EARLY POSTNATAL GROWTH OF
THE SPOTTED DOLPHIN, *STENELLA ATTENUATA*, IN
THE OFFSORE EASTERN TROPICAL PACIFIC

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ABSTRACT

Estimates of length at birth and early postnatal growth are made for the northern and southern popula-
tions of the offshore spotted dolphin in the offshore eastern tropical Pacific. Length at birth is estimated
to be 85.4 cm for the northern population and 83.2 cm for the southern population. Analyses of series
of monthly distributions of length revealed two cohorts born each year in the northern population, at
least in the northern inshore part of its geographic range, but only one cohort born each year in the southern
population. Growth curves fitted to the means of the monthly distributions of length gave estimates of
length at 1 year of 126.2 and 132.6 cm and length at 2 years of 154.3 and 154.9 cm for the two cohorts
in the northern population, and length at 1 year of 127.9 cm for the southern population. A growth curve
fitted to lengths and ages (in dental growth layer groups) from the northern population gave estimates
of lengths at 1 and 2 years of 123.0 and 143.0 cm, respectively.

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 aging of a sample of fish of known length and the following of a series 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, provided that the aged sample is a representative one.

For most species of fish, length-age relationships may be appropriate for the entire life of the animals, or at least for the period of interest to a commercial fishery. In marine mammals, however, length changes little, if at all, after attainment of physical maturity. Growth rates may change markedly even while the animal is maturing, being high for an initial period after birth and then declining quite rapidly. In delphinids, the growth rate has been found to be high in the first year, with animals typically increasing by 50-70% of their birth length (Sergeant 1962; Kasuya et al. 1974; Kasuya 1976; Miyazaki 1977; Hohn 1980; Perrin and Henderson 1984), but then declined rapidly in 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. Consequently, length-age relationships for these animals are most useful from birth until about 2 yr.

In this paper, we have used both the technique of following a series of length distributions from month to month and the technique of aging a sample of dolphins of known length to estimate the rate of growth in the spotted dolphin, *Stenella attenuata*, in the offshore eastern tropical Pacific (hereafter referred to as the offshore spotted dolphin). In neither of these two techniques did we have an absolute measure of age. Consequently, we have estimated length at birth independently and used this to fix time at birth. Growth curves were fitted to the length data by relative age and then length at birth was substituted in order to predict length-at-age.

THE SAMPLE

The field data and specimens used in the following analyses were collected by National Marine Fisheries Service (NMFS) and Inter-American Tropical Tuna Commission (IATTC) scientific technicians aboard commercial tuna purse seiners from 1968 to 1982. Procedures for collecting sample data and specimens have been described by Perrin et al. (1976). In all the following analyses, the data have been stratified into northern and southern popula-

tions divided by lat. 1°S, based on a division selected by Perrin et al. (1979). Areas 1 and 2 in Figure 1 correspond to the region occupied by the southern offshore spotted dolphin and areas 3-8 correspond to the region occupied by the northern offshore spotted dolphin.

ESTIMATION OF LENGTH AT BIRTH

An accurate estimate of length at birth is important because it establishes a point through which any growth curve should pass. This extra degree of freedom allows greater accuracy in fitting growth curves and estimating growth rates. Neither of our methods of relating length to age, described below, allows us to fix absolute age so it is essential here for us to calculate an independent estimate of length at birth.

A commonly used method of estimating length at birth when a sufficient sample is available is to regress the percent postnatal at each length interval on length and to calculate the length at which 50% of the specimens are predicted to be postnatal. This method, using a linear model, has been employed to estimate length at birth for spotted dolphins (Perrin et al. 1976), for striped dolphins, *S. coeruleoalba*, (Miyazaki 1977), and for spinner dolphins, *S. longirostris*, (Perrin et al. 1977), and using a nonlinear model for spinner dolphins (Perrin and Henderson 1984). Another method commonly employed when a small sample is available is to estimate the average length at birth as the mean length of known neonates or the mean length of full-term fetuses and small calves combined. This method has been used to estimate length at birth for long-finned pilot whales (Sergeant 1962), for spotted dolphins (Kasuya et al. 1974), for bottlenose dolphins, *Tursiops truncatus*, (Ross 1977; Hohn 1980), and for
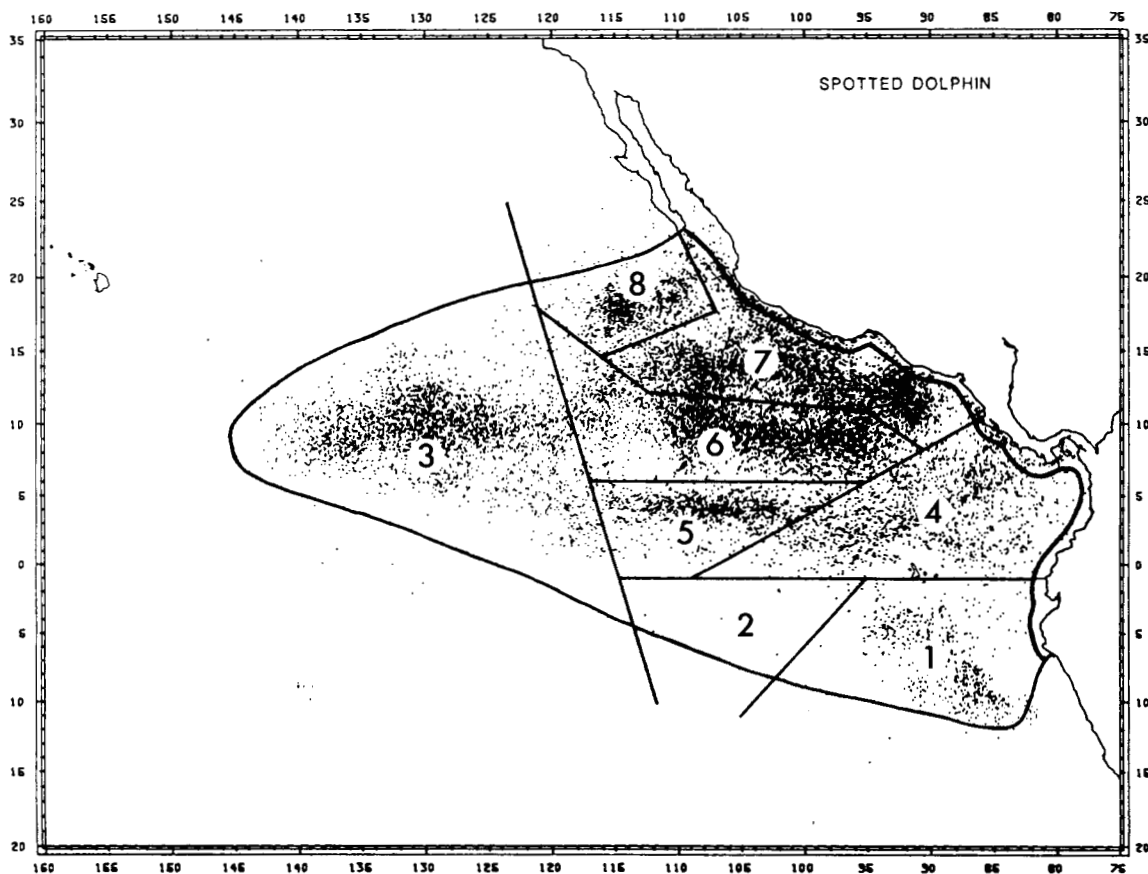

