Age, growth, and calving season of bottlenose dolphins, *Tursiops truncatus*, off coastal Texas

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Life history studies of bottlenose dolphins, *Tursiops truncatus*, in North America began over a century ago with observations by True (1890) on dolphins captured in a directed fishery along the coast of Cape Hatteras, North Carolina. He detected an approximately equal sex ratio but variability in size among individuals in almost every catch. He noted tooth development (eruption) and state of fissure of the umbilical cord in young dolphins, as well as reproductive state in females (i.e. lactating or pregnant). Furthermore, he suggested that calving took place primarily in the spring. Since then, much of the knowledge of life history of bottlenose dolphins in the western Atlantic has been obtained from dolphins captured incidentally during fishing operations or directly for research or display, and from stranded animals (Sergeant et al., 1973; Hohn, 1980; Hersh, 1987; Barros and Odell, 1990; Mead and Potter, 1990). More recent and extensive information on age, growth, and population biology has been obtained from a long-term study of free-ranging bottlenose dolphins in Sarasota Bay, Florida (e.g. Hohn et al., 1989; Scott et al., 1990; Wells and Scott, 1990; Read et al., 1993).

Equivalent life history studies have not been conducted on bottlenose dolphins from the north or western Gulf of Mexico, although this is the most common cetacean inhabiting the coastal waters of the northwestern Gulf (Barham et al., 1980; Fritts et al., 1983; Leatherwood and Reeves, 1983; Mullin et al., 1990). It also is the most commonly stranded species along the Gulf coast, particularly along the coast of Texas. Strandings of bottlenose dolphins have been recorded routinely in Texas since 1974 (Jones, 1987; Schmidly and Shane[1]). Since late 1980, the Texas Marine Mammal Stranding Network (TMMSN) has recovered over 800 carcasses. In the spring of 1990 and 1992, the TMMSN documented the highest frequency of bottlenose dolphin strandings since the program began (Hansen[2]). Unusually high mortalities among bottlenose dolphins along the Texas coast have emphasized the need for baseline information on their life history to allow better interpretation of the impacts of these mortalities on the populations. The available source of data and samples to begin such studies is the strandings themselves. This study of stranded specimens was conducted to estimate 1) age structure of stranded specimens, 2) growth from length-at-age data, 3) mean length at birth, 4) calving season, and, where possible, 5) age and length at sexual and physical maturation. These data provided the material for a preliminary examination of the life history of bottlenose dolphins that inhabit the coastal waters of Texas.

Materials and methods

From January 1981 through December 1990, 898 stranded bottlenose dolphins (373 males, 292 females, and 233 specimens of unknown sex) were recovered by members of TMMSN along the 715-km Texas coastline. Tooth sections were prepared for 205 specimens (Table 1), which comprised the entire sample of specimens from which teeth were collected. The teeth were fixed in 10% buffered formalin and processed following the decalcification, sectioning, and staining protocol described by Hohn et al. (1989). Age was estimated by counting the number of GLG's (growth layer groups, Perrin and Myrick, 1980) in dentine and cement without reference to data on the sex and length

[1] Schmidly and Shane. 1978. A biological assessment of the cetacean fauna of the Texas coast. Rep. U.S. Mar. Mamm. Comm., contract report MMC-74/05, 38 p.

[2] Hansen, L. J. 1992. Stranding rate and trends. *In* L. J. Hansen (ed.), Report on investigation of 1990 Gulf of Mexico bottlenose dolphin strandings, p. 15–20. National Marine Fisheries Service, Southeast Fisheries Center, Contribution MIA-92-93-21.

Manuscript accepted 26 June 1997.
Fishery Bulletin 96:357–365 (1998).

Table 1

Sample sizes and sex ratios of bottlenose dolphins, *Tursiops truncatus*, stranded along the Texas coast from January 1981 through December 1990 and of the subsample for which age was estimated.

Sample	Males	Females	Sex unknown	Sex ratio (M:F)
Total	373	292	233	1.3 : 1
Aged	78	81	36	1 : 1.04
<1.0 yr old	22	10	7	2.2 : 1
1–20 yr old	46	39	22	1.2 : 1
>20 yr old	10	32	7	1 : 3.2

of the animals. The age structure of males and females was compared by using the nonparametric Kolmogorov-Smirnov (K-S) test (Sokal and Rohlf, 1981).

Growth was determined by fitting the nonlinear, least-squares Gompertz model to length-at-age data (SAS Institute, 1985):

$$S(t) = A\left(\exp\left(-b\exp(-k)\right)\right), \quad (1)$$

where S = a measure of size (cm);
A = asymptotic length;
b = the constant of integration;
k = the rate of growth constant; and
t = age (yr) (Laird, 1966).

Total body length was measured to the nearest centimeter in a straight line from the tip of the upper jaw to the notch of the fluke (Norris, 1961). Predicted asymptotic lengths for males and females were compared by using the approximate t-test (Sokal and Rohlf, 1981). These lengths were then compared with the corresponding asymptotic lengths for male and female bottlenose dolphins from Sarasota Bay, Florida (Read et al., 1993).

Length at birth was estimated in three ways: 1) as the mean length of 21 specimens from the entire data set (n=898) determined to be neonates on the basis of the presence of remains of the umbilical cord or folded dorsal or caudal fins; 2) as the mean length of 21 specimens (no overlap with the previous sample of 21) estimated to be <0.1 year old because the neonatal line in tooth sections had not yet formed or had just started to form (Hohn and Hammond, 1985); 3) as the predicted value from the Gompertz model. Calving season was also identified in three ways: as the date of stranding of 1) neonates, 2) specimens <0.1 year old, and 3) specimens measuring 90–120 cm in length.

Reproductive data were available for 57 females from the total sample of stranded females from which some data were collected (n=292). Teeth were available for 25 of these. Sexual maturity of females was determined by noting 1) the presence or absence of a corpus of ovulation from external examination of ovaries or 2) the presence of a fetus or an extended uterus, indicating a pregnancy. Sexual maturity of males could not be evaluated because few data or samples from testes were collected.

Vertebrae from 24 males, 25 females, and 12 dolphins of unknown sex were collected. All were examined for state of physical maturity. From this sample, teeth were available for only 11 males, 12 females, and 8 specimens of unknown sex. Physical maturity was determined by noting the degree of fusion of the epiphysis to the centrum of thoracic and lumbar vertebrae. Three categories were used to classify the specimens: a) not fused (immature), b) fusing (maturing), and c) fused (mature).

Results

Age and sex composition

Estimates of age were obtained for 78 males, 81 females, and 36 specimens of unknown sex (Table 1; Fig. 1). For an additional 10 dolphins (5 males, 3 females, and 2 dolphins of unknown sex), only minimum ages, ranging between 12+ to 20+ years, were obtained because poor-quality tooth sections precluded accurate age estimates. These 10 specimens were excluded from all analyses. Occlusion of the pulp cavity was not seen in any of the tooth sections.

The oldest male and the oldest specimen of unknown sex were 33 years old and the oldest female was 41 years old (Fig. 2). Age distributions for males and females were significantly different (K-S test, P<0.01). Specimens less than 1 year old accounted for a relatively large part (20%) of the aged sample and were skewed towards males, but with increasing age, the proportion of females in the sample increased significantly (chi-square (χ^2) P=0.003, for data stratified by age group 0–0.9, 1.0–9.9, 10.0–19.9, and ≥20 years; Table 1). Because of the relatively large number of males less than one year of age, the K-S test was rerun with that age class excluded for both males and females. The difference was still significant (K-S test, P<0.01).

Growth

The Gompertz model gave predicted asymptotic lengths of 263.5 cm for males and 244.7 cm for fe-

males. Trends in the residuals, however, showed that the fit was poor for a number of age classes (Fig. 3). To obtain a better predictor, the model was fitted to a data set that excluded all specimens less than 1 year of age, analogous to the procedure in Read et al. (1993) where the Gompertz model was found to describe well the growth of bottlenose dolphins from Sarasota Bay, Florida. With this subset of data, asymptotic length was slightly higher for males (268.0 cm) and for females (246.7 cm) but neither were significantly different from the predicted values from the total sample (approximate t-test, $P>0.05$, Table 2). Trends in the residuals showed that predicted length at age was a better fit for ages 1–9 years and was slightly overestimated at asymptote.

In an attempt to find a fit with evenly dispersed residuals, the Gompertz model was modified to fix length at birth at 109.5 cm, as calculated below by independent means, rather than by solving for the asymptotic value, A:

$$S(t) = 109.5\left(\exp\left(b\left(1 - b\exp(-k)\right)\right)\right). \qquad (2)$$

Predicted asymptotic length was 261.7 cm for males and 244.4 cm for females. Predicted length from birth through age 2 years was very similar to that estimated from the total sample with the Equation 1 version of the Gompertz model. Length at age was still underestimated and this derivation of the model did not improve the fit.

Although none of the iterations produced a fit that represented all age classes well, the best overall predicted values occurred with Equation 1) when specimens <1 year of age were excluded (Fig. 3) and, for comparative purposes, predicted lengths were taken from this model (268 cm for males and 246.7 cm for females). Males were significantly larger than females at asymptotic length (approximate t-test, $P<0.05$). Asymptotic lengths of males and females were not significantly different (approximate t-test, $P>0.05$) between dolphins from Texas and Sarasota Bay, Florida (Table 2).

Length at birth and calving seasonality

There was no difference in length at birth between male and female neonates or between males and females <0.1 year old (t-test, $P>0.05$). Therefore, data were combined to produce a single estimate with each method (Table 3). Mean length at birth from combined data was not significantly different between these two methods (t-test, $P>0.05$), therefore the total data set was combined (males, females, and sex unknown, $n=42$) to give an estimated length at birth of 109.4 cm (SD=8.5). Length at age 0 estimated from the Gompertz curve was greater than length at birth estimated from the more direct measures. In addition, because the best-fit version of the Gompertz

Figure 1

Midlongitudinal stained thin sections from the tooth of a 29-year-old, 261-cm female bottlenose dolphin, *Tursiops truncatus*, stranded in Texas. Growth layer group (GLG) boundaries were considered to be the relatively thin dark layers; most of these are easily visible. Boundaries between the first few layers are marked with a small black line on the upper left side of the section. The last few, very fine GLG's near the pulp cavity are difficult to see at this low magnification.

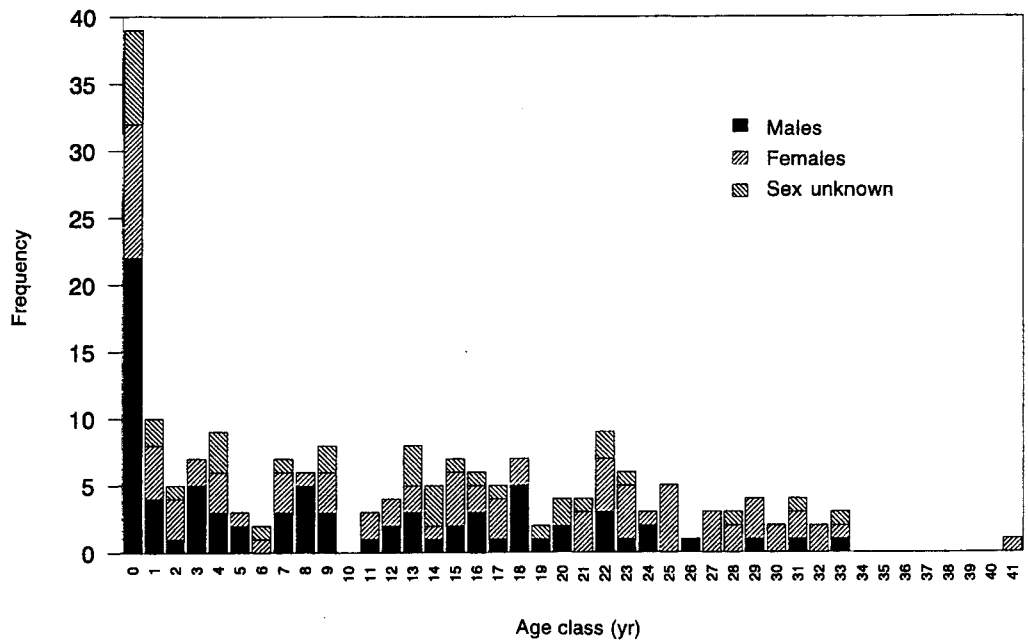

Figure 2

Age distribution of bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas from 1981 to 1990.

Table 2

Parameter values and their asymptotic standard errors (SE) from the Gompertz growth model fit to two sets of length-at-age data from bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The first set included all the available data; the second set was a subset of the first set that excluded specimens <1.0 yr of age. A = asymptotic length, b = the constant of integration, and k = the rate of growth constant. n = number of dolphins in each sample.

	n	$A \pm$ SE	$b \pm$ SE	$K \pm$ SE
Female length				
All data	78	244.7 ± 1.90	0.755 ± 0.0423	0.497 ± 0.0490
Specimens of age <1.0 yr excluded	68	246.7 ± 2.22	0.482 ± 0.0873	0.294 ± 0.0655
Male length				
All data	75	263.5 ± 2.93	0.785 ± 0.0308	0.351 ± 0.0313
Specimens of age <1.0 yr excluded	54	268.0 ± 3.64	0.592 ± 0.0679	0.234 ± 0.0388

model excluded specimens less than 1-yr-old extrapolation to age 0 to estimate length at birth was inappropriate. The ratio of mean length at birth to asymptotic length was 40.8% for males and 44.4% for females.

The mode in strandings of neonates (n=12 of 21) and specimens <0.1 year of age (n=11 of 21) occurred in March (Fig. 4). In both data sets, 86% of the specimens stranded during March and April. Except for five specimens found in November and December, all neonates stranded from February through June.

Sexual and physical maturation

Because reproductive data were collected from only 57 females (Table 4), the sample size was too small to estimate the mean age and length at sexual maturation. Only seven pregnant females were noted; the smallest was 233 cm and the longest was 335 cm. The latter, an extremely large female, also had the largest fetus (122-cm male) recorded in the TMMSN stranding database. Teeth were available for three of the seven pregnant females, and they were esti-

mated to be 9.8, 23, and 27 years of age. A 4.8-year-old pregnant female, 245 cm long, was excluded from this sample owing to possible mislabeling of samples. No reproductive data were available for males.

Mean age and length at physical maturation could not be calculated owing to the small sample sizes (Table 4). Two specimens, a 280-cm male and a 253-cm female, were notable because they were relatively large yet physically immature.

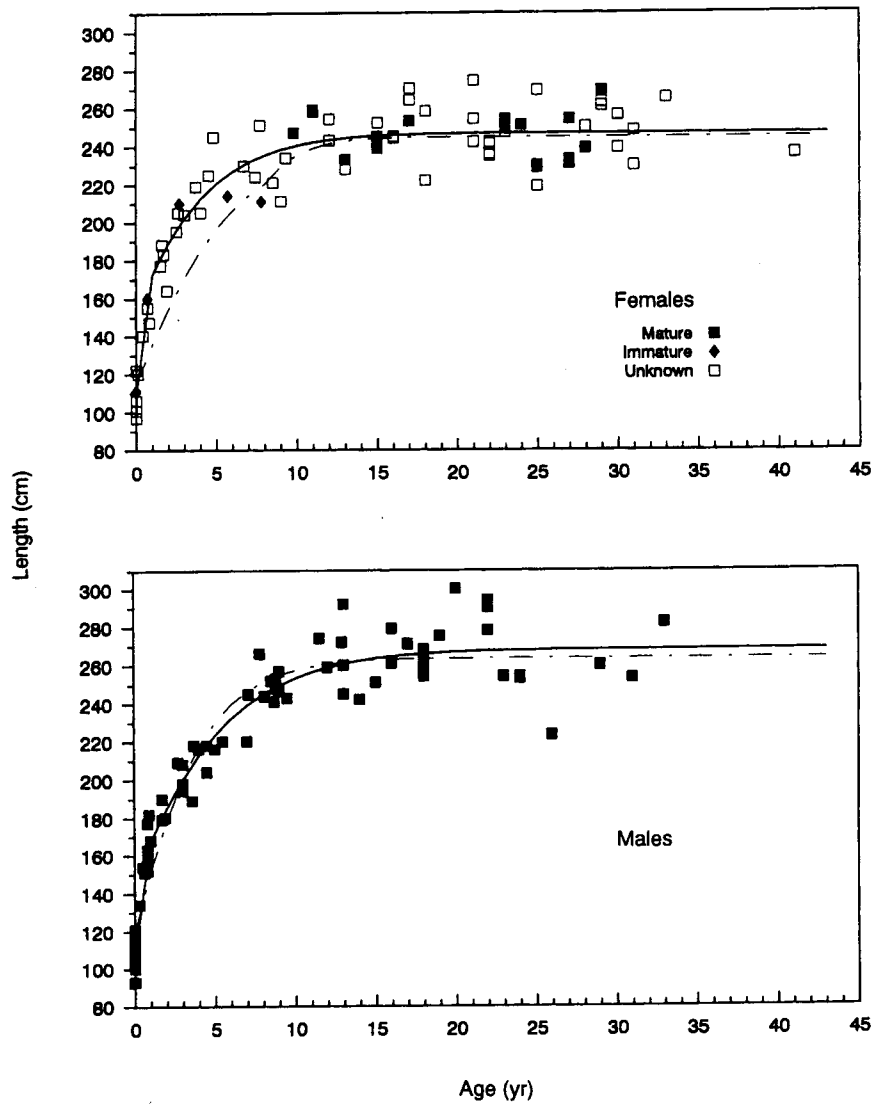

Figure 3

Scatterplots of length at age for female and male bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The solid lines represent the predicted growth trajectory from the Gompertz model when specimens less than 1 yr old are excluded; growth between birth and age 1 was determined by using the independently estimated length at birth and the predicted length at age 1. The dashed lines represent the predicted growth trajectory from the Gompertz model with the entire data set. Although the asymptotic lengths are similar, the growth trajectories are different, particularly for females.

Discussion

Despite the widespread distribution and high abundance of bottlenose dolphins along the Atlantic and Gulf of Mexico coasts of the United States, the majority of biological information for this species has come from a few locations, a relatively small number of studies, and small sample sizes. Basic questions still remain throughout much of the range. The current data provided the opportunity to begin to evaluate similarities and differences in bottlenose dolphin life history in relation to areas where previous studies had been conducted.

Results from this study support the hypothesis that in bottlenose dolphins sexual dimorphism in body length is not exhibited at birth (Sergeant et al., 1973; Hohn, 1980; Kasuya et al., 1986; Cockcroft and Ross, 1990) but does occur in adults (Read et al., 1993). Although a number of studies have concluded that sexual dimorphism in adult size does not exist in bottlenose dolphins from the Atlantic and Gulf of Mexico coasts of the United States (for example, Hohn, 1980; Hersh, 1987; Hersh et al., 1990; Mead and Potter, 1990), the contradictory results could be explained partly because sample sizes in earlier studies were small but also because these other studies did not fit a growth curve to obtain predicted asymptotic lengths that could be directly compared (Read et al., 1993). The dimorphism at asymptotic length may result from females diverting energy to reproduction at the same ages that males are gaining girth and mass (Read et al., 1993) and thus would explain why sexual dimorphism occurs in adults, but not at birth.

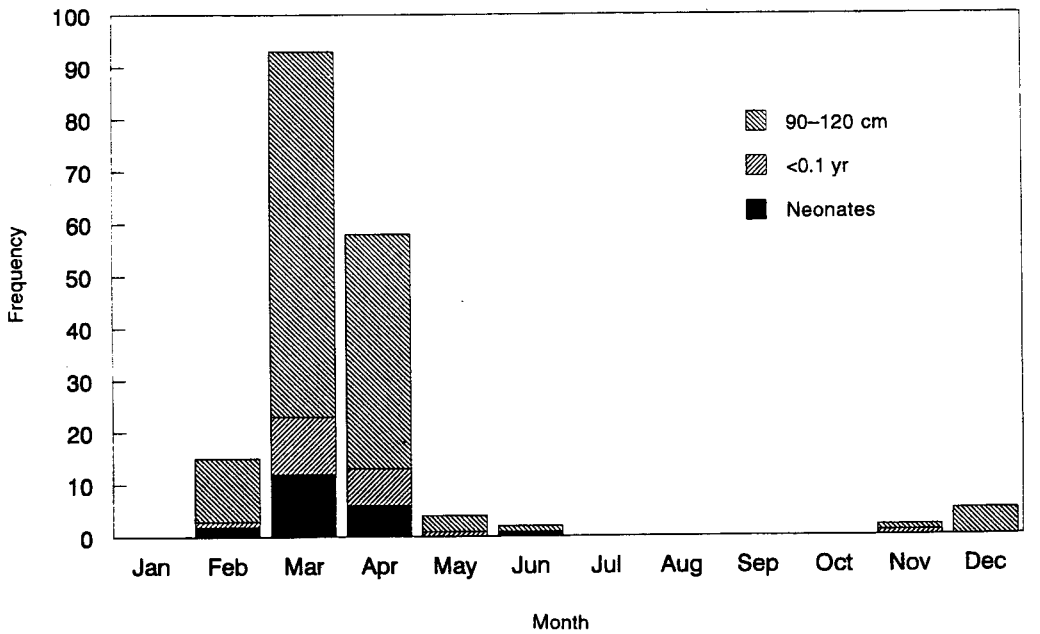

Figure 4

Calving seasonality illustrated as the monthly distribution of strandings of neonates, specimens <0.1 years old, and specimens 90–120 cm in length.

Table 3

Estimated length at birth (cm) for bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The two methods of defining a newborn animal ("neonates" and "specimens <0.1 yr") are described in the text. The Gompertz values were the predicted lengths at age 0 (L_0) from the Gompertz curve fitted to age-at-length data for males and females. The samples for neonates and specimens <0.1 yr are independent. *n* = number of dolphins in each sample.

	Males	Females	Sex unknown	Total
Neonates				
mean	109.5	111.2	107.3	109.5
SD	9.3	13.6	5.0	9.3
n	12	5	4	21
range	94–124	91–128	102–112	91–128
Specimens < 0.1 yr				
mean	109.7	107.4	113.7	109.7
SD	7.7	9.7	3.5	7.5
n	13	5	3	21
range	93–121	97–122	110–117	93–122
Gompertz				
mean	128.2	115.1		
SD	3.6	4.9		
n				
range				

Bottlenose dolphins from the coast of Texas are not significantly different in adult size from those in Sarasota Bay, Florida (Read et al., 1993), the only other western Atlantic or Gulf of Mexico area for which growth curves have been fitted to length-at-age data. Contrary to the analysis of Read et al. (1993), however, we found that the Gompertz curve did not adequately describe growth across all age classes. The curve did not respond readily enough to simulate rapid growth during the first couple of years. The fit was improved by excluding specimens less than 1 year of age, the phase of growth where the rate and absolute incremental increase are greatest. Although this approach provided a data set comparable in range of ages to that used in Read et al. (1993), the Gompertz model proved a better predictor for the Sarasota Bay, Florida, sample where the predicted length of young animals was larger. The large and unbiased sample of live animals that represented most of the individuals in Sarasota Bay probably accounts for these differences. The fit might be further improved if the sample was large enough to allow for a two-stage Gompertz fit (e.g. see Perrin et al., 1976) that would accommodate the growth spurt occurring at maturation (Cheal and Gales, 1992; Read et al., 1993).

Estimates of length at birth are not available for the Sarasota Bay animals. Along the mid-Atlantic

coast of the United States, however, Mead and Potter (1990) estimated length at birth (117 cm) as the mean length of 13 specimens classified as neonates on the basis of a folded or flaccid dorsal fin. Using the equivalent data set from the Texas sample (neonates), we found that the length at birth of mid-Atlantic coastal bottlenose dolphins was significantly different (*t*-test, P=0.02) from the estimate of 109.4 cm for Texas animals, but this result should be considered preliminary until larger sample sizes are available.

Mean length at birth may best be estimated by using morphological characteristics. Tooth-layer deposition patterns proved to be accurate in comparison to results from morphological data and can be valuable when morphological characteristics are not recorded. The method, however, is more time consuming. In contrast, use of predicted lengths of 0-yr-old animals from a fitted growth curve may be inaccurate, as was the case with this sample.

Strandings of neonates along the Texas coast are highly seasonal, with a mode in March. Using stranding data, Urian et al. (1996) found a significant difference in calving season between bottlenose dolphins from the coast of Texas (citing this data set) and those from the central-west coast of Florida, including Sarasota Bay. Stranding patterns may not accurately reflect actual calving, however, because neonates that did not survive may be those that were born earlier or later than calves that did survive. In the Sarasota Bay area, Urian et al. (1996) found that the mean date of birth estimated from stranded neonates was 16 days earlier than that estimated from sighting records of females with new calves, although this difference was not significant. They suggested that the photo-identification data may also be biased owing to unequal and discontinuous distribution of survey effort, a finding also made by Caughley and Caughley (1974). Further error may arise from lack of detection of neonates that stay very close to the female. Photo-identification studies of calving season along the Texas coast identified a peak in number of neonates in May (Shane, 1977). This later detection of neonates, in comparison with stranded animals, is consistent with the results from the central-west coast of Florida and limitations of the photo-identification method.

The increase in proportion of females with age in the Texas sample is similar to a general pattern identified in delphinids, with a slight bias towards young males and old females (Ralls et al., 1980; Perrin and Reilly, 1984; Wells and Scott, 1990). Some authors have attributed this shift to higher natural mortality rates in males (Kasuya, 1976; Miyazaki, 1977; Wells and Scott, 1990). No direct or unbiased estimates of mortality are available for bottlenose dolphins from Texas, and patterns from stranded animals may not accurately reflect the population.

Table 4

Sample sizes and descriptions of sexual and physical maturity in bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. Reproductive data were not collected for males.

Sample	Females	Males	Sex unknown
Total stranded with at least minimum data collected	292	373	233
With reproductive data	57		
Number immature	17		
Number mature	40		
Largest immature (cm)	235		
Shortest mature (cm)	225		
With reproductive and age data	25		
Number immature	6		
Number mature	19		
Oldest immature (yr)	7.8		
Youngest mature (yr)	9.8		
Youngest pregnant (yr)	9.8		
With vertebrae examined for physical maturity	25	25	12
Number immature	10	16	8
Number maturing	2	2	0
Number mature	13	7	4
Largest immature (cm)	253	280	253
Shortest mature (cm)	219	237	231
With physical maturation and age data	12	11	8
Number immature	2	7	4
Number maturing	1	1	0
Number mature	9	4	4
Oldest immature (yr)	15	16	9.9
Youngest mature (yr)	13	18	20

The proportion of specimens less than 1 year of age in the sample of stranded animals is higher than expected. In bottlenose dolphins from Sarasota Bay, Florida, Wells and Scott (1990) calculated that animals in the same age class represented 3.4% of the population, and that the crude birth rate was 5.5% annually (range of 1.1–10.4% over eight years). The higher percentage (20%) of calves in the Texas sample most likely is due to the high rate of mortality in neonates and young calves. It is also interesting to speculate that cows with young calves may occupy more protected waters and, therefore, are more likely to wash ashore when they die, contributing to a stranding sample not representative of the population.

Some of the specimens in the sample were notably large, e.g. a 300-cm male, a 335-cm female, a 280-cm

physically immature male, and a 253-cm physically immature female. Although the sample is assumed to consist predominantly of the coastal form of bottlenose dolphins, it is possible that specimens from the larger offshore form (Duffield et al., 1983; Hersh and Duffield, 1990; Hersh et al., 1990) were included. These specimens remained in the sample because they were not specifically identified as offshore individuals from independent criteria. The inclusion of offshore individuals of various lengths may be responsible for some of the variability in length at age seen in this study.

Results from this study show that bottlenose dolphins from the coast of Texas have some similarities and some differences with bottlenose dolphins from the west coast of Florida and the mid-Atlantic coast of the United States. However, samples size are small, precluding, for example, any substantial reproductive analyses. We strongly encourage the routine collection of reproductive and other samples from stranded specimens. Such basic information as the average age at sexual maturation and calving interval remains unknown even though large numbers of bottlenose dolphins are found stranded each year.

Acknowledgments

This research was funded by National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory (SEFSC) and was conducted primarily at the SEFSC, Galveston Laboratory. We thank Raymond Tarpley (Founder and first President) and Graham Worthy (current President) of the Texas Marine Mammal Stranding Network (TMMSN) for providing access to samples and data. We are particularly grateful to Elsa Haubold for facilitating access to database records and assisting with clarification of questions about the data. Efforts by regional coordinators and volunteers from Texas A&M University at Galveston who collected data on these specimens are greatly appreciated.

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