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GROWTH IN THE FIRST YEAR OF THE OFFSHORE SPOTTED DOLPHIN, Stenella attenuata, IN THE EASTERN TROPICAL PACIFIC

by

Aleta A. Hohn and P. S. Hammond

ADMINISTRATIVE REPORT LJ-83-08

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GROWTH IN THE FIRST YEAR OF THE OFFSHORE SPOTTED DOLPHIN, *STENELLA ATTENUATA*, IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

Estimates of length at birth and growth in the first year were made for northern and southern offshore spotted dolphins. Length at birth, the length at which 50% of the specimens are postnatal, in northern offshore spotted dolphins in the eastern tropical Pacific has been estimated to be 85.4 cm. The estimate is a function of kill per set and data were stratified accordingly to investigate and account for this. Average length at birth for southern offshore spotted dolphins has been estimated to be 83.2 cm, although sample sizes are considerably smaller for this stock. An analysis of monthly distributions of length revealed that two cohorts are born per year in the northern offshore spotted dolphin, at least in part of their geographical range, but only one in the southern offshore spotted dolphin. Growth curves were fitted to the progressions of mean length by month to give estimates of length at one year of 129.4 cm for the northern offshore spotted dolphin (the mean of the estimates from the growth curves of the two cohorts), and either 127.9 cm or 130.6 cm for the southern offshore spotted dolphin depending, respectively, upon whether length at birth was estimated using southern data or the combined data. Length at one year was estimated to be 123 cm for the northern stock from a growth curve fitted to the lengths and ages of specimens aged by dental growth layer groups (GLGs).

INTRODUCTION

The average growth rate of individual animals in a population is an important characteristic because of its correlation with other population parameters. In fisheries biology, two commonly employed techniques used to estimate growth rates are the ageing of a sample of fish of known length and the following of a progression of length distributions through time. These techniques allow the relationship between length and age (or relative age) to be applied to a much larger sample of fish, providing that the aged sample is a representative one.

In commercial fisheries, length-age relationships may be appropriate for the entire life of a fish. This is not true of marine mammals where length changes little after an initial period of relatively rapid growth. In delphinids, the rate of growth is high in the first year with animals increasing 50-70% of their birth length (Sergeant, 1961; Kasuya, Miyazaki and Dawbin, 1974; Kasuya, 1976; Miyazaki, 1977; Perrin and Henderson, 1979; Hohn, 1980a) but declines rapidly in the second year. Consequently, length-age relationships for these animals are only useful from birth until some time during the second year. During this period, growth rates are high relative to the variability in age-at-length so that length distributions are distinguishable as separate age groups.

In this paper, we have used both the technique of following a progression of length distributions from month to month and the technique of ageing a sample of dolphins of known length to estimate the rate of growth of offshore spotted dolphins in the first year. For the progression of lengths technique, the age axis was relative and unfixed in time so that time of birth was unknown. Consequently, length at birth has been estimated independently and used to fix time of birth. This is not necessary for the ageing technique if age is absolute. However, it has been incorporated here also because the ageing technique has not been calibrated. Rate of growth has been estimated in both techniques by fitting a growth equation to the length data by age (or relative age). These growth rates have been compared and possible explanations for the differences have been discussed.

THE SAMPLE

The field data and specimens used in the following analyses were collected by NMFS and Inter-American Tropical Tuna Commission scientific technicians aboard commercial tuna purse-seiners from 1968 to 1982. Procedures for collecting sample data and specimens have been described by Perrin, Coe, and Zweifel (1976). In all the following analyses, the data have been grouped into northern and southern strata, based on a dividing line of 1° south of the equator. This is a similar division to that used in Smith (1979).

The sample for each analysis was necessarily different. Analyses to estimate length at birth used data collected between 1973 and 1981. Data prior to 1973 were collected on a non-random basis (Perrin et al., 1976) and, at the time of the analysis, data collected in 1982 were not all available for analysis. In addition, three northern specimens less than 68 cm in length, which were identified as "calves" by dolphin observers, were judged to have been misidentified aborted fetuses and were not included in the analysis, and one 91 cm southern "fetus" was excluded as an outlying data point. Analyses of the means of length distributions by month used all available data from 1968-1982 except for the three "calves" judged to have been misidentified above. The sample of specimens aged for the age-length analysis was selected from data collected between 1973 and 1978. This sample consisted of 800 male and 800 female northern offshore spotted dolphins selected randomly without further stratification of the sample.

LENGTH AT BIRTH

An accurate estimate of length at birth is important because it establishes a point through which any growth curve can pass. This extra degree of freedom allows greater accuracy in estimating growth curves and growth rates. Two methods have been commonly employed to estimate length at birth. The first method involves regressing percentage postnatal at each length on length, then finding the length at which 50% of the specimens in a length interval are postnatal (calves) and 50% prenatal (fetuses). This method, using a linear model, has been employed to estimate length at birth for spotted dolphins (Perrin et al., 1976), for striped dolphins (Miyazaki, 1977), and for spinner dolphins (Perrin, Holts and Miller, 1977; Perrin and Henderson, 1979). The second method estimates the average length at birth as the mean of the lengths of known neonates in the sample or the mean of the lengths of full-term fetuses and small calves combined. It may be more appropriate than the first method when samples are not sufficient to allow regression of percentage postnatal on length. This second method has been used to estimate length at birth for long-finned pilot whales, Globicephala melaena (Sergeant, 1962), for spotted dolphins, Stenella attenuata (Kasuya, Miyazaki, and Dawbin, 1974), for bottlenose dolphins, Tursiops truncatus (Ross, 1977; Hohn, 1980a) and for the Franciscana dolphin, Pontoporia blainvillei (Kasuya and Brownell, 1979).

Methods

Length at birth was estimated by regressing percent postnatal at each length, weighted by the inverse of the variance, on length in 1 cm intervals using a logistic model and a linear model. Initially, this was done for all northern data (N=465) and all southern data (N=23). However, Powers and Barlow (1979) have shown that in sets in which the kill of northern offshore spotted dolphins was less than or equal to 40 (small-kill sets), about twice as many calves were killed as a proportion of the total kill as in sets where the kill was greater than 40 (large-kill sets). This introduced a bias in the estimate of length at birth in the regression procedure because the ratio of calves to fetuses was larger in small kill sets, hence the average length at birth was underestimated. Since most of the sample (approximately 90%) was from small kill sets, the effect of this bias was investigated. Estimates of average length at birth in northern offshore spotted dolphins were calculated after stratifying the data by kill per set. Because the sample size for sets with kill >40 was small, the data were also stratified using kill <30 and >30 per set. The small sample available for southern offshore spotted dolphins (N=23) prevented any stratification of the data.

Results

The estimates of length at birth for the non-stratified sample of 465 northern specimens using the logistic and linear models were 82.0 cm and 82.4 cm, respectively. The largest fetus was 91 cm long and the smallest calf was 72 cm long. The mean length of 216 fetuses and 249 calves in this length

range was 82.6 cm, although this method provides a less accurate estimate of length at birth.

In the four samples stratified by kill size, estimates of length at birth were similar using either logistic or linear models (Table 1). However, based on minimizing sums of squares, the logistic curve provided a better overall fit. For instance, the error mean square for kill greater than 40 is 1.13 and 1.31 for the logistic and linear fits, respectively, with the difference between the fits increasing with sample size. Asymmetrical logistic-type models were investigated but did not improve the fit.

When the sample was stratified by kill per set, the estimate of length at birth in small-kill sets was lower than the estimate based on the unstratified sample and that in large-kill sets was higher than the estimate based on the unstratified sample (Table 1). There was little difference in the estimate of length at birth (81.6 cm) between the samples from sets where the kill was ≤40 (Figure 1) and <30 (N=384 and 321, respectively). A small difference in the estimate occurred in large kill sets when the cut-off occurred at kill >30, 84.6 cm, rather than at kill >40, 85.4 cm (N=105 and 36, respectively), indicating that the estimate of length at birth was still a function of kill per set at this level. The proportion of specimens in the neonatal color phase, i.e., young calves (Perrin, 1970; Perrin *et al.*, 1976), was not significantly different ($\chi^2 = 0.98$, $p>0.10$) between sets with kill >30 and sets with kill >40. However, the estimate of length at birth was assumed to be more representative in sets with kill >40 (Figure 2) since the difference in length between the two levels of kill suggested that the bias had not been eliminated at the cut-off level of kill >30. Further stratification to extract data for sets with larger kills was not possible due to sample-size considerations.

The estimates of length at birth for the southern offshore spotted dolphin using logistic and linear models were 83.2 cm and 82.1 cm, respectively, for 13 fetuses and 10 calves from 78 to 85 cm in length. The mean length of calves and fetuses in this length range was 81.0 cm.