FIGURE 1.—Areas inhabited by the offshore spotted dolphin. The numbered regions refer to strata investigated in analyses of monthly distributions of length. In all analyses, the southern population is from areas 1 and 2, and the northern population is from areas 3 through 8.

the franciscana dolphin, *Pontoporia blainvillei*, (Kasuya and Brownell 1979).

Methods

The data used in this analysis were from all fetuses and calves sampled between 1973 and 1981 except for three specimens <68 cm identified as calves and one specimen of 91 cm identified as a fetus (n = 609). These four specimens were judged to have been misidentified. The data were stratified by area, north and south of lat. 1°S, and the northern sample was further stratified by the size of kill in each net set. Powers and Barlow (1979[3]) have shown that in net sets in which the kill of spotted dolphins from the northern offshore regions was ≤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 >40 (large-kill sets). This would introduce a bias in the estimate of length at birth in the regression procedure because about 90% of all northern specimens were from small-kill sets. The effect would be to underestimate length at birth because the ratio of calves to fetuses was too high in most of the sample. To investigate the extent of the bias, we calculated average length at birth for all northern specimens, for specimens from sets with kill ≤40 and >40, and for specimens from sets with kill ≤30 and >30 because the sample size for sets with kill >40 was small. The small sample available for southern specimens prevented any further stratification of the data.

Length at birth was estimated by fitting a logistic model to the percent postnatal at each length interval, weighted by the inverse of the binomial variance of each percentage, and estimated by calculating from the fitted curve the length at which 50% of the specimens were predicted to be postnatal. We also investigated linear and asymmetric logistic-type models.

Results

Figure 2 shows the length-frequency data for northern specimens from sets with kill ≤40, and the logistic model fitted to the data. Figure 3 is the equivalent for northern specimens from sets with kill >40. Table 1 gives the results for all stratifications described above using the logistic model. Using the linear or asymmetric logistic-type models did not

[3]Powers, J. E., and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, Status of Porpoise Stocks Workshop, La Jolla, CA, 27-31 August 1979. Unpubl. MS.

improve the fit and gave similar results.

Table 1 shows that the estimates of length at birth for northern specimens using the unstratified data (82.0 cm) and using specimens from sets with kill ≤30 (81.6 cm) or ≤40 (81.6 cm) are lower than the estimates using specimens from sets with kill >30 (84.6 cm) or >40 (85.4 cm), demonstrating that the bias resulting from an overrepresentation of calves in small-kill sets is significant. Furthermore, the estimate for kill >40 is higher than that for kill >30, indicated that the proportion of calves in the sample may still be a function of kill-per-set at this level. Further stratification to investigate whether or not estimates of length at birth continue to rise at higher thresholds of kill-per-set was not possible because of small sample size.

The estimate of length at birth for southern specimens is 83.2 cm. No stratification was possible because of the small sample.

Estimates of standard deviations of the estimates of length at birth are not given because, in fitting the logistic model, sums of squares were minimized for differences between observed and predicted percent postnatal and it was unclear how to calculate the standard deviations.

TABLE 1.—Estimates of length at birth stratified by number of offshore spotted dolphins killed per set. The range of length classes includes the last 0% postnatal length class and the first 100% postnatal length class.

	Sample size	Range (cm)	Length at birth predicted from the logistic model (cm)
Northern offshore spotted dolphin			
Unstratified data	586	71-92	82.0
Sets with kill ≤30	321	73-92	81.6
Sets with kill ≤40	384	71-92	81.6
Sets with kill >30	105	71-89	84.6
Sets with kill >40	36	78-89	85.4
Southern offshore spotted dolphin			
Unstratified data	23	78-85	83.2

Discussion

Our estimate of length at birth of 82.0 cm from the unstratified northern data is similar to that of Perrin et al. (1976), who estimated length at birth at 82.5 cm, based on a sample of 73 northern specimens (calves and fetuses) grouped into 3 cm intervals from 74 to 92 cm.

Estimates of length at birth in large-kill sets are less biased because of the overrepresentation of calves in small-kill sets. A future larger sample from large-kill sets may allow for additional stratification by kill-per-set, enabling estimates to be calculated
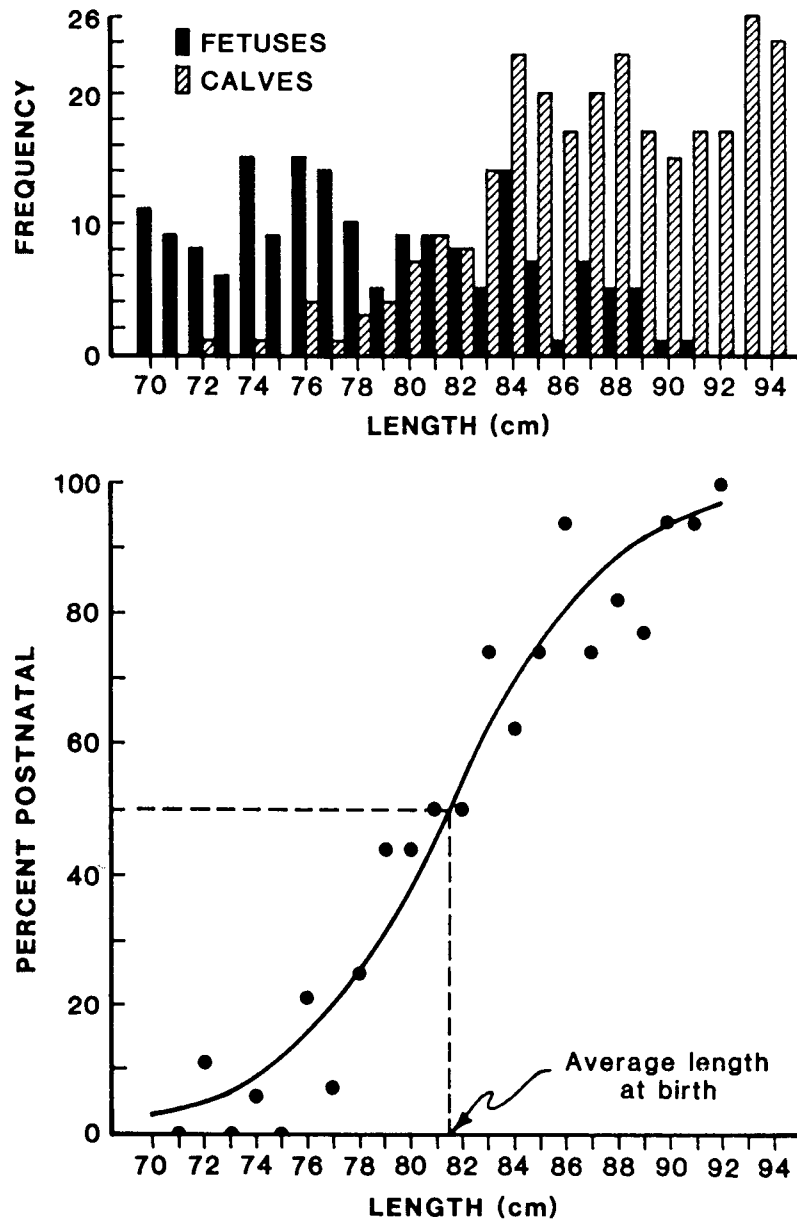
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FIGURE 2.—Length-frequency data for specimens from sets with kill ≤40 grouped in 1 cm intervals for 163 fetuses and 221 calves from the northern offshore population of spotted dolphins, and the logistic model fitted to the percentage of animals that were postnatal.

using specimens from sets with higher levels of kill. It may then be possible to determine at what level of kill-per-set the estimate ceases to increase. Until additional data are available, we consider 85.4 cm to be the best estimate of length at birth in northern offshore spotted dolphins.

Our estimate of length at birth in the southern offshore spotted dolphin of 83.2 cm is more ques-

tionable because we were unable to stratify by kill-per-set. As adults, southern specimens are about 2.5 cm shorter than their northern counterparts (Perrin et al. 1979). This small, but statistically significant, difference may or may not imply that length at birth is smaller in the southern population. The small sample of 23 specimens used in our calculation of length at birth raises doubts concerning the
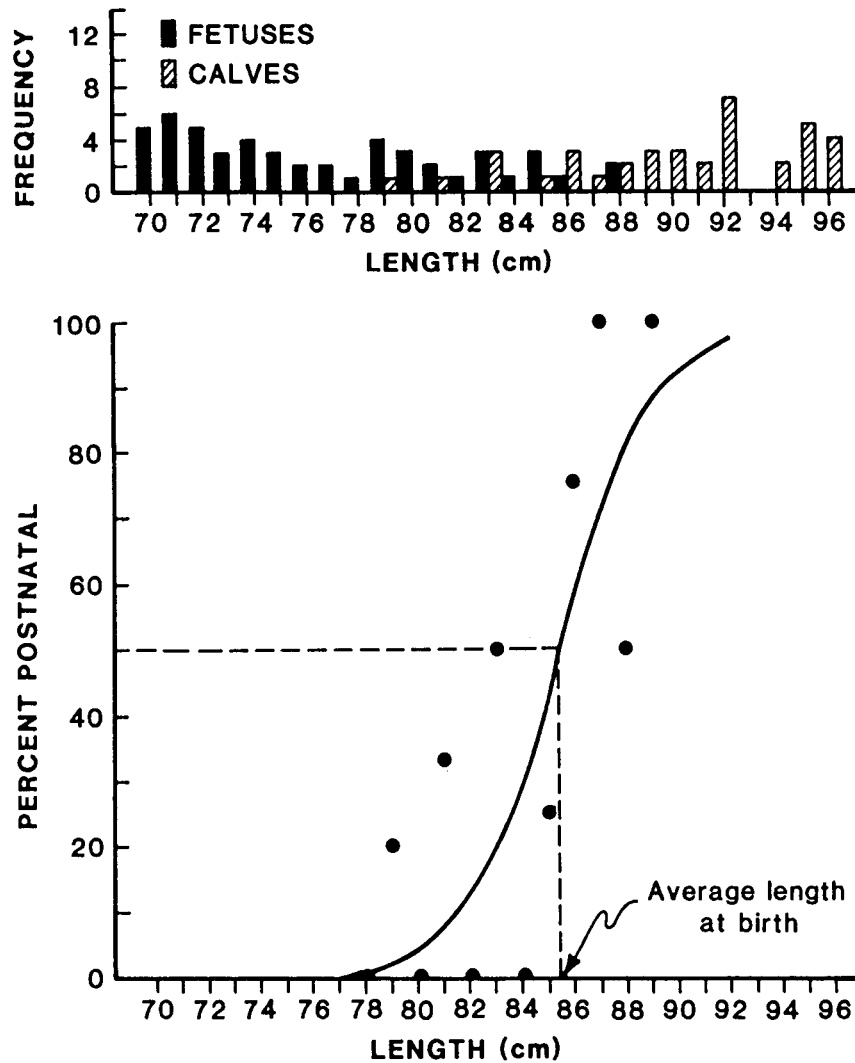
FIGURE 3.—Length-frequency data for specimens from sets with kill >40 grouped in 1 cm intervals for 21 fetuses and 15 calves from the southern offshore population of spotted dolphins, and the logistic model fitted to the percentage of animals that were postnatal.

accuracy of this estimate. For these reasons, we take the estimate from all southern specimens of 83.2 cm as our provisional best estimate of length at birth for southern offshore spotted dolphins while recognizing that this estimate may be biased downwards because of a possible overrepresentation of calves in the sample.

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 the means of normal distributions fitted to length-frequency data by month to estimate the length of the offshore spotted dolphin at 1 yr of age. Perrin and Henderson (1984) used the same technique for the spinner dolphin. 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 is characterized by a distribution of lengths, identifiable as 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, mean lengths can be followed from birth until

growth slows to an extent that distributions of lengths from different cohorts cannot be distinguished. A growth curve can then be fitted to the monthly mean lengths.

Since the analysis of Perrin et al. (1976), the sample of measured lengths from offshore spotted dolphins has increased from about 3,500 to over 15,000. Consequently, we were able to analyze the available data more extensively than had been done previously.

Methods

Length measurements from all postnatal specimens, made between 1968 and 1982, were used in the analyses except for three specimens <68 cm which were judged to have been erroneously identified as calves. The data were stratified into eight areas based upon apparent hiatuses in distribution from examination of sightings and effort data (Fig. 1). Areas 1 and 2 comprise the southern population and areas 3-8 the northern population.

For the northern data, no consistency could be found in preliminary analyses of lengths when data from all areas were included. When area 3 was excluded, consistency was much improved. When areas 4 and 5 were also excluded, consistency was improved further for the months of February through June. This indicated that there were nonseasonal or seasonal but asynchronous elements in areas 3, 4, and 5 at least at certain times of the year. Consequently, in our analyses of northern data we used lengths from areas 6, 7, and 8 only for February through June and lengths from areas 4-8 for January and July through December. A similar situation occurred for the southern data where the elimination of area 2 improved consistency for January through May. In our analyses of southern data, therefore, we used lengths only from area 1 for these months.

The data were grouped in interval widths of 4 cm. This gave four possible ways of grouping the data because lengths were measured to the nearest whole centimeter. Each of these four groupings were investigated, there being no reason to prefer a starting point of the first interval as, for example, 76, 77, 78, or 79 cm.

A mixture of normal distributions was fitted to each data set using a version of the computer program NORMSEP (Hasselblad 1966). The program requires the number of distributions to be specified, and this was varied in order to determine the most likely number of distributions present. The model selected as most representative of the length-frequency data was that which gave the highest χ^2 value, and therefore the highest probability that a greater χ^2 value could be obtained by chance alone, and also gave biologically feasible results based on prior knowledge of delphinid growth. (Some model fits had a very high probability of a greater χ^2, but the mean lengths could not be accounted for by any reasonable regime of growth.)

We chose Laird's (1969) form of the Gompertz (1825) growth equation to fit to the monthly mean lengths. A linear model is clearly inadequate to describe growth except over a very short time period. We also investigated the use of the von Bertalanffy (1934) growth equation but found it to be less flexible than the Gompertz model.

Each model of growth was fitted to the mean lengths using the midpoint of the first month as time zero. In fact, this is not necessarily the time of birth so we fixed time of birth by substituting our estimate of length at birth into the fitted equation. Lengths at age were then calculated by substituting that age plus the difference between the midpoint of the first month and our calculated time of birth into the fitted equation.

Results

Northern Population

Figure 4 shows, as examples, the fitted mixture of normal distributions to the length-frequency data for August and October. The arrows indicate the positions of the means of the fitted distributions.

Table 2 shows the estimates of mean length of the fitted normal distributions for each month. The estimates are presented so that the increases from month to month can be clearly seen. The two final columns of Table 2 are mean lengths of the two distributions to the right of the length-frequency plots. These mean lengths are consistent from month to month. The table shows that there are actually two series of mean lengths: one beginning at 86.7 cm in September and continuing through columns 2 and 4 of the mean lengths, and the other beginning at 84.5 cm in April (the estimate of 92.7 cm for March is an anomaly for which we have no explanation) and continuing through columns 1, 3, and 5. These represent two cohorts born each year about 6 mo apart in the spring and autumn. Note that each series of mean lengths continues only for about 24 mo. This is because after this time growth has slowed to an extent that it is not possible to distinguish distributions of length from different cohorts. The
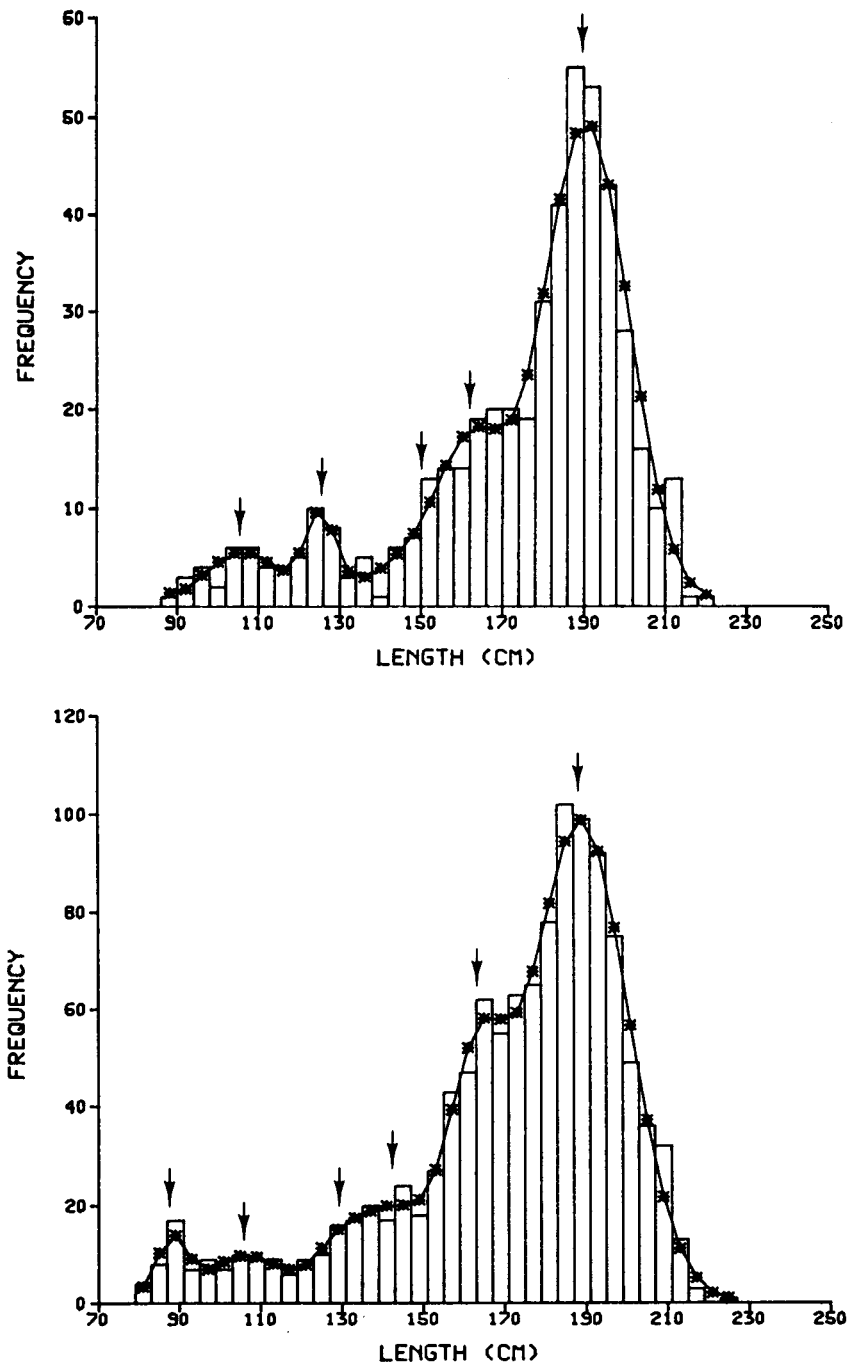
FIGURE 4.—Histograms of length and the fitted mixture of normal distributions for data for the northern offshore spotted dolphin in (A) August and (B) October. The arrows indicate the positions of the means of the fitted distributions.

mean length of 105.9 cm for June was not included in further analyses because its inclusion more than doubled the residual sums of squares for the model fit. We consider it an outlier.

Figure 5 shows Gompertz models of growth fit-

ted separately to the mean lengths, excluding the 92.7 cm point for March, from columns 1, 3, and 5 (curve A) and, excluding the 105.9 cm point for June, from columns 2 and 4 (curve B) of Table 2. Time at birth and lengths at 1 and 2 yr were calculated as

TABLE 2.—Mean lengths of the fitted normal distributions for the northern offshore spotted dolphin.

Month	Sample size	Mean lengths of fitted distributions (cm)					
September	536		86.7	105.0	129.4		161.3	186.9
October	1,159		87.9	106.3	129.4	142.7	163.1	188.8
November	616		91.9	113.9	129.6	145.7	159.4	187.7
December	223		97.5		127.7	149.9		187.4
January	2,926		102.9		142.4		161.9	187.4
February	2,772		104.1		140.7	151.8	161.5	186.3
March	866	¹92.7	113.2	131.4			160.7	188.7
April	700	84.5	113.6		146.0		163.6	188.5
May	423	84.5	108.7	133.9	147.5		165.9	187.9
June	300	90.7	¹105.9	135.5			165.2	189.5
July	266	91.8	118.0	136.1	150.8		164.5	190.1
August	486	105.7	125.1		151.8		162.6	190.5

¹These mean lengths were not included in further analyses.

$$L_t = 82.0e^{\frac{0.059}{0.079}[1-e^{-0.079t}]}$$

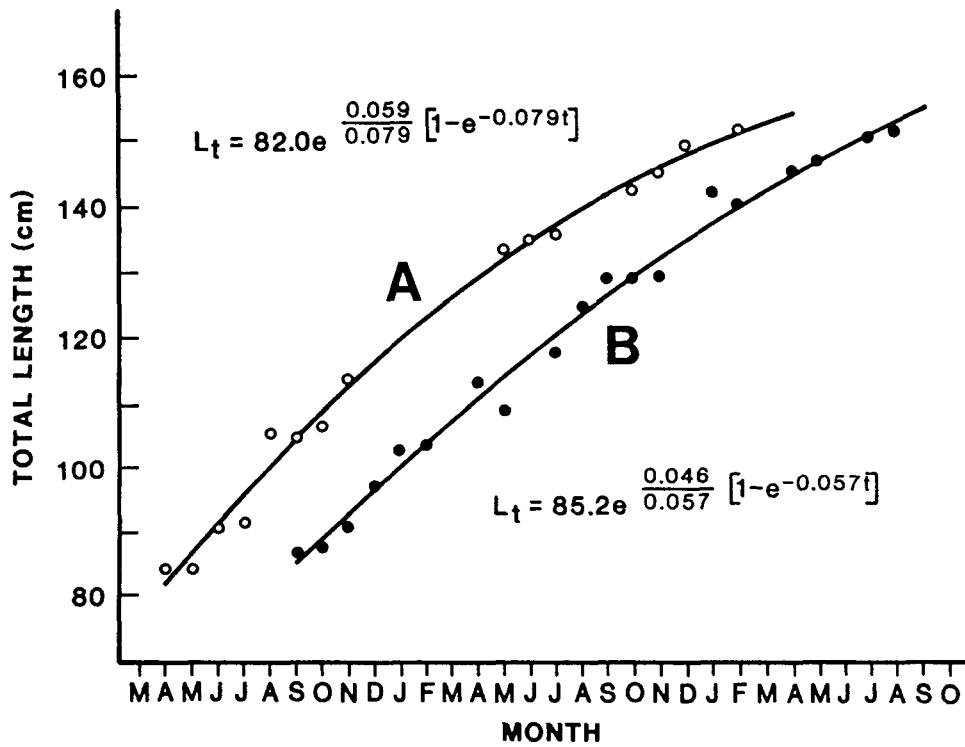$$L_t = 85.2e^{\frac{0.046}{0.057}[1-e^{-0.057t}]}$$

FIGURE 5.—Mean values of monthly distributions of length from data for the northern offshore spotted dolphin. The two curves represent two annual cohorts fitted separately 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.

described above with the following results:

	Growth curve A	Growth curve B
Fixed length at birth (estimated in this paper)	85.4 cm	85.4 cm
Estimated time of birth	May 9	September 11
Estimated length at 1 yr	132.6 cm	126.2 cm
Estimated length at 2 yr	154.9 cm	154.3 cm

Rates of growth as centimeters per month for the two fitted curves adjusted for length at birth are as follows:

	Rate of growth	
Months after birth	Curve A	Curve B
0	5.03	3.80
6	3.94	3.43
12	2.76	2.89
18	1.81	2.33
24	1.14	1.82

Southern Population

Table 3 shows the estimates of mean length of the fitted normal distributions for each month. For these data it is clear, apart from the mean lengths of 105.0 cm in January and 127.5 cm in May, that there is only one cohort born each year in the southern summer. As a result of this and the much smaller sample sizes, distributions of length could only be distinguished up to about 18 mo. The two final columns of Table 3 show the mean lengths of the two distributions to the right of the length-frequency plots. These are quite consistent from month to month, as with the northern data.

Figure 6 shows the Gompertz model of growth fitted to the mean lengths from columns 1 and 3 of Table 3. Time at birth and length at 1 yr were calculated as described above with the following results:

Fixed length at birth (estimated in this paper)	83.2 cm
Estimated time of birth	6 January
Estimated length at 1 yr	127.9 cm

Rates of growth for this fitted curve do not decrease from birth as they do for the northern population because the curve has a point of inflection at approximately 50 mo. The rates of growth at 0, 6, 12, and 18 mo after birth are 3.29, 3.72, 4.12, and 4.47 cm/mo, respectively.

TABLE 3.—Mean lengths of the fitted normal distributions for the southern offshore spotted dolphin.

Month	Sample size	Mean lengths of fitted distributions (cm)				
December	47	81.0		123.5	165.7	187.9
January	254	87.0	[1]105.0	131.0	164.5	187.8
February	412	85.1		134.9	165.6	188.0
March	57	90.0		139.3		189.7
April	43	97.9		140.8	163.3	189.5
May	212	97.1	[1]127.5	144.3	157.7	182.6
June	42	99.0			163.8	185.3

[1]These mean lengths were not included in further analyses.

Discussion

There are several sources of variability in the estimates of mean length by month to which the growth models have been fitted. There is individual variation in time of birth, length at birth, and growth rate. The calving season may vary from year to year and area to area. The specimens which were measured are subject to the usual sampling variation. Sampling in a particular year may not have been random with respect to time in each month. Given these sources of variability, it is interesting that the results should appear so consistent.

The growth curves were fitted to the unweighted mean lengths. 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 a weighted regression. We believe that this is not necessarily the case and that the unweighted regressions represent the best descriptions of growth for these data. When weighted regressions were performed the fitted curves changed negligibly.

The most important potential problem is that the method relies upon being able to analyze a sample of data in which reproduction is seasonal and in which the timing of seasonality is constant. 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 series of mean lengths because offshore spotted dolphins appear to have different calving 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.

In this analysis we pooled the data from several years for our monthly samples, rather than attempt-

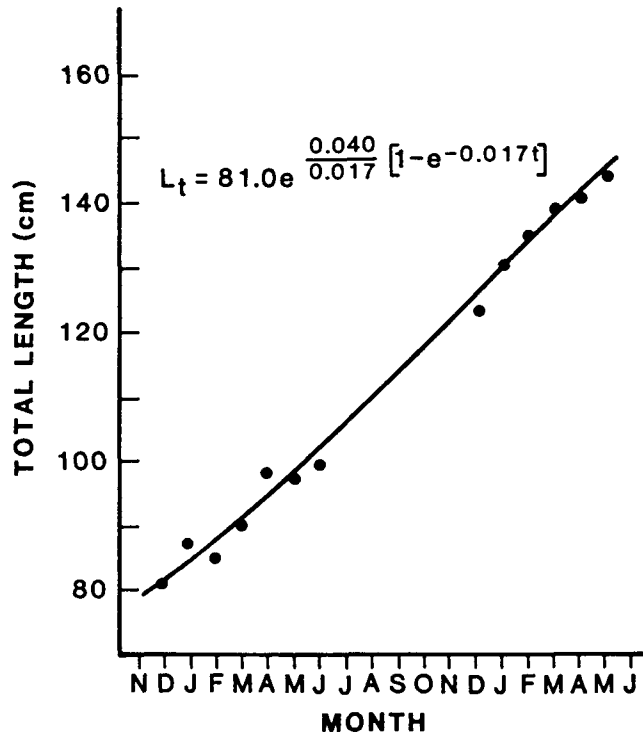$$L_t = 81.0e^{\frac{0.040}{0.017}\left[1-e^{-0.017t}\right]}$$

FIGURE 6.—Mean values of monthly distributions of length from data for the southern offshore spotted dolphin. The curve represents one annual cohort fitted by the Gompertz model of growth. The open circles were not included in the fitting of the curve. 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.

ing to follow actual cohorts of animals from individual years as did Perrin et al. (1976) in their analyses. Combining the data from several years introduces additional variation in the data if the timing of the calving season varies from year to year, but it increases sample sizes and minimizes bias caused by nonrandom timing of sampling within months. In addition, we are mainly interested in an average growth rate which is best estimated from several years of data.

Perrin et al. (1976) fitted a linear model to mean lengths estimated in the months of October 1972, January, February, March, and April through June 1973 from which they extrapolated to obtain an estimate of length at 1 yr of 147.5 cm for the northern offshore spotted dolphin. The authors recognized that this estimate was biased upwards because growth rates of delphinids do decrease in the first year and revised this estimate downwards based on aged specimens. We believe our analyses to be more

accurate than those of Perrin et al. (1976) and our results to be a substantial improvement.

Barlow (1984) found an indication of two peak calving seasons for spotted dolphins north of the Equator, in the spring and autumn, but that the animals were born throughout the year. South of the Equator he found a single season peaking around April. These results are similar to ours but the timing of the southern season does not agree. The difference can be explained by Barlow's use of Perrin et al.'s (1976) growth curve which predicted a mean length of 138.0 cm for 1-yr-old animals. Our growth equations predict animals of this length to be from 14 to 16 mo old.

The two growth curves fitted to the mean lengths from the two cohorts in the northern region predict different lengths-at-age and are characterized by very different growth rates. It is possible that these two cohorts actually grow at different rates because of environmental factors, but we believe that the dif-

ferences are more likely a result of variability in the data. We suggest, therefore, that the mean of the estimates from both growth curves be used for estimates of lengths-at-age for the northern offshore spotted dolphin.

For the southern population, the mean lengths of 105.0 and 127.5 cm for January and May, respectively, suggest that there may be two calving seasons in this area. At present, the sample size is too small to assess whether or not this is the case.

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

Increments of tissue are deposited in teeth as a function of time. The most important incremental pattern in odontocete teeth is comprised of 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, p. 48-49). These 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 with absolute time is available. However, a few known-age captive and minimum-known-age captive bottlenose dolphins (Sergeant 1959; Sergeant et al. 1973; Hui 1978) and captive tetracycline-marked specimens of other species (*Lagenorhynchus obscurus*, Best 1976; *Delphinus delphis*, Gurevich et al. 1980; *S. longirostris*, Myrick et al. 1984) have provided evidence that the GLG as defined and calibrated by these workers represents an annual deposition pattern. In the absence of any known-age specimens of spotted dolphins, we have assumed that a GLG pattern similar to that described in the above species represents the same amount of time.

Methods

A sample of 800 males and 800 females, selected randomly from the specimens collected between 1973 and 1978, and all 312 female specimens collected in 1981 made up the sample of animals from which teeth were aged.

The teeth were decalcified in RDO[4], a commercial decalcifying agent, cut longitudinally into 24 μm thin sections using a freezing microtome, stained in

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

haematoxylin, and mounted in 100% glycerin. Detailed procedures for the preparation technique and interpretation of GLGs are described by Myrick et al. (1983).

Teeth from each of the 1,600 specimens collected between 1973 and 1978 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 2 yr. 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 et al. 1983). Only one age reading was made by each reader for the 312 specimens collected in 1981, and the mean of these two readings determined. For lack of a preference for one reader's estimates, growth rate analyses used the pooled mean and mean age estimates. Growth models were fit to the age-length data for males and females separately.

Growth rate was estimated by regressing length on number of GLGs (age) using Laird's (1969) form of the Gompertz model. The data were truncated at ≤3.0 GLGs in order to reduce the effects of older animals on our estimates of growth in the first 2 yr, in case the chosen model failed to describe growth adequately over a wider range of ages. Length at birth was fixed at the independently estimated value of 85.4 cm (see above).

Results

There was no difference in growth between males and females at this age. Therefore, the data were pooled. Figure 7 shows the Gompertz model of growth fitted to the pooled data. The model gives a predicted length of 123 cm (SD = 0.7 cm) at 1 yr and a predicted length of 143 cm (SD = 0.6 cm) at 2 yr. These standard deviations are underestimates because they do not incorporate variability in the age of individual specimens resulting from between reader differences.

Figure 7 also shows that lengths predicted by this model may be underestimated up to about 8 mo and overestimated from about 8 to 13 mo. For comparison with predicted length at 1 yr from the model, the mean length of specimens aged between 0.9 and 1.1 yr (*n* = 24) is 121 cm with a range of 101-140 cm.

The estimated monthly growth rate is 3.84 cm/mo initially, falling to 3.11 cm/mo at 6 mo, 2.33 cm/mo at 12 mo, 1.67 cm/mo at 18 mo, and 1.15 cm/mo at 24 mo.

Discussion

The accuracy of these length-at-age estimates

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depends upon the representativeness of the sample, the accuracy of the readings, the assumptions that 1 GLG equals 1 yr, and the adequacy of the growth model.

The sample analyzed was a simple random sample, stratified only by sex, taken from all specimens collected between 1973 and 1978. These were themselves a sample of the animals killed incidental to fishing operations, which were a sample of the population. Although Powers and Barlow (fn. 2) have shown a bias towards a higher proportion of calves killed in purse seine nets, we have no reason to believe that the relationship between length and age is different in our sample than in the population.

Teeth were read as accurately as possible. Reilly et al. (1983) have investigated the precision of the readings but, without known-age animals, it is not possible to validate their accuracy.

Our assumption that 1 GLG equals 1 yr is based on captive, tetracycline-marked Hawaiian spinner dolphins (Myrick et al. 1984) a distantly related species. Known-age, captive or marked spotted dolphins are not available for direct GLG calibration. If differences are found between GLG in spotted and spinner dolphin teeth when data from known-age spotted dolphins are available, these estimates of growth based on GLGs will need to be revised.

It is often assumed that when one GLG is deposited each year the first GLG begins with the neonatal line immediately at birth and ends precisely 1 yr later. Yet it is possible, as suggested by Perrin et al. (1977) for *S. longirostris*, that the first GLG is not always complete. Teeth from young, known-age dolphins from the same stock born at different times during the year are needed to address this question.

It is also possible that the neonatal line may not be deposited immediately at the time of birth. In bottlenose dolphins, stranded on the mid-Atlantic coast of the United States, variability has been found in the time of deposition of the neonatal line in 18 neonatal specimens (Hohn unpubl. data). These specimens were identified as neonates because they lacked the umbilicus (indicating that the calf was not stillborn) and their dorsal fin and flukes were folded (Tavolga and Essapian 1957). Some of these stranded specimens showed no neonatal line while others had part of a neonatal line deposited. Similarly, in our sample of offshore spotted dolphins from northern areas there is not neonatal line in some postnatal specimens so that the amount of time since birth is unknown. This difference in timing of neonatal line deposition may be due to individual variation in tooth growth and mineralization or small difference in gestation time.

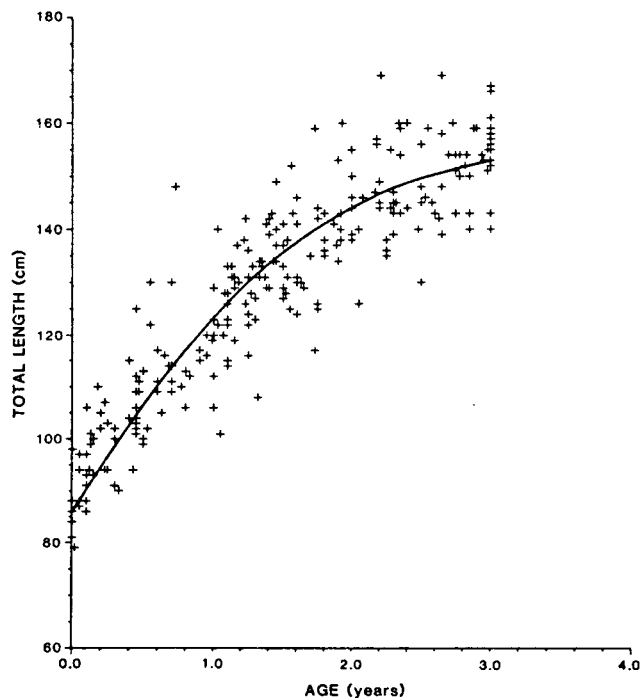The precise timing of the deposition of the first

FIGURE 7.—Length-age [GLGs, (growth layer groups), pooled mean estimates] data for northern offshore spotted dolphins up to 3.0 GLGs, and the fitted Gompertz model of growth.

GLG (beginning with the neonatal line) is important in estimates of age in young animals. For a specimen estimated to be 0-yr-old based on GLGs but which is known not to be a neonate, the age must necessarily be an underestimate of the actual age of that specimen, and, consequently, the average length of "0-yr-olds" would be greater than the average length of new-born specimens. When the Gompertz model (with L_0 not fixed) is fitted to the age data, the predicted length at age 0 is 89.6 cm, 4.2 cm higher than the length-at-birth estimate. The age at which the predicted length is 89.6 cm when L_0 is fixed at 85.4 cm is about 0.1 GLGs. This indicates a possible bias of about 0.1 GLGs for young animals. However, this difference between predicted length for fits of the model with fixed and floated L_0 diminishes rapidly and at 0.7 GLGs predicted length is 114.0 cm for both models.

The Gompertz model appears to be generally suitable in describing the early growth of the offshore spotted dolphin based on GLG readings. However, the pattern of points around the fitted line in Figure 7 up to about 1.1 GLGs indicates that growth during this period may not be adequately described by a single curve. This pattern may be a result of either sampling variation or errors in reading, but it may be due to changes in growth rate during this period resulting from changes in food intake. Perrin et al. (1976) have estimated that weaning occurs at about 11 mo in the offshore spotted dolphin so that during the period from about 8 to 13 mo, milk intake will be decreasing and the intake of solid food will be increasing. