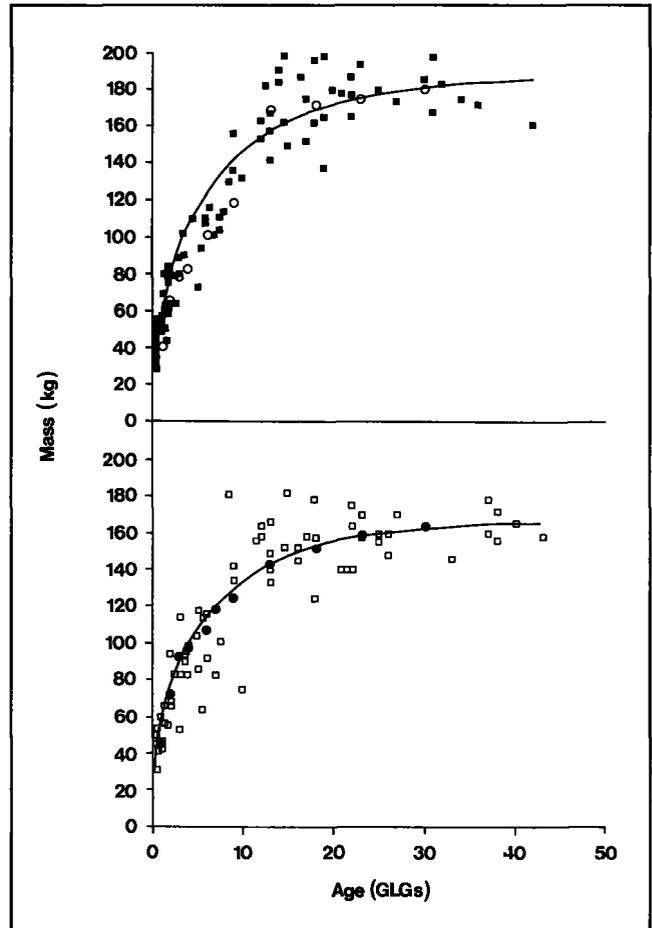
Figure 4

The increase in mass with age of male (■) and female (□) bottlenose dolphins captured off southern Africa. A four-stage von Bertalanffy growth curve is fitted to these data (see text). Mean mass for various age classes of males (O) and females (●) is also shown.

Table 1

Parameters derived from a four-stage von Bertalanffy growth curve $(L(t) = L_{inf}(1 - e^{-k(t-t_0)})^p)$ fitted to age-length and age-mass data for male and female bottlenose dolphins captured off southern Africa.

	Males		Females	
Parameter	Length	Mass	Length	Mass
L_1	102.775	14.7865	102.0206	14.64186
L_2	245.016	185.217	239.9296	165.7209
t_0	−0.02261	−0.0676	−0.056844	−0.05725
L_{inf}	245.611	187.254	239.9625	166.8249
k	0.09712	0.09105	0.167249	0.099103
L_{t0}	103.4	14.9	102.3	14.8
n	100	88	88	84

L_1 = Smallest length or mass in the sample k = Constant of catabolism
L_2 = Largest length or mass in the sample p = Power constant
t_0 = Age corresponding to zero length L_{t0} = Estimated length of mass at birth
L_{inf} = Asymptotic length or mass n = Sample size

Table 2

Range in age (growth-layer-group) at which the vertebral epiphyses of male and female bottlenose dolphins captured off southern Africa were unfused, fusing, and fused.

	Unfused	Fusing	Fused
Males	0–8	4–14	>12
Females	0–6	4–13	>12

Table 3

Length, mass, and brain mass of six stranded or captive-born neonate bottlenose dolphins captured off southern Africa.

	Length (cm)	Mass (kg)	Brain mass (g)
	100	12.4	562
	105	17.7	680
	106	14.8	738
	106		595
	108	13.0	635
	109	13.4	625
Mean	106	14.3	639

Figure 5

Fetal growth in length and mass of bottlenose dolphins captured off southern Africa, and a regression of the form (length = 23.914 + 0.006 × mass) drawn through these data.

shows a clear discontinuity between 10 and 13 years of age (Fig. 4), indicating that a two-stage growth curve may better fit these data.

The mean length and mass of the first five year-classes (calculated from calves displaying whole, completed GLGs only) showed that growth rate during the first year far exceeded that in any other. Mass increases in the first year by some 255% of mean birth mass, but increases over the subsequent 4 years slow to 49%, 13.5%, 10.6% and 3.8%, respectively. In contrast, length increase is much less rapid over this same period and is approximately 57%, 15.2%, 3.7%, 4%, and 5.5%, respectively. In both males and females the relationship between mass and length, up to asymptotic values, is well defined by power curves (males, log mass = −5.1 + 3.06 × log length, $r = 0.97$; females, log mass = −4.7 + 2.9 × log length, $r = 0.95$).