Discussion

Our unstratified analysis of 465 northern offshore spotted dolphins yields similar results to that of Perrin *et al.* (1976), which estimated a length at birth in northern offshore spotted dolphins of 82.5 cm, based on a sample of 73 specimens (calves and fetuses) grouped into 3-cm intervals from 74 to 92 cm.

The difference between the estimates of length at birth based on samples from large- and small-kill sets is, as described above, a function of the over-representation of calves in small-kill sets. The estimate of length at birth in large-kill sets is therefore less biased. A future larger sample from large-kill sets may allow for additional stratification by kill per set so that the estimate can be recalculated at higher levels of kill until a bias is no longer detected, i.e., the estimate does not change with increase of the

kill-size cut-off. Until additional data are available, 85.4 cm is considered the best estimate of length at birth in northern offshore spotted dolphins.

The best estimate of length at birth in southern offshore spotted dolphins is more questionable. As adults, southern offshore spotted dolphins are about 2.5 cm shorter than their northern counterparts (Perrin, Sloan, and Henderson, 1979). This small, but statistically significant, difference may or may not mean that length at birth is smaller in the southern population. The small sample size (N=23) for calculating the length at birth may not be adequate for a reliable estimate. For these reasons, we use two estimates of length at birth in southern offshore spotted dolphins: 82.6 cm from the unstratified southern data and 85.4 cm, the best estimate for the northern data.

ESTIMATION OF LENGTH AT AGE USING ANALYSES OF MONTHLY DISTRIBUTIONS OF LENGTH

Perrin et al. (1976) used the technique of fitting a growth curve to a progression of the means of monthly length distributions to estimate the length of the offshore spotted dolphin at one year of age. Perrin and Henderson (1979) used the same technique for the eastern spinner dolphin, Stenella longirostris. The technique is based on the assumption that breeding in these dolphins is seasonal and that a cohort of animals born at approximately the same time can be identified as a distribution of lengths, identifiable by a mode in the overall length distribution, which can be followed from month to month as mean length of the cohort increases. If there are sufficient data in each month to follow this progression from birth to one year and beyond, a growth curve can be fitted to mean length by month to give an estimated length at one year.

Since the analysis of Perrin et al. (1976), the sample of measured lengths from offshore spotted dolphins killed incidental to the purse-seine fishery for tunas in the eastern tropical Pacific has increased from some 3,500 animals to over 15,000 animals. Consequently, we were able to analyze the data for offshore spotted dolphins more extensively than had been done previously.

Methods

In order to be able to compare results for offshore spotted dolphins in the northern and southern areas of the purse seine fishery for tunas, these strata were analyzed separately. The data were grouped by month of capture for all years combined and flagged by area of capture for further stratification as required. These areas were determined subjectively by dividing the entire area based upon apparent hiatuses in animal distribution as observed by examining distributions of sightings of offshore spotted dolphins (Figure 3) and the searching effort expended by scientific technicians.

The data for each month were analyzed separately using a version of the computer program NORMSEP (Hasselblad, 1966, modified by Patrick K. Tomlinson of the Inter-American Tropical Tuna Commission), which fits a specified number of normal distributions to length-frequency data. This was the same program used by Perrin et al. (1976) and Perrin and Henderson (1979). Program NORMSEP requires that the data be grouped into intervals of predetermined width and initial value of the first interval, that the number of distributions be specified, that the approximate ranges of the mean and standard deviation of each distribution be given, and that a set of cut-points separating the approximate means of the distributions be provided. Output from the program includes the set of fitted means and standard deviations describing each distribution, the percentage of the total sample accounted for by each distribution, and a χ^2 statistic indicating the goodness of fit of the model.

The procedure for a given month of data from all years involved using an interval of 4 cm in width. It was found that a width of 5 cm tended to mask some information and that 3 cm introduced too much variation in the data. Program NORMSEP was then used to fit distributions to the data grouped in four different ways depending upon the initial value of the first interval. For example, if the smallest length in the sample was 79 cm, the data would have been fitted by groupings in which the first interval was 76-80, 77-81, 78-82 or 79-83. By inspection of the data, by review of other length-at-age studies and by feedback from results of this analysis, the number of distributions and the approximate ranges of likely means and standard deviations were chosen. Cut-points were selected so that each of the points fell between successive ranges of the likely means.

In each application of the model, a combination of criteria were used to determine the overall model fit chosen as most representative of the month. The criteria taken into consideration were as follows: 1) how well the number of distributions and the means of these distributions conformed to those expected based on knowledge of the growth of delphinids from other studies, 2) how well the model fitted the data (χ^2 test), and 3) how large the approximate sample size was in each distribution. An additional criterion was employed when the results of the analyses were compared between months: how well the monthly progression of fitted mean lengths conformed to the expected progression based on knowledge of delphinid growth from other studies.

The distributions of interest were those of the smallest animals but the model fitted largely based on the greater number of larger animals. Consequently, the data for two months (August and October) were truncated at a range of lengths in order to investigate the effects on the model fits of excluding the larger animals. The results of this were as expected. Because of the overlap between distributions, truncation of the data caused the means of the closest distributions to the truncation length to be biased. They were biased upwards if a significant amount of data from the next distribution were included, and downwards if a significant amount of data from the last distribution before the truncation length were excluded. Consequently, in the absence of a robust criterion upon which to select a truncation length, the data were analyzed in their untruncated form.

Results

Northern Offshore Spotted Dolphin

Initially, data for the entire northern stratum were analyzed for each month. The results from this analysis were confusing because monthly progressions of the mean lengths of the fitted distributions were not at all consistent. This indicated that there may be non-seasonal or seasonal but asynchronous elements in the data which could be masking the progression of cohorts from each year born in the same season. In order to try to identify these, the data for each month were stratified by area where there was a sufficient sample to do this.

As a first attempt to obtain consistency, data were eliminated which were collected in the offshore area of the fishery (Area 3). The results of the analyses of these data showed far more consistency than those from the initial analyses of all northern data. However, the results from some months still did not agree with the clear progression of mean lengths shown by the other months. Consequently, the data were stratified further by eliminating lengths from animals collected in the southern part of the northern area (Areas 4 and 5). However, this was possible only for the months of January through June because sample sizes were considered to be too small for the other months. The results from the analyses of the data from these months were now more consistent with those from the other months except that the results for January did not change. Table 2 describes the fitted distributions chosen to represent each month in this analysis. Figure 4 shows, as an example, the length data from August and from October plotted as histograms. Superimposed upon the histograms are the curves from the fitted models chosen to represent the data from these months. The arrows indicate the positions of the means of the fitted distributions. Mean lengths estimated for data collected in March and for the second distribution in June were still inconsistent and were not included in further analyses. The reasons for these inconsistencies are unknown.

Figure 5 shows the means of the fitted distributions plotted as a monthly progression up to approximately 24 months from approximate month of birth. The means have been plotted to show two clear growth curves in the figure representing two cohorts born each year approximately six months apart in the spring and autumn.

In choosing a growth curve to fit to the set of monthly mean lengths, three models of growth were investigated. These were a linear equation, the Gompertz (1825) equation, and the von Bertalanffy (1934) equation. The Gompertz equation fitted the data well and better than the other two models, and only the curves from this model are shown in Figure 5. Time of birth was determined by substituting the length at birth determined in this paper into the model. Length at one year was then calculated by substituting time of birth plus one year into the model. This was done for both growth curves with the following results:

	Growth curve A	Growth curve B
Fixed length at birth (determined in this paper)	85.4 cm	85.4 cm
Estimated mean time of birth	May 7	September 15
Estimated length at one year	131.6 cm	127.2 cm

These results are from unweighted non-linear regressions. If the variation in the mean length of a distribution is considered to be due largely to sampling error, then there is a justification for regressing mean lengths weighted by the reciprocal of the variance on time. When this was done, the results for curves A and B changed slightly but not significantly. For curve A, the time of birth changed to April 28 and the length at one year to 130.1 cm. For curve B, time of birth and length at one year changed to September 19 and 128.2 cm. The weighted regressions resulted in the two curves becoming more similar. It is possible that curves A and B represent two cohorts with different growth rates. However, if the weighted regressions are thought more appropriate, this seems less likely. We believe that sampling variation is not necessarily the largest source of variation in the monthly mean lengths and that a weighted regression cannot be justified from first principles. Consequently, we present the results of the investigated regressions as the best estimates of length at one year and, without additional data and in the absence of any obvious reason to prefer one or the other curve, present a best estimate of 129.4 cm, the mean of the two estimates.

Southern Offshore Spotted Dolphin

Results from analyses of all southern data showed inconsistencies which were similar to those found in the results for the northern data. Consequently, data were eliminated from Area 2 for those months where this was possible, allowing for sample size considerations. These months were January through May. The results from analyses of the stratified data showed more consistency than those for all the available data, indicating once again that the offshore data may be less seasonal or timed to a different seasonal pattern than the nearshore data. Table 3 describes the fitted distributions chosen to represent each month.

Figure 6 shows the means of the fitted distributions plotted as a monthly progression up to approximately 18 months from approximate month of birth. For these data, it is clear that there is only one growth curve, indicating only one cohort of young born each year. However, there is some evidence for the presence of another cohort (distribution 2 in January and distribution 2

in May in Table 3) and its absence may be a result of the very small sample sizes. The data were again fitted using the Gompertz growth model using the length at birth estimate from the analysis of southern data and that from the analysis of northern data with the following results:

	Length at birth from analysis of southern data	Length at birth from analysis of northern data
Fixed length at birth (determined in this paper)	83.2 cm	85.4 cm
Estimated mean time of birth	January 6	January 24
Estimated length at one year	127.9 cm	130.6 cm

Weighted regressions, as described above in the results for the northern offshore spotted dolphin, gave practically identical results.

Discussion

There are several sources of variability in the monthly estimates of mean length to which the growth models have been fitted to estimate length at one year. Four of these are biological in nature. There is individual variation in the time of birth; animals may be born at different lengths; animals may grow at different rates; and the calving season may vary from year to year, from area to area and within areas. In addition, the monthly distributions are subject to sampling error. All these factors combine to produce the variation about the mean lengths.

One potential bias is that caused by non-random sampling within a month with respect to time. This could occur because the data have been grouped by calendar month and fixed in time at the center of each month. If the actual average sample date is not at the center of the month, this will result in a bias in the time axis which translates into a bias in mean length by month. This is difficult to adjust for since the individual animals in a distribution cannot necessarily be identified because distributions may overlap. Such a bias would be most important in the sample data contributing to the mean lengths of the younger animals where growth rate is fastest. However, because data have been collected over a number of years and bias could be in either direction, overall bias in a given month is likely to be negligible. Furthermore, since direction of bias for any month should be random, the fitted growth curve and estimated length at one year should be effectively unbiased.

An additional potential bias is that caused by mean time of birth not being at the center of the first month where data occur. A similar bias to that described above could result if mean time of birth were towards the end of the first month because there would be a higher proportion of animals in the cohort still to be born than had already been born. Since offshore spotted dolphins grow approximately 4-5 cm a month in the first few months of life, the effective bias in mean length in the first month can be no more than 2.5 cm. In practice, however, since data have been collected over several years, variation in the exact timing of the birthing season is likely to eliminate any bias due to this effect. Given if the bias were not eliminated, a bias in this one monthly mean length should again have a negligible effect on the fitted growth curve and consequently on the estimated length at one year.

Perrin et al. (1976) followed actual cohorts of animals from individual years in their analyses. Combining the data from several years introduces variation in the data if the timing of the birthing season varies from year to year, but it increases sample sizes and minimizes bias caused by non-random timing of sampling within months.

Barlow (in press) has predicted approximate seasons of birth for the northern and southern offshore spotted dolphin using forward projection of birthdates of fetuses and backward projection of birthdates of calves along growth curves described by Perrin et al. (1976). The results for the northern data indicate two peak seasons, in the spring and autumn, but that animals are born throughout the year. The results for the southern data show one birthing season peaking around April. This is three to four months later than the mean time of birth estimated here. The difference can be explained in the use of different growth curves. Barlow (in press) used a growth equation which predicted animals of 138 cm in length to be one year old whereas the growth equations used here predict an age of 15-16 months for an animal of this length. This accounts for the difference precisely. There should also be a difference in the fetal growth curve but this has not been investigated here.

Following progressions of means of monthly distributions of length may give misleading results for a number of reasons. Firstly, the mean length for each mode is subject to a large amount of variation so that the estimated value for each mean is liable to differ considerably from its actual value. Secondly, the method of estimating the mean lengths makes the assumption that lengths of dolphins captured within any calendar month over several years are distributed normally within the younger age classes. This is unlikely to be true and could cause the estimated means to be unrepresentative of the lengths of a cohort. Thirdly, the method relies upon being able to analyze a sample of data in which reproduction is seasonal. In addition, the seasonality should be the same. This analysis has shown that this may be difficult to achieve. Only by stratification of the data by area could consistent results be obtained. Stratification of the data by area improves the consistency of the progressions because offshore spotted dolphins appear to have different birthing seasons depending upon the area of capture. In probability, this seasonality is not actually a function of area but of schools or groups of schools which tend to inhabit different areas with different environmental conditions. Thus, even with the best stratification scheme, there may always

be asynchronous seasonal elements in a sample of data from any given area affecting the estimation of the mean lengths of the cohorts.

Despite these reservations, the results presented here are encouraging and may provide the best estimates of length at one year currently available for the offshore spotted dolphin.

ESTIMATION OF LENGTH AT AGE USING GROWTH LAYER GROUP (GLG) AGEING

Increments of dentine are deposited in teeth as a function of time. The most important incremental pattern in odontocete teeth are growth layer groups (GLGs), defined as "a repeating or semi-repeating pattern of adjacent groups of incremental growth layers within the dentine, cementum, or bone which is defined as a countable unit" (Perrin and Myrick, 1980:48-49). GLGs are used for age determination in many species of odontocetes, as well as pinnipeds and sirenians (see review by Scheffer and Myrick, 1980), but in most species no calibration of GLGs is available. However, a few known-aged captive and minimum known-age captive bottlenose dolphins (Tursiops truncatus) (Sergeant, 1959; Sergeant, Caldwell, and Caldwell, 1973; Hui, 1978) and captive tetracycline-marked specimens of other species (Gurevich, Stewart, and Cornell, 1980, Delphinus delphis; Myrick, Shallenberger, Kang, and MacKay, unpubl. MS, Stenella longirostris; Best, 1976, Lagenorhynchus obscurus) have provided evidence that the GLG, as defined and calibrated by these workers, represents an annual deposition pattern. In species for which known-aged specimens are not available, e.g., spotted dolphins, it has been assumed that a GLG pattern similar to that described in the above species represents the same amount of time.

Methods

The teeth were decalcified in RDO[1], a commercial decalcifying agent, cut longitudinally into 24 μm thin sections using a freezing microtome, stained in haematoxylin, and mounted in 100% glycerin. Detailed procedures for the preparation technique and interpretation of GLGs are described by Myrick, Hohn, Sloan, Kimura and Stanley (1983).

Teeth from each of the 1,600 specimens were "read" for age at least three times, to the nearest 0.1 GLG in young animals, by each of two readers over a period of two years. The series of age estimates was averaged for each reader, and the resulting two mean age estimates were again averaged to produce a pooled mean age estimate (see Reilly, Hohn, and Myrick, unpubl. MS). Growth rate analyses were performed using the pooled mean age estimate,

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[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

for males and females separately. In addition, each analysis was re-run using the average of the last age count for each specimen by each reader, since both readers thought that improvement in technique throughout the tooth-reading exercise resulted in the last reading being the most accurate.

Growth in the first year was determined by regressing length on GLG age using the Laird (1969) modification of the Gompertz model as described by Perrin et al. (1976), a modification of the von Bertalanffy model using length at birth, and a linear model. In each case length at birth, L_0, was fixed at 85.4 cm. Each non-linear model was run twice on each of the two age estimates using cut-offs at $\leq$1.2 and $\leq$3.0 years of age. Increasing the age to $\leq$3.0 years increased the sample size from 101 to 248 and reduced the effect of any discrepancies in the data for animals close to one year of age. The linear regression was run on ages up to 1.0 and 1.2 years.

Results

The predicted lengths at one year, error mean squares and parameter values for each of the three fitted models are presented in Table 4. There is no difference in growth between males and females up to age 3.0, so the data was combined for the remaining analyses. Although the fits are slightly better using the last count for each specimen, estimated length at one year is essentially the same with both sets of age data and both non-linear models. Predicted length at one year is always slightly higher for the non-linear models run on age $\leq$3.0. The linear regression yielded error mean squares close to the non-linear functions, but there are trends in the residuals caused by forcing a straight line through a curve. The Gompertz model should provide the most appropriate fit for mammalian growth (Perrin et al., 1976; Laird, 1969), and for consistency with the previous analysis, it is assumed to do so, giving a length at one year of about 123 cm. However, the Gompertz fit to length on age up to 3.0 years (Figure 7) shows that lengths predicted by this model may be underestimated up to about 8 months and overestimated from 9 to 12 months. The mean length of specimens aged between 0.9 and 1.1 years in the sample is 121 cm.

The estimated average monthly growth from age data is 3.2 cm during the first year. However, the growth rate is not constant. The initial growth is high and decreases quickly after birth up to approximately 9 months, at which time the decrease in rate is not as great (Table 6). Figure 8 shows predicted growth each month for two years for the age data and the results from the monthly progression of mean length analysis presented above. The rate of decrease of the growth rate estimated from age data is similar to that of curve A from monthly modes, although the predicted average monthly growth is slightly less when estimated from the age data. Curve B data show a slower initial growth and a slower decrease in growth rate to the end of the second year. Average monthly growth for the first year from curve A is 3.9 cm and from curve B, 3.4 cm.

Discussion

The accuracy of the estimate of length at one year depends on the representativeness of the sample and the accuracy of the age determination technique. The sample is a random sample of the specimens collected in the purse-seine fishery, although Powers and Barlow (1979) have shown that the sample collected may be biased. There is no evidence that specimens in the sample are on the average smaller than the unsampled animals.

Age determination methodology must be based on known-age animals. The calibration of GLGs for these spotted dolphins has been extrapolated from captive, tetracycline-marked Hawaiian spinner dolphins, a related species (see Myrick et al., unpubl. MS). Known-age, captive or marked spotted dolphins are not available for direct GLG calibration. If differences are found between GLGs in spotted and spinner dolphin teeth when known-age spotted dolphins are available, these estimates of growth based on GLGs may have to be revised.

The precise timing of the deposition of the first GLG (the neonatal line) is important in estimates of age in young animals. For a specimen estimated to be Ø year old based on GLGs but which is not known to be a neonate, the age must be an underestimate of the actual age of that specimen, and, consequently, the average length of "Ø year olds" would be greater than the average length of specimens actually new born. When the Gompertz model with L_0 not fixed is fitted to age data, the predicted length at age Ø is 89.6 cm, 4.2 cm higher than the length at birth estimate. The age at which the predicted length is approximately 90 cm when L_0 is fixed at 85.4 is 0.1 GLGs. Therefore, the estimates of age based on GLGs may be underestimated by 0.1 GLGs for young animals. The estimates of length at age for fixed and floating L_0 are identical beginning at 0.7 GLGs (114 cm) and the predicted length at one year (1 GLG) does not change.

The Gompertz model seems to describe growth adequately for most of the range of ages considered. The apparent under estimate of average length in specimens less than 8 months old and over estimate in specimens approximately 9 to 12 months old may be due to errors in age determination methodology, sampling variation, or actual inherent changes in growth rates in animals approaching one year of age. A marked change in growth at this age may be caused by an increase in solid food or weaning. Perrin et al. (1976) estimated that weaning occurs at about 11 months in this population. It is possible that a two-cycle Gompertz model would provide a better description of the decrease in growth for animals approaching one year of age, similar to the two-cycle Gompertz model used by Perrin et al. (1976) and Perrin et al. (1977) in spotted and spinner dolphins, respectively, to describe a secondary surge in growth in pre-adult or adolescent animals that is typical of mammalian growth.

CONCLUDING REMARKS

Assuming there is little or no bias in the monthly progression of length analysis, the results of length at one year from this method can be used to

calibrate the aging methodology. Perrin et al. (1976) used the mean length progression analysis to help calibrate dentinal GLGs. Their estimate of length at one year (138 cm), resulting from the linear fit to monthly means and extrapolation from other species, caused them to predict that two layers are laid down during the first year. Using a length at one year of 129 cm from the current monthly progression of length analysis, the model from Perrin et al. (1976) shows that 1.5 layers would be deposited in the first year.

If the monthly progression of mean length analysis accurately estimates length at one year, it would require more than one GLG in the current age sample for the average northern offshore spotted dolphin to reach 129 cm, because the length at one year from GLG counts has been estimated to be 123 cm. The largest difference in growth rates between the two methods occurs at the beginning of the first year (Figure 8), indicating that any error in ageing methodology is probably in animals shortly after birth. Possible explanations for this are that the neonatal line (the beginning of the first GLG) may not be deposited immediately at the time of birth. In this sample, there is not a neonatal line in some postnatal specimens, although the actual amount of postnatal time is unknown.

In Tursiops stranded on the mid-Atlantic coast of the U. S., there is variability in the deposition of the neonatal line (Hohn, unpubl. data). The specimens were identified as neonates by lack of umbilicus (indicating that calf was not still born) and by the folded dorsal fin and flukes; the dorsal fin is erect within 24 hours in captive Tursiops (Tavolga and Essapian, 1957). Some of these stranded specimens show no neonatal line while others have part of a neonatal line deposited. Although these animals were probably ill prior to stranding, this variability may be found in other neonates. Individual variation in gestation time may also contribute to variation in neonatal line deposition.

Another possibility is that the first GLG may not always be complete. For example, if the first GLG is always laid down during April for all animals in a cohort, animals born in May would have only 11/12ths of the first GLG deposited the following April when the second GLG would begin. The factors influencing or regulating the deposition of GLGs are still unknown. If the timing of the deposition of the GLG is influenced by some temporal cue (endogenous or exogenous) in addition to the time of birth, then all the neonates and near-term fetuses comprising a cohort may begin deposition of the first GLG simultaneously, at least in seasonally breeding populations. Fetuses that are not near-term, however, may not be affected because of developmental or other biological factors. In non-seasonal breeders, the deposition of the neonatal line would be triggered primarily by time of birth and less affected by seasonal or other temporal cues.

If length at one year is 129 cm, and assuming that most if any error in the ageing methodology occurs shortly after birth when growth rates are highest, about 1.1 GLGs would have to be deposited in the first year. However, except for the possible small biological variance (+0.1 GLG), using GLG counts for age has some advantage over analysis of monthly distributions of length to estimate length at one year. Seasonal (or non-seasonal) effects probably introduce less error in age estimation from GLG deposition than that

from the analysis of monthly distribution of length. In addition, GLGs in teeth from related species have very similar patterns, regardless of the geographic distribution of the species, so an absolute measure of GLG age can be obtained once the pattern is identified. Use of GLGs may provide a more accurate method of estimating age and growth.

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Table 1. Estimates of length at birth by number of dolphins killed per set. The range of length classes includes the first zero percent postnatal length class and the first 100 percent postnatal length class.

	Sample size	Range (cm)	Predicted Length at Birth (cm)	
			Logistic model	Linear model
Northern Offshore Spotted Dolphins				
Unstratified data	586	71-92	82.0	82.4
Sets with kill ≤40	384	71-92	81.6	81.7
Sets with kill ≤30	321	73-92	81.6	81.9
Sets with kill >40	36	78-89	85.4	85.0
Sets with kill >30	105	71-89	84.6	83.8
Southern Offshore Spotted Dolphins				
Unstratified data	36	78-85	83.2	82.1

Table 2. Fitted distributions of length, in centimeters, by month and area, in northern offshore spotted dolphins.

Month	Areas	N		Fitted Distributions 1	2	3	4	5	6	Probability of a greater χ^2
January	4,5,6,7,8	2926	$\bar{x}$	102.9	142.4	161.9	187.4			0.051
			SD	(11.7)	(12.4)	(6.1)	(11.8)			
			% of sample	8.2%	14.0%	11.5%	66.4%			
February	6,7,8	2772	$\bar{x}$	104.1	140.7	152.0	161.5	186.3		0.184
			SD	(11.0)	(10.1)	(3.9)	(6.0)	(12.3)		
			% of sample	11.0%	10.2%	2.4%	11.3%	65.0%		
March*	6,7,8	866	$\bar{x}$	92.7	113.2	131.4	160.7	188.7		0.689
			SD	(6.3)	(10.5)	(15.7)	(11.7)	(11.5)		
			% of sample	4.4%	5.6%	7.3%	23.2%	59.5%		
April	6,7,8	700	$\bar{x}$	84.5	113.6	146.0	163.6	188.5		0.092
			SD	(4.3)	(8.1)	(11.0)	(5.4)	(12.0)		
			% of sample	1.7%	3.9%	11.4%	13.8%	69.2%		
May	6,7,8	423	$\bar{x}$	84.5	108.7	133.9	147.5	165.9	187.9	0.039
			SD	(3.4)	(9.4)	(10.9)	(14.5)	(7.5)	(10.8)	
			% of sample	0.7%	7.2%	4.5%	6.3%	20.9%	60.4%	
June	6,7,8	300	$\bar{x}$	90.7	105.9*	135.5	165.2	189.5		0.050
			SD	(7.6)	(2.1)	(14.8)	(8.1)	(11.4)		
			% of sample	3.1%	3.1%	13.6%	16.9%	63.3%		

Table 2. Continued

Month	Areas	N		Fitted Distributions 1	2	3	4	5	6	Probability of a greater χ^2
July	4,5,6,7,8	266	$\bar{x}$ SD % of sample	91.8 (6.0) 3.4%	118.0 (3.3) 1.1%	136.1 (4.4) 4.1%	150.8 (7.1) 4.7%	164.5 (7.0) 19.9%	190.1 (10.4) 66.9%	0.495
August	4,5,6,7,8	486	$\bar{x}$ SD % of sample	105.7 (9.2) 6.5%	125.1 (3.5) 3.9%	151.8 (15.5) 9.5%	162.6 (8.3) 14.0%	190.5 (10.3) 66.1%		0.461
September	4,5,6,7,8	536	$\bar{x}$ SD % of sample	86.7 (3.2) 1.5%	105.0 (9.8) 4.0%	129.4 (8.5) 7.7%	161.3 (8.9) 13.0%	186.9 (13.7) 73.9%		0.527
October	4,5,6,7,8	1159	$\bar{x}$ SD % of sample	87.9 (3.8) 2.7%	106.3 (9.5) 5.1%	129.4 (6.2) 3.8%	142.7 (7.5) 7.3%	163.1 (7.4) 19.2%	188.8 (11.6) 62.0%	0.483
November	4,5,6,7,8	616	$\bar{x}$ SD % of sample	91.1 (7.3) 5.4%	113.9 (5.0) 5.2%	129.6 (5.5) 5.2%	145.7 (3.7) 3.9%	159.4 (5.0) 10.2%	187.7 (12.5) 70.1%	0.676
December	4,5,6,7,8	223	$\bar{x}$ SD % of sample	97.5 (10.5) 7.2%	127.7 (5.7) 6.3%	149.9 (14.3) 14.2%	187.4 (12.7) 72.4%			0.570

*Mean lengths estimated from data collected in March and the mean length from distribution 2 in June were not included in the data set to which the growth models were fitted.

Table 3. Fitted distributions of length, in centimeters, by month and area, in southern offshore spotted dolphins.

Month	Areas	N		Fitted Distributions 1	2	3	4	5	Probability of a greater χ^2
January	1	254	$\bar{x}$	87.0	105.0	131.0	164.5	187.8	0.897
			SD	(1.0)	(2.0)	(4.1)	(12.6)	(10.5)	
			% of sample	0.4%	0.8%	4.1%	35.0%	59.8%	
February	1	412	$\bar{x}$	85.1	134.9	165.6	188.0		0.305
			SD	(5.5)	(6.5)	(9.4)	(7.6)		
			% of sample	1.7%	8.9%	34.1%	55.4%		
March	1	57	$\bar{x}$	90.0	139.3	189.7			0.961
			SD	(2.0)	(7.8)	(14.6)			
			% of sample	3.5%	13.5%	83.0%			
April	1	43	$\bar{x}$	97.9	140.8	163.3	189.5		0.647
			SD	(18.1)	(3.7)	(3.0)	(8.8)		
			% of sample	12.1%	13.5%	13.5%	60.9%		
May	1	212	$\bar{x}$	97.1	127.5	144.3	157.7	182.6	0.796
			SD	(7.9)	(5.0)	(2.7)	(3.6)	(12.7)	
			% of sample	15.7%	1.8%	4.5%	9.7%	68.4%	
June	1,2	42	$\bar{x}$	99.0	163.8	185.3			0.886
			SD	(5.7)	(14.4)	(9.9)			
			% of sample	19.1%	29.0%	52.0%			

Table 3. Continued

Month	Areas	N		Fitted Distributions 1	2	3	4	5	Probability of a greater χ^2
October*	1,2	33	$\bar{x}$	111.0	175.0	187.1			0.747
			SD	(8.0)	(2.0)	(12.0)			
			% of sample	6.1%	7.8%	86.1%			
December	1,2	47	$\bar{x}$	81.0	123.5	165.7	187.9		0.454
			SD	(2.0)	(17.0)	(6.0)	(6.4)		
			% of sample	4.2%	9.0%	21.4%	65.4%		

*Mean lengths estimated from the data collected in October were not used in the data set to which the growth model was fitted.

Table 4. Summary of predicted length at one year based on GLG counts.

Method	Pooled Mean Age Estimate		Last Age Count		Model
	≤1.2 years	≤3.0 years	≤1.2 years	≤3.0 years	
von Bertalanffy					
Predicted length at 1 year	121.9	123.1	122.5	122.8	$L_t = \frac{85.4}{1-b}(1-be^{-kt})$
Error mean square	66.9	68.4	60.5	65.1	where t = age in years
b	0.37	0.46	0.38	0.48	and L_t = length at time t
k	1.31	0.64	1.23	0.63	
Gompertz					
Predicted length at 1 year	121.9	123.0	122.5	122.6	$L_t = 85.4\ e^{\frac{a}{\alpha}[1-e^{-\alpha t}]}$
Error mean square	67.2	69.3	60.9	66.2	where t = age in years,
a	0.73	0.54	0.72	0.54	a = rate of exponential growth
α	1.67	0.86	1.6	0.85	and α = rate of decay of exponential growth
	≤1.0 years	≤1.2 years	≤1.0 years	≤1.2 years	
Linear Regression					
Predicted length at 1 year	125.9	123.8	123.8	122.9	$L_t = 85.4 + bt$
Error mean square	77.3	78.7	66.2	60.8	where t = age in years
Slope (b)	40.5	38.4	32.8	31.6	

Table 5. Average monthly growth, in centimeters, in northern offshore spotted dolphins calculated from the fitted Gompertz model. Perrin et al. (1976) estimated that two layers are deposited in the first year.

Month	Monthly Modes		Age Data		Perrin et al., 1976	
	Curve A Growth	Curve B Growth	Years	Growth	Layers	Growth
1	4.73	3.87	0.1	4.57	0.1	3.81
2	4.61	3.81	0.2	4.40	0.2	3.73
3	4.47	3.75	0.3	4.23	0.3	3.54
4	4.32	3.68	0.4	4.05	0.4	3.46
5	4.16	3.60	0.5	3.86	0.5	3.32
6	3.99	3.52	0.6	3.67	0.6	3.19
7	3.82	3.43	0.7	3.48	0.7	3.06
8	3.65	3.34	0.8	3.28	0.8	2.93
9	3.47	3.24	0.9	3.10	0.9	2.79
10	3.30	3.15	1.0	2.91	1.0	2.65
11	3.13	3.05	1.1	2.74	1.1	2.54
12	2.96	2.95	1.2	2.56	1.2	2.41
13	2.80	2.85	1.3	2.40	1.3	2.28
14	2.64	2.75	1.4	2.24	1.4	2.16
15	2.48	2.65	1.5	2.08	1.5	2.05
16	2.34	2.55	1.6	1.95	1.6	1.93
17	2.19	2.45	1.7	1.81	1.7	1.82
18	2.06	2.36	1.8	1.68	1.8	1.73
19	1.93	2.26	1.9	1.55	1.9	1.62
20	1.80	2.17	2.0	1.45	2.0	1.52
21	1.69	2.08				
22	1.57	1.99				
23	1.47	1.91				
24	1.37	1.82				

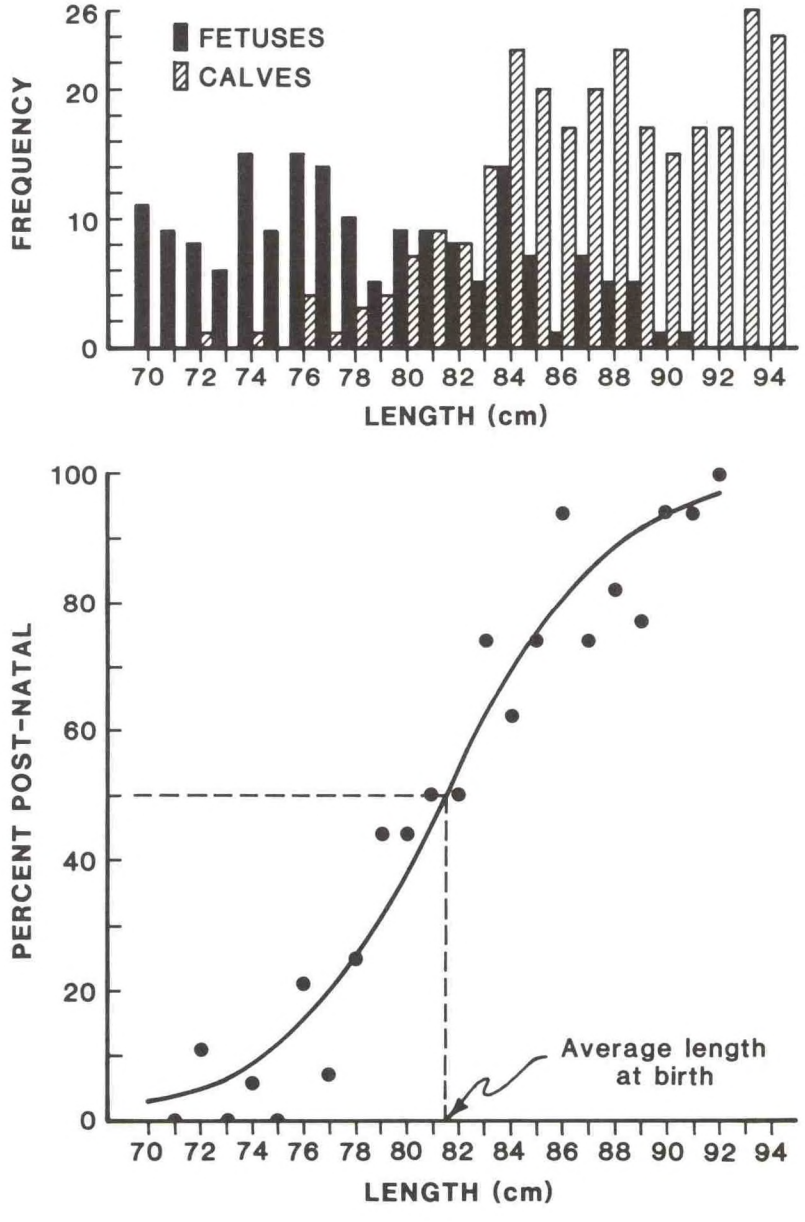


Figure 1. Length-frequency data for kill <40 grouped in 1 cm intervals for 163 fetuses and 221 calves of the northern offshore spotted dolphin and the logistic model (see text) fitted to the percentage of animals that are postnatal.

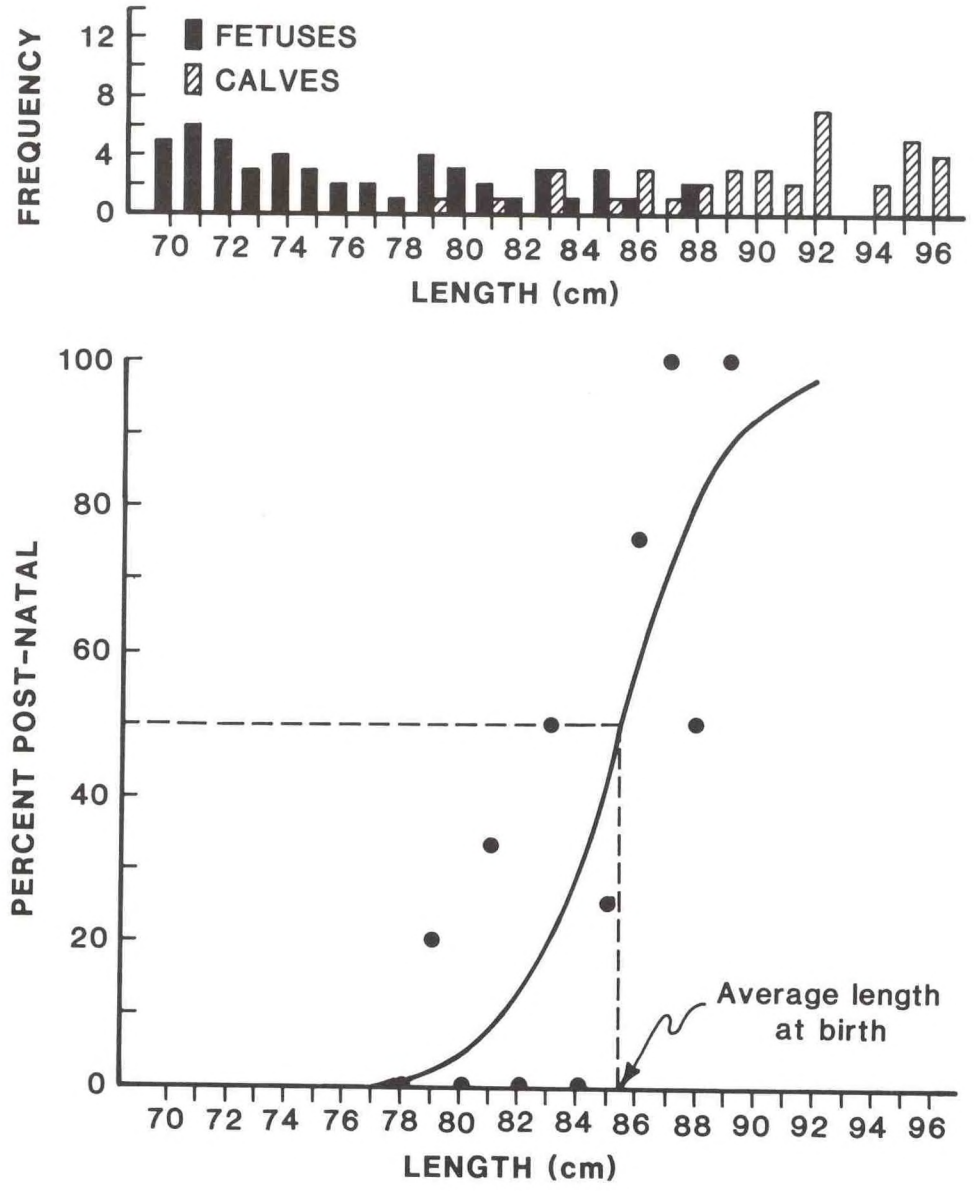
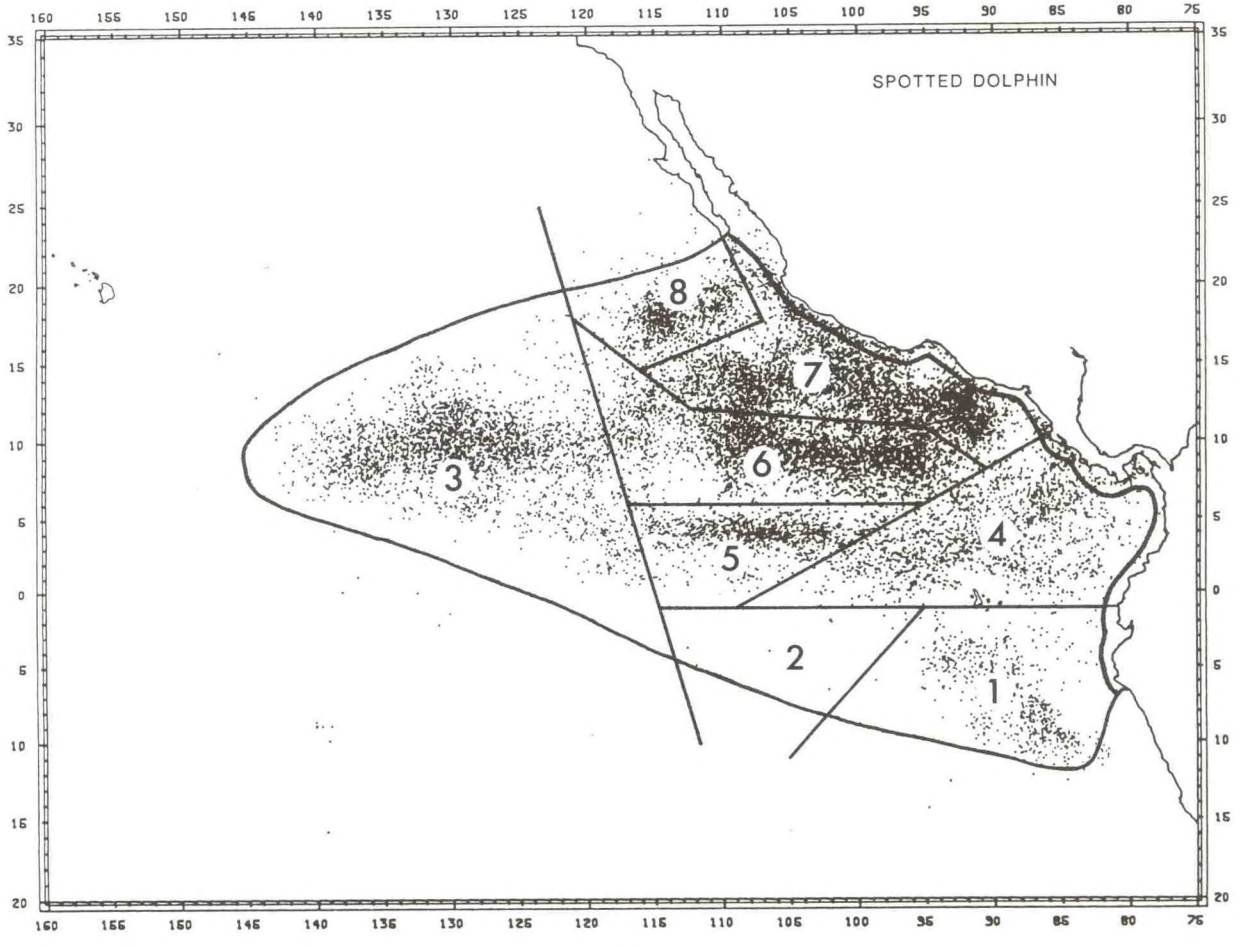


Figure 2. Length-frequency data for kill >40 grouped in 1 cm intervals for 21 fetuses and 15 calves of the northern offshore spotted dolphin and the logistic model (see text) fitted to the percentage of animals that are postnatal.



Figure

Figure 3. Areas selected for stratification of offshore spotted dolphin data for the analysis of monthly distributions of length.

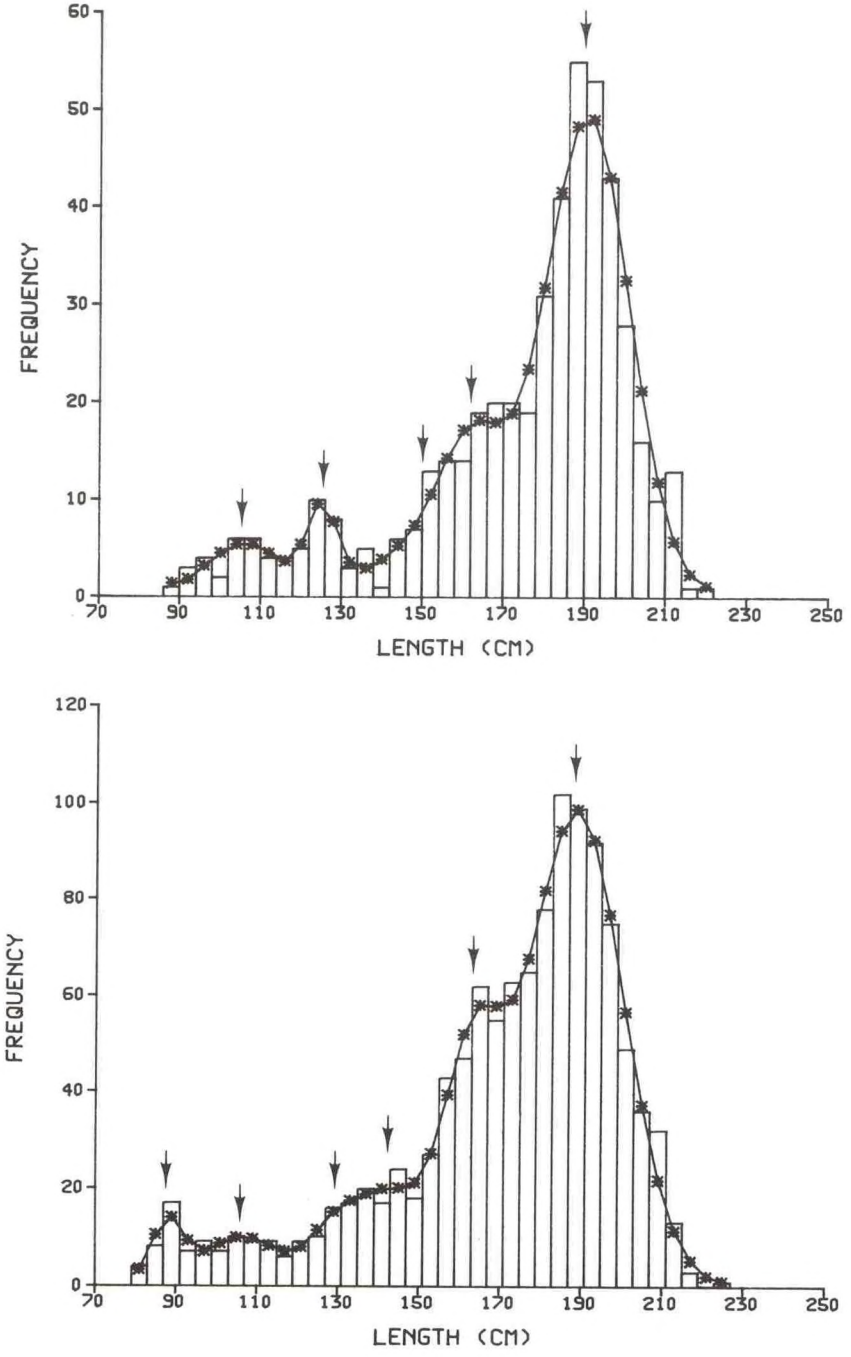


Figure 4. Histograms of length and the curve of the fitted model chosen to represent the data for northern offshore spotted dolphins in (a) August and (b) October.

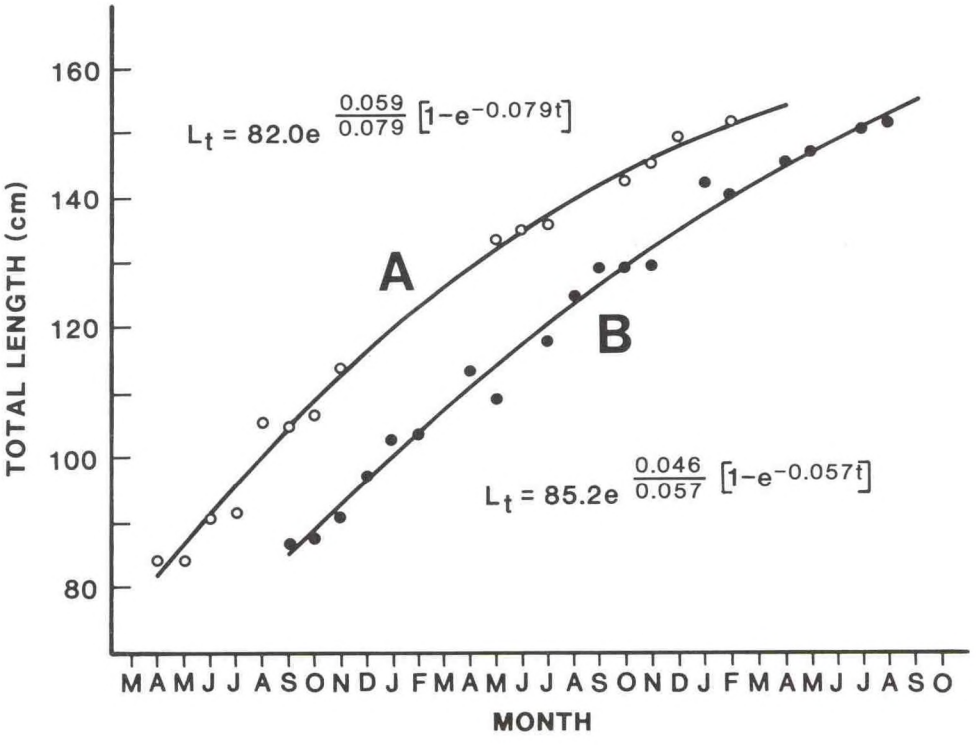


Figure 5. Mean values of monthly distributions of length for northern offshore spotted dolphin data stratified by area. The two curves represent two annual cohorts fitted by the Gompertz model of growth. NOTE: The equations were fitted using relative time and are not therefore accurate models of growth. To obtain such growth models, relative time can be converted to absolute time using the estimate of length at birth and the equation refitted to these data.

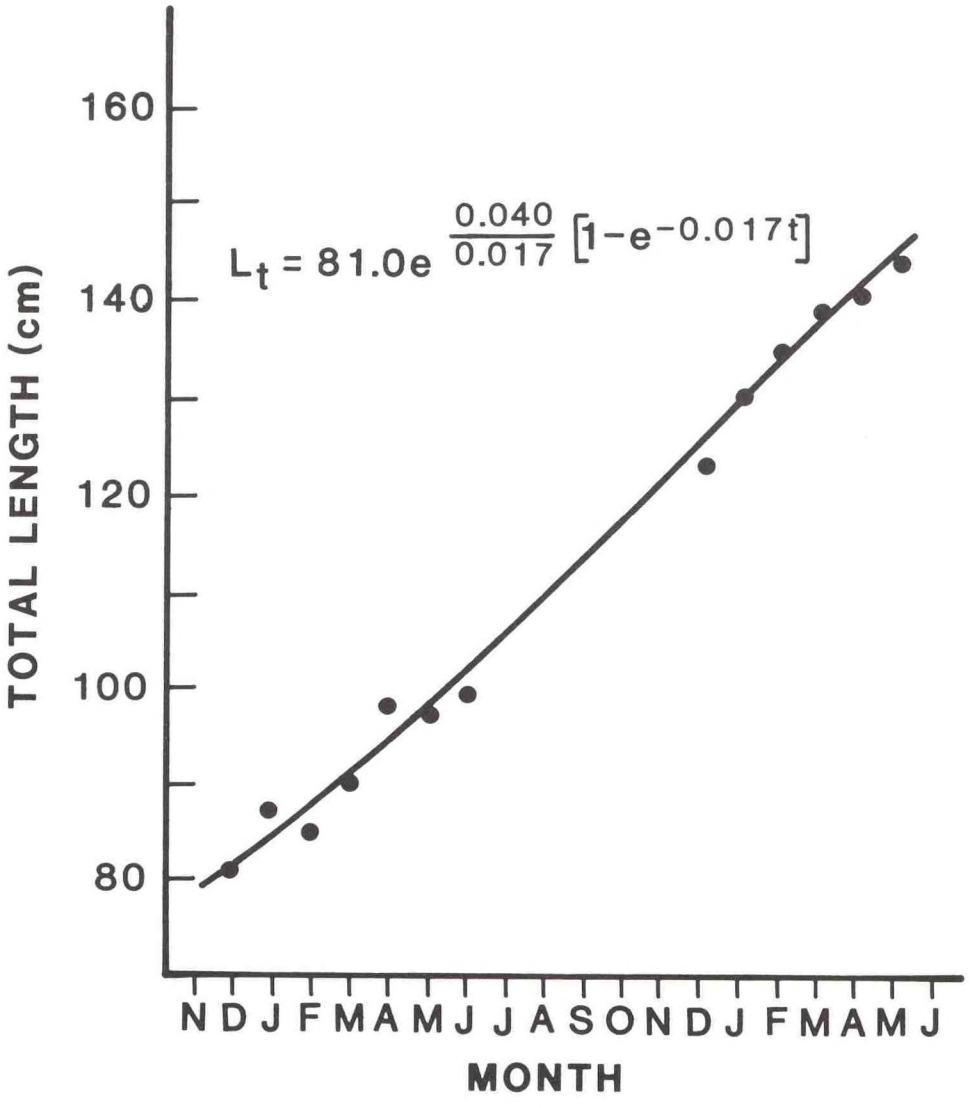


Figure 6. Mean values of monthly distributions of length for southern offshore spotted dolphin data stratified by area. The curve represents one annual cohort fitted by the Gompertz model of growth. NOTE: The equations were fitted using relative time and are not therefore accurate models of growth. To obtain such growth models, relative time can be converted to absolute time using the estimate of length at birth and the equation refitted to these data.

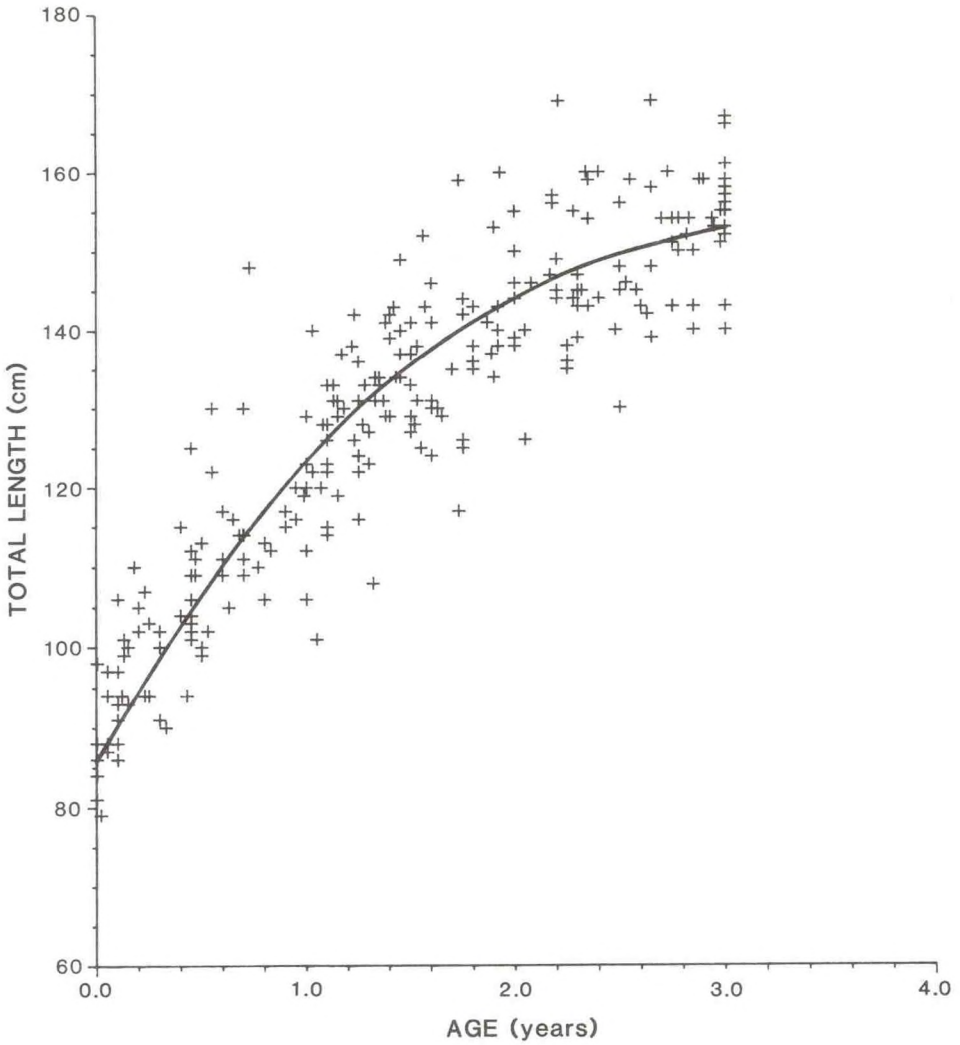


Figure 7. Total length vs. age in years (GLGs, pooled mean estimates) for northern offshore spotted dolphin data up to 3.0 years fitted by the Gompertz model of growth.

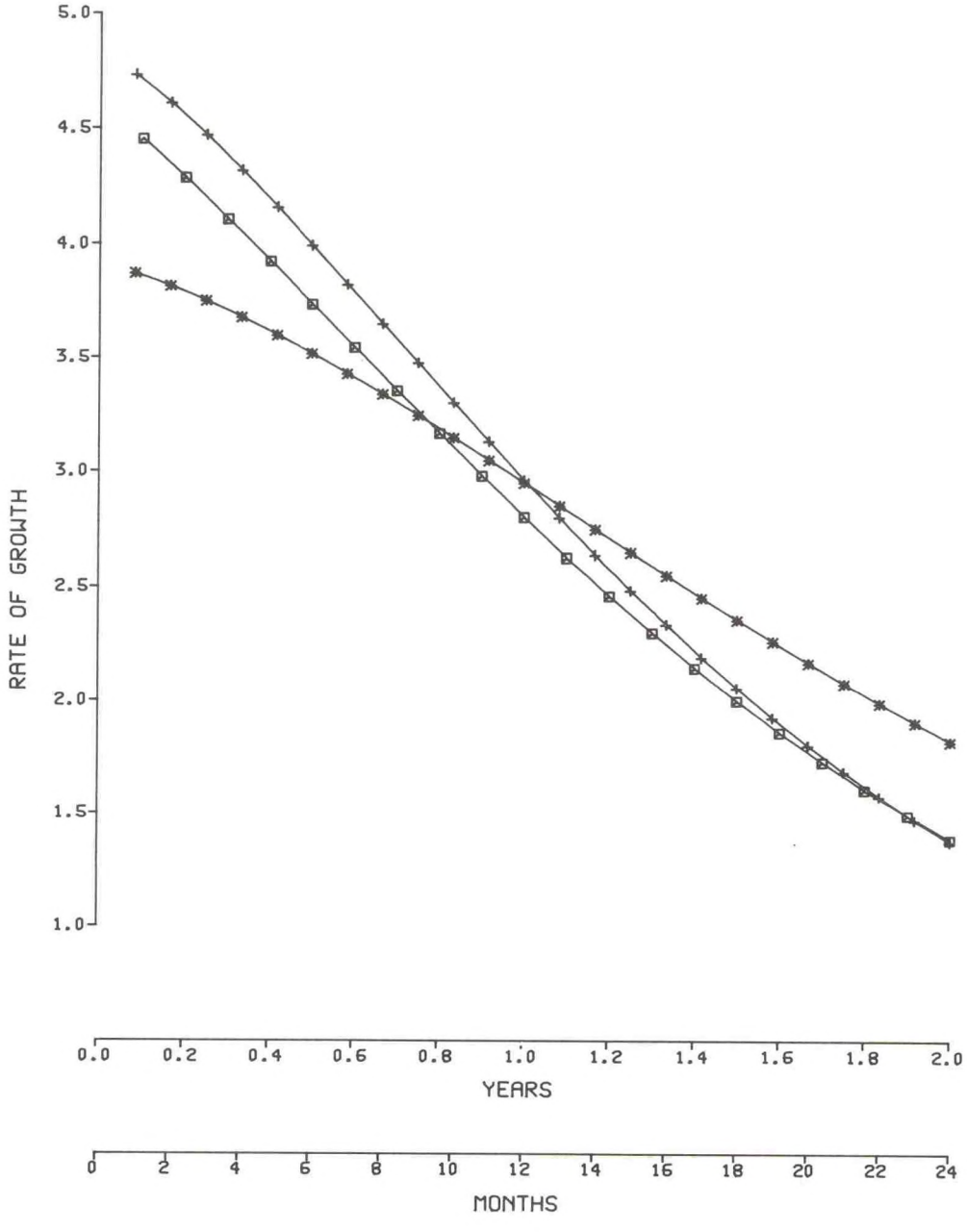


Figure 8. Average monthly growth in centimeters of northern offshore spotted dolphins plotted as the first derivative of the fitted growth curves. '+' is from curve A in Figure 5; '*' is from curve B in Figure 5; '□' is from the age-length curve in Figure 7.