Both male and female bottlenose dolphins appear to reach physical maturity between 12 and 15 years of age (Table 2). The youngest physically mature animal was 12 years old while the oldest nonphysically mature animal was 14 years old (Table 2).

Female reproduction

Only six (2.8% of the total catch and 12% of mature females) of the captured females were pregnant, and the growth of the six fetuses—length (cm) against mass (kg)—was well defined by a linear regression (Fig. 5). Although no estimate of gestation period was possible

from these data, an estimate was obtained from the relationship between neonatal and adult brain mass (Sacher and Staffeldt 1974, in Perrin et al. 1977). A neonatal brain mass of 639 g was estimated from the mean brain mass of six stranded or captive-born neonates in which the umbilicus was unhealed (Table 3). An asymptotic brain mass of 1460 g was calculated from the mean brain volume of physically mature females, although the variation in maximum size of females would obviously affect this. Application of the Sacher and Staffeldt equation gives a gestation period of some 372 days. An alternative method of estimating gestation period based on the relationship between birth length and gestation period (Perrin et al. 1977) yielded an estimate of 12.3 months or 374 days, assuming a birth length of 103 cm.

Birth date, to the nearest month, was back-calculated for 25 captured calves less than 1-year-old by measuring the width of deposited dentine as a proportion of the mean width of the first GLG (Fig. 6). The mean width of the first GLG layer was 279 μm ($N = 29$, range 229–331 μm) with a 95% CI of 10 μm, indicating a maximum error of about 13 days. The subtraction of age from date of capture (Fig. 6) suggests that most births occurred in summer.

In all females the majority of ovarian scars (80%) occurred in the left ovary. The maximum number of scars in any ovary was 11, with no indication that ovary mass decreased with the number of scars (Fig. 7). Age-, mass-, and length-related ovulation rates appear extremely varied in bottlenose dolphins (Fig. 8). In only one female was there one scar, so calculation of mean age at first ovulation was impossible. This 13-year-old
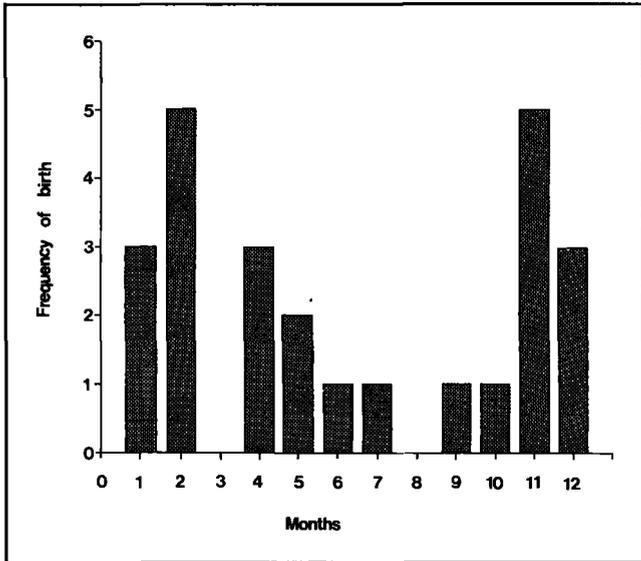
Figure 6
Birth month of 25 bottlenose dolphin calves captured off southern Africa back-calculated from the width of the first dentinal growth-layer-group.
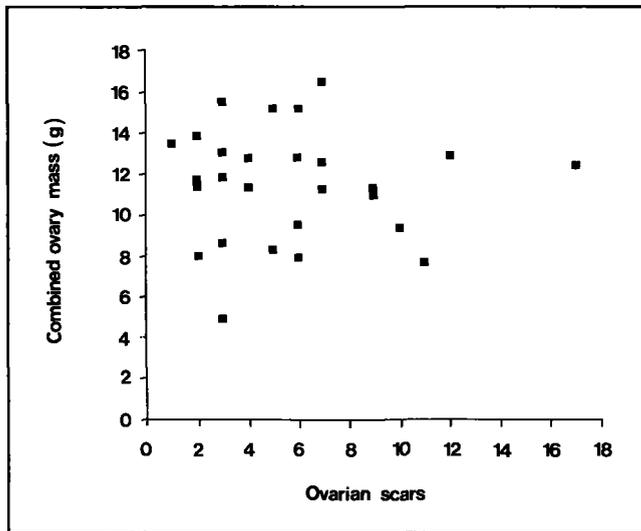
Figure 7
Relationship between combined ovary mass and the total number of ovarian scars for female bottlenose dolphins captured off southern Africa.

Figure 8
Increase in the number of ovarian scars with mass, age, and length of female bottlenose dolphins captured off southern Africa. A linear regression (no. ovarian scars = 0.58 - 0.29 x age) fitted to this relationship in postpubertal females is shown.

female had a *corpus albicans* measuring 10 x 8 x 8 mm (index volume 640 mm^3) and was lactating, indicating she probably had a suckling calf. Extrapolation from a regression of calf length on an index of largest corpora volume, for mother-calf pairs (Fig. 9), suggests that the calf would have been some 184 cm in length or 18 months old (Figs. 3,4), implying that her first

ovulation and conception occurred at approximately 10.5 years of age.
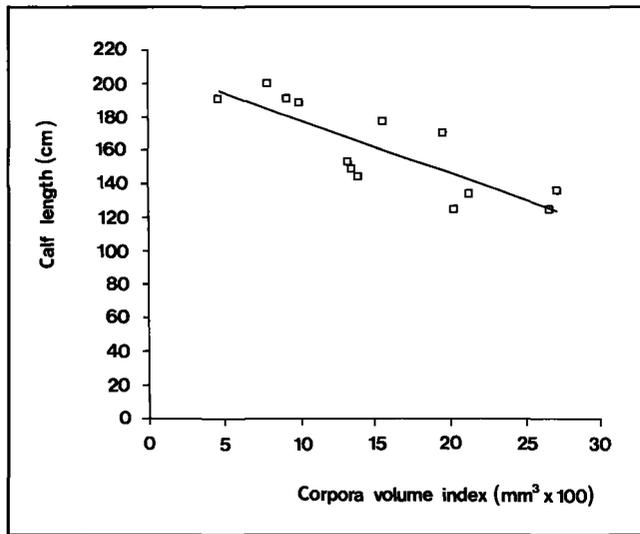
Figure 9
Relationship between the length of a bottlenose dolphin calf and an index of the volume of the most recent or largest corpus in the mother. The fit of a linear regression (calf length in cm = 209.61 − 0.032 × corpora volume index) to these data is shown.

Figure 10
Relationship between the mass of a bottlenose dolphin calf and an index of the volume of the mother's mammary glands.

Two other females, 12 and 13 years old, which had each undergone two ovulations, were lactating and the index volumes of their largest *corpora albicans* were 900 mm³ and 2100 mm³, respectively. Extrapolation from Figure 9 suggests that the calves of these females were approximately 181 cm or 18 months old, and 143 cm or 6 months old, respectively. These data imply that at conception of the calves, these two females were about 10.5 and 9.5 years old, respectively. The above data, and the presence of 10-year-old females that had not ovulated, imply that first ovulation occurs between 9.5 and 11 years of age. One 17-year-old female had undergone two ovulations, was lactating, and had a 170-cm calf of approximately 1-year-old. This suggests that this female was 15-years-old at the time of conception of this calf, although she may have undergone a previous pregnancy.

A regression fitted to the number of ovarian scars on age of sexually mature females has a slope of 0.29 ($r = 0.6$, $N = 32$), implying that mature females, in general, ovulate at least every third year (Fig. 8). A similar regression of log of age on log of number of *corpora albicantia* was linear (log age = −0.61 + 1.03 · log # scars, $r = 0.62$), indicating no decrease in ovulation rate with age.

Length of lactation calculated from the catch statistics of animals on the Natal coast (Cockcroft and Ross In press) where 27% and 5.2% of females were lactating and pregnant, respectively, gave an estimate of 5.2 years (proportion lactating/proportion pregnant;

Perrin and Reilly 1984). As this is obviously exaggerated by the overabundance of lactating females and dearth of pregnant females, alternative means of estimating lactation period are required. The relationship between calf mass and an index of mammary gland volume (length × height × depth) in 13 mother and calf pairs suggests that the mammary glands increase in size during lactation, until the calf's mass is between 60 and 70 kg, after which the mammary volume decreases (Fig. 10). Extrapolation from the growth curves suggests that calves of this mass are about 18-months-old. An examination of the stomach contents of captured calves and juveniles showed that solids first appear in stomachs at about 6 months of age, although milk remains were still evident in calves of up to 3 years of age.

Of the 20 known mother and calf pairs, ten calves were 1 year old or less, five were 1–2 years old and a further five were greater than 2 years old; the mother of one of the latter was pregnant with a fetus of only 38.5 g. Although only solids were found in the stomach of her 69-kg calf, she was still lactating, the only one of six pregnant females simultaneously lactating. These facts imply a mother and calf association of up to 3 years before a subsequent pregnancy.

Female resting period calculated from gestation period (1 year), proportion of females resting (5.3%) and the proportion of females pregnant (Perrin and Reilly 1984) yielded an estimate of about 1 year.
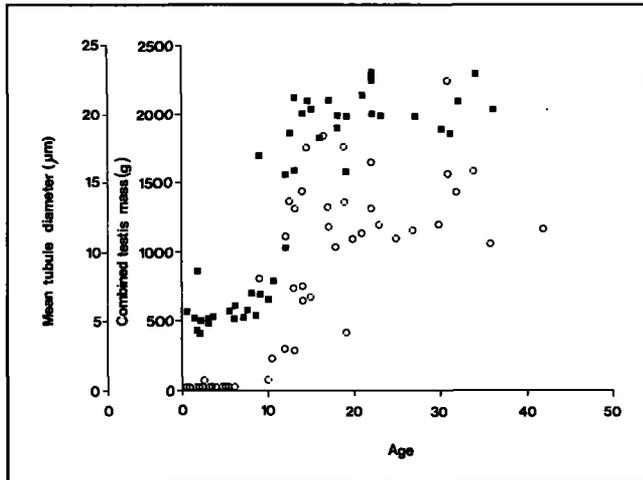
Figure 11
Increase of mean seminiferous tubule diameter (■) and combined testis mass (O) with age in male bottlenose dolphins captured off southern Africa.

Table 4
Mean age, mass, and length of male bottlenose dolphins captured off southern Africa, with testes showing no mature tubule development (stage 1), some (~half) mature tubule development (stage 2), and 75–100% of tubules mature (stage 3/4).

	Testis development stage		
	1	2	3/4
Age	4.68	14.3	20.6
Mass (kg)	90.8	151	174
Length (cm)	201	228	241
n	22	6	25
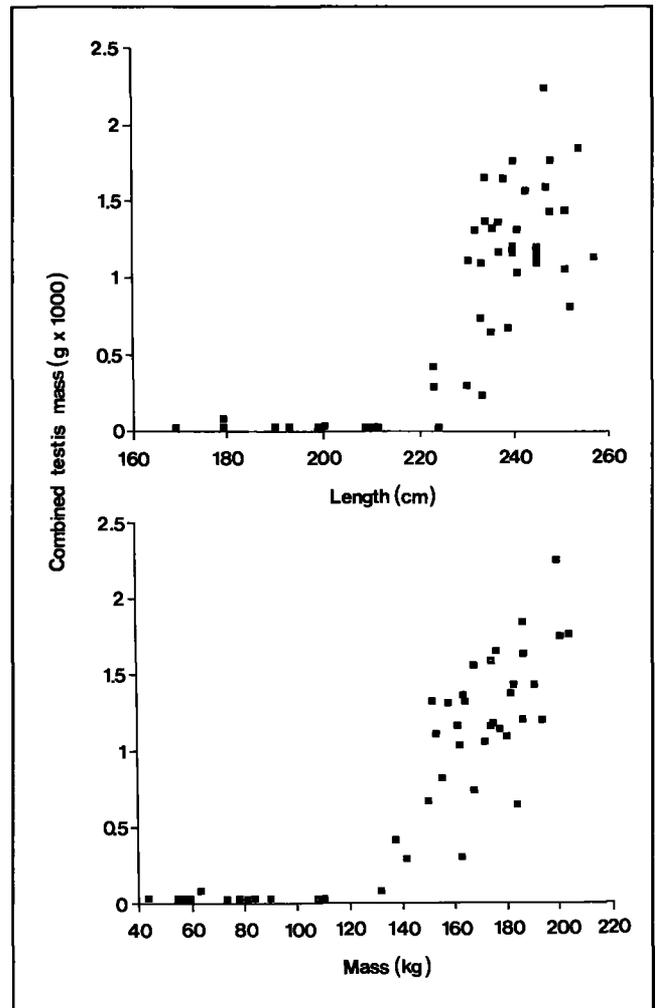
Figure 12
Increase in combined testis mass with mass and length in male bottlenose dolphins captured off southern Africa.

Male reproduction

No consistent differences were found between mean seminiferous tubule diameter of samples taken from the outer, middle, and inner sections of testes. In general, left and right testes were of similar mass ($r = 0.95$, $N = 46$). Combined testis mass remained low (<100 g) up to approximately 10 years of age, approximately 140 kg body mass, and a length of 225 cm, but thereafter increased rapidly (Figs. 11,12). Tubule diameter growth and state of testes development (Mitchell and Kozicki 1984) showed a similar pattern of growth with age, mass, and length (Table 4, Fig. 11), although development of tubules appeared to occur earlier than did the increase in testis mass. The maximum mature testis (stage 4) mass of any male was 1160 g and the largest apparently immature testis (stage 1) was 130 g. The smallest testis at stages 2, 3, and 4 were 140 g,
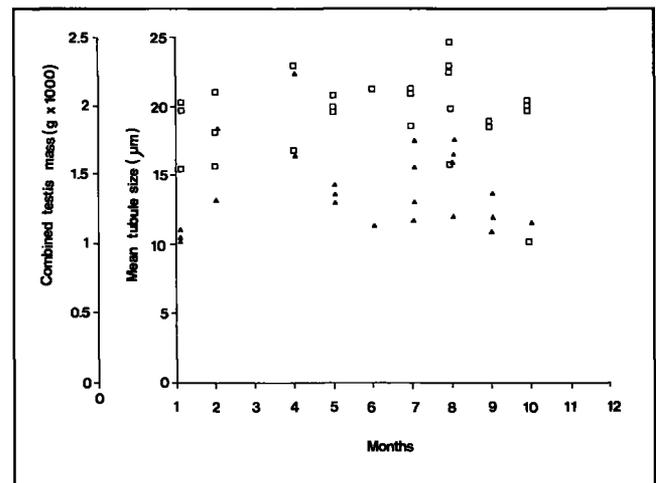
Figure 13
Influence of season (month) on combined testis mass (▲) and mean testis seminiferous tubule diameter (□) in male bottlenose dolphins captured off southern Africa.

320 g and 310 g, respectively. Mean age, mass, and length of males according to testis development stage are given in Table 4. Puberty in male *Tursiops* from the Indian Ocean may begin as early as 9 years of age but primarily between 10 and 12 years (Fig. 11). However, sexual maturity (50% each of stages 2/3 and 4) occurs only at about 14.5 years of age, a length of 240 cm and a mass of 165 kg.

There was no evidence of a seasonal pattern in either combined testis mass and tubule size (Fig. 13) or the presence of sperm in the epididymis.

Discussion

The similarity of dentinal GLG counts to "Dolfie's" actual age indicates an annual deposition of dentinal GLGs for at least the first 6 years. Ross (1984) superimposed the growth rate of this animal on a length-versus-age (dentinal GLGs) relationship in bottlenose dolphins from Natal and the Eastern Cape, and concluded that "the best fit of the points to the curve is reached when the accumulation rate of dentine layers is equal to one per year." Similarly, when the growth rate of another captive Indian Ocean animal (Cockcroft and Ross 1990b) is fitted to the curve, the relationship is best explained by an annual deposition of dentinal GLGs, also proposed for *Tursiops* in other areas (Sergeant et al. 1973, Hui 1980).

In contrast to apparently continuously deposited dentinal GLGs, cemental GLGs appear to be rapidly deposited and only accumulate as whole layers in the teeth of *Tursiops*. Nevertheless, the strong correlation between dentinal and cemental age estimates up to occlusion of the pulp cavity, and the similarity of dentinal and cemental GLG counts in teeth of the captive animal, suggest that cemental GLGs also accumulate annually and are reliable estimators of age in bottlenose dolphins from the Indian Ocean, at least up to an age of 12 years. Despite the lack of direct evidence, it seems likely that cemental GLGs are deposited annually even after 12 years.

Male and female Indian Ocean bottlenose dolphins may attain an age greater than 40 years (cf. Ross 1977) with little difference in the apparent maximum ages of the sexes. In excess of 20% of the Natal net catch were older than 20 years, indicating a long-lived species. Few data are available on the longevity of *Tursiops* elsewhere, and most existing studies have used dentinal age estimates. Sergeant et al. (1973) estimated the longevity of *Tursiops* from northeast Florida to be about 25 years, with no apparent differences in the life expectancy of males and females. Hohn (1980), in a study of *Tursiops* from the southeast coast of the United States, found animals with up to 27 dentinal

GLGs, males and females reaching similar ages. In contrast, the maximum age of spotted dolphins, estimated from cemental GLGs, is in excess of 45 years (Kasuya 1976). Thus, the use of cemental GLG age estimates in future studies of bottlenose dolphins may yield greater estimates of maximum age.

The estimated mass and length at birth of Indian Ocean bottlenose dolphins in this study are comparable with those calculated by Ross (1984). Subsequent to birth, growth is rapid, particularly in terms of mass, but decreases gradually with age. The proportional length increase is similar to that previously recorded for bottlenose dolphins from Natal and the eastern Cape (Ross 1977, 1984; Cockcroft and Ross 1990b) and also those from other areas such as northeast Florida (Sergeant et al. 1973), the western North Atlantic (Hohn 1980) and captive animals from the Pacific coast of Japan (Kasuya et al. 1986). An enormous increase in mass during the first (suckling) year is well known in seals and balaenopterid whales but has not often been recorded for delphinids. Presumably, a large initial mass increase reflects the rapid development of the calf and its need to reach thermoregulatory equilibrium as well as some social and motor independence from its mother (Cockcroft and Ross 1990b) before the female's involvement with the next pregnancy and calf.

The asymptotic length and mass values obtained in this study and those of Ross (1977, 1984) are less than those for bottlenose dolphins from the western North Atlantic (Hohn 1980), Florida (Sergeant et al. 1973), and the Japanese Pacific (Kasuya et al. 1986). It is unclear why bottlenose dolphins from different areas have varying asymptotic sizes. Some authors have suggested that this may warrant the separation of the various populations to the specific level (Ross 1977), although Ross and Cockcroft (1990) have suggested that there is little morphometric evidence to suggest this and that such differences may only have resulted from environmental conditions, particularly temperature.

The asymptotic lengths of male and female Indian Ocean bottlenose dolphins are only slightly different (243 cm and 238 cm, respectively). In the western North Atlantic, Hohn (1980) found no difference in the maximum lengths of males and females. These results support the findings of Sergeant et al. (1973) that the total lengths of male and female delphinids, in general, do not appear to be different, although they found that the asymptotic length of male *Tursiops* from Florida was 20 cm greater than that of females.

In contrast, fully grown male Indian Ocean bottlenose dolphins are considerably heavier (9%) and more robust than females (176 kg and 160 kg, respectively). Lactating and nonlactating females had a similar mean mass, indicating that this mass difference cannot be

attributed to stress and blubber mass loss through lactation (Cockcroft and Ross 1990a,b). Some of this mass difference between the sexes may be a direct consequence of the male mass growth spurt between 10 and 12 years of age. It is unclear why this growth spurt is not reflected in the length of males; it may be that robusticity and not length is important in male and female interaction.

Despite this, the male growth spurt at the onset of puberty may be similar to the two-stage growth that Perrin et al. (1976, 1977) described for male and female spotted and spinner dolphins in the eastern tropical Pacific where growth showed a pubertal secondary growth spurt. In male bottlenose dolphins, this spurt occurs 4–5 years later than in spotted or spinner dolphins but also at the onset of puberty, suggesting that such growth spurts may be directly related to the attainment of sexual maturity. It is possible that this growth spurt may also be evident in female bottlenose dolphins but is not discernible owing to the small sample size.

Females mature sexually some 2 or 3 years prior to the attainment of physical maturity in contrast to males, where sexual maturity is attained just before physical maturity. In both sexes, however, physical maturity occurs almost in concert with the occlusion of the tooth pulp cavity, supporting previous suggestions that animals with occluded pulp cavities are sexually and physically mature (Ross 1977, 1984). Females attain sexual maturity at least 2 years earlier and at a lesser length and mass than do males, although the reduced number of first-time ovulators and high occurrence of females with multiple ovulations will have biased this upwards. It is not unusual for female delphinids to attain sexual maturity sometime before and at a smaller size than males. Female *Tursiops* in the western North Atlantic also appear to follow this pattern (Sergeant et al. 1973). Female spotted and spinner dolphins reach sexual maturity about 3 or 3–4 years, respectively, before males and both are smaller than their male counterparts (Perrin et al. 1976, 1977). It has been proposed that this disparity ensures more sexually mature females than males in the population (Bryden 1972). Intensive behavioral field work is needed before this suggestion can be confirmed.

Although no direct estimate of gestation period was available from the fetal growth data, both derived estimates were in excellent agreement, about 373 days. A 373-day gestation period is slightly longer than previous estimates for Indian Ocean *Tursiops*, which range from minimums of 342 and 341 days (Saayman and Tayler 1977) to maximums of 364 and 368 days (Ross 1984) in captive bottlenose dolphins. Similar estimates of the gestation period in captive *Tursiops* from other areas have been given by Tavolga and Essapian (1957), McBride and Kritzler (1951), and Kasuya (1985).

Although the sample was too small for an assessment of the age at first ovulation, the onset of ovulation in females is apparently rapid. Thereafter, there was considerable variability in the ovulation rates. Some 12- or 13-year-old females had particularly high ovulation rates, possibly a result of several initial infertile ovulations (Harrison et al. 1972). Others of the same age had low corpora counts, were all lactating, and one was pregnant, indicating that fertilization occurred on the first or second ovulation. Indirect evidence, which shows that lactational transfer of organochlorines in female bottlenose dolphins occurred after one or two ovulations (Cockcroft et al. 1989), supports the view that the majority of females conceive after one or two ovulations. The variation in ovulation rates of older females may be due, in part, to the same factors which apply to younger females and to additional reasons such as calf mortality or aborted pregnancies.

Overall, the calculated annual ovulation rate for female bottlenose dolphins was 0.28, a substantially lower rate than that observed for *Tursiops* from northeast Florida (Sergeant et al. 1973). There was little sign of reproductive senescence in females from Natal, as ovulation rate did not appear to decline with age, and there was no reduction in ovary mass with an increasing number of ovarian scars. Also, the oldest captured female was lactating, and a number of older females were captured with calves and had enlarged *corpora* in their ovaries. Results from organochlorine residue studies in these females also indicate that older females do not become senescent (Cockcroft et al. 1989). These data imply that older females do not act as "wet nurses," which is contrary to suggestions for several other species of odontocetes that manifest age-related declines in fecundity. Senescent females invest more in quality calf-rearing and a longer lactational commitment than in quantity calf-bearing, as their reproductive potential fails (Kasuya and Marsh 1984, Marsh and Kasuya 1986). However, sample numbers in this study were small and certain female-calf pairs showed an extended relationship, though there was no indication that this was restricted to older females.

Taken in combination, these facts indicate that some Indian Ocean bottlenose dolphin females are probably reproductively active until an advanced age. A similar conclusion was reached by Kasuya (*in* Marsh and Kasuya 1986) who found that although the annual pregnancy rate and the number of resting females in a sample of *Tursiops* from the Pacific declined with age, pregnant and lactating females were present in all age groups, presenting no conclusive evidence of senescence.

Although births apparently occur throughout the year, there is a peak in summer, between November and February, when over 60% of births occur. However, as birth dates were back-calculated, this may reflect the greater catch of dolphins in these months and the bias of the net catch for larger calves (Cockcroft and Ross In press), although previous work in this region noted that births occurred predominantly in late spring and summer (Ross 1977). No seasonal cycle of either testis mass, tubule diameter, or occurrence of sperm in epididymis was evident in mature males. These data also imply no distinct mating or breeding season in Indian Ocean *Tursiops*. In Florida waters, the main mating and calving season is apparently February to May (Essapian 1963), or spring to early fall (Irvine et al. 1981), which is similar to that found in the present study. In contrast, bottlenose dolphins off Argentina show a distinct summer calving and mating season (Wursig 1978). These geographical variations, however slight, indicate the adaptability of coastal *Tursiops* to local conditions.

Although it has been suggested that suckling as a nutritional source probably only lasts 1 year (Kasuya and Marsh 1984, Cockcroft and Ross 1990b), there is evidence that suckling may last at least 18 months in *Tursiops* and that non-nutritional suckling may continue for as long as 3 years for some mother and calf pairs. An estimate of the duration of lactation is difficult, where suckling extends over long periods and may serve a non-nutritional purpose such as enhancing the cow-calf bond (Brodie 1969). Of the calves from lactating female-calf pairs, 25% were over 1 year old and a further 25% were over 2 years old, and some of the latter had both milk and solids in their stomachs. The mammary glands from these lactating females, only one of which was pregnant, increased in size with calf size, until calves were at least 18 months old. In combination, these data indicate that lactation in Indian Ocean bottlenose dolphins lasts more than 1 year and in some instances may extend to more than 2 years.

This is slightly longer than previous estimates of lactation length and age at weaning based on studies of captive and captured free-ranging bottlenose dolphins (McBride and Kritzler 1951, Gurevich 1977, Saayman and Tayler 1977, Kasuya 1985, Cockcroft and Ross 1990b) and suggests a prolonged mother-calf association that may extend in free-ranging bottlenose dolphins for at least 15 months (Irvine et al. 1981). Such extended mother-calf interaction may indicate a stable school structure, such as that postulated for short-finned pilot whales off the Pacific coast of Japan, which may be indicative of late maturing, long-lived animals (Kasuya and Marsh 1984). This may equally apply to *Tursiops* where a lengthy mother-calf bond may be important in the calf's development and be a reflection of the smaller school size and inshore habitat, mastery of which may require greater maternal care and a longer learning period (Cockcroft and Ross 1990b).

During a study of captive bottlenose dolphin mother and calf association, Cockcroft and Ross (1990b) have shown that the calf's suckling rate decreased with age, although its energy requirements probably grow with its level of independence and activity. As there was no evidence of energy changes in delphinid milk during lactation (Arvy 1974) to compensate for this, the authors proposed that the quantity of milk ingested may increase as the calf's stomach volume increased (Cockcroft and Ross 1990b). This explanation is supported by the present findings that a female's mammary glands increase in size, probably increasing the volume of milk produced, during lactation.

In view of the extended lactation period of female bottlenose dolphins and the early and probably increasing intake of solid food by the calf, it is unlikely that females require a substantial interval between the end of lactation and the next pregnancy. A 1-year resting period, estimated from the catch statistics data, is almost certainly an overestimate due to catch bias. Kasuya (1985) estimated a 3-month resting period for *Tursiops* in the western north Pacific, and it is probable that Indian Ocean *Tursiops* are similar. Considering that gestation lasts about 1 year and that lactation probably lasts 18 months to 2 years, a calving interval of around 3 years can be estimated for Indian Ocean bottlenose dolphins. This estimate is in good agreement with the projected ovulation rate of one every 3 years, but assumes that all calves survive and ignores the effects of differential calf mortality (Perrin and Reilly 1984) that would lower the mean calving interval considerably.

Nothing is known of the age and sex structure of the Natal bottlenose dolphin population. The only available information is from the catch of these animals in the Natal shark nets, the sex, size, and age structure bias of which have been discussed (Cockcroft and Ross In press). Given these biases, attempts to calculate reproductive parameters from these data are flawed but provide the only means of calculating the reproductive potential of this population.

The relevant proportions in the net catch of females—mature, lactating, pregnant, and resting—are 56%, 43%, 27%, 5.2%, and 5.8%, respectively (Cockcroft and Ross In press). Annual pregnancy rates (APR; Perrin and Reilly 1984) calculated from these catch data and lactation period (either 1 or 2 years) range between 5.2% and 27%. Changes in either the proportion of females lactating or the length of lactation greatly influence this calculation, but even the highest estimate is low in comparison with values calculated for *Tursiops* in other areas; 63% in the Black Sea (Danilevsky and

Tyutyunnikov 1968, *in* Perrin and Reilly 1984) and 43.6% and 40.4% for the western north Pacific (Kasuya and Izumisawa 1981, *in* Perrin and Reilly 1984; Kasuya 1985).

Gross annual reproduction rate (GARR) (Perrin and Reilly 1984) calculated from catch statistics and the range of APR values yields estimates between 0.043 and 0.065. Although biases in the catch will influence these GARR estimates, they are useful for comparative purposes. The former GARR estimate is greater than that calculated for an unexploited stock of *Tursiops* from eastern Australian waters, although this was based on an unreliable technique of estimating calf numbers from aerial surveys (Lear and Bryden 1980, *in* Perrin and Reilly 1984). The latter GARR figure, although probably an overestimate, is some 40% and 500% lower than those estimated for exploited populations of *Tursiops* off Iki Island, Japan (Kasuya 1985) and in the Black Sea (Danilevsky and Tyutyunnikov 1968, *in* Perrin and Reilly 1984), respectively.

The probable biases in the calculated APR and GARR estimates suggest that an assessment of the theoretical maximum natural rate of increase (ROI) of the Natal bottlenose dolphin population would be more practical. Assuming a calving interval of 2–3 years, age at first breeding of 10 years, and an annual survival rate of less than 0.97, an ROI of 4–6% can be calculated (Reilly and Barlow 1986). The ROI makes allowances for adult and calf mortality not accounted for by a GARR estimate, which, therefore, infers that even the greater GARR figure may be an underestimate. Given an annual increase of as much as 6% of the estimated 900 population, the mean annual mortality of bottlenose dolphins in shark nets—32 dolphins per year including about 4 reproductive females—in conjunction with whatever other sources of man-induced mortality, such as the probable death of first-born neonates through pollutant toxicity (Cockcroft et al. 1989), implies that mortalities may be close to or exceed the likely replacement rate of this population. However, this conclusion should be viewed with some caution, as it is based on an estimated population of only some 900 dolphins, although biases of aerial counts suggest that numbers may be greater (Cockcroft et al. In press). Additionally, other factors may also influence understanding of the reproductive capacity of this population. If bottlenose dolphins on the Natal coast are geographically separated for long periods (Cockcroft et al. 1989) with little mixing even of adjacent groups (Cockcroft et al. In press), then reproductive parameters for females in different areas may vary and have a profound effect on calculated replacement potentials.

The incidental mortality and probable depletion of long-lived dolphins, that invest many years in the care and socialization of their young and are resident in areas with which they are familiar, is of concern. The future management of the Natal bottlenose dolphin population requires accurate population figures and an unbiased estimate of age and sex structure. Regular aerial, boat, and shore-based surveys along the Natal coast are needed to define the former. The latter is best obtained through a combination of intensive field observational work on free-ranging dolphins and a continued monitoring of captured animals.

Acknowledgments

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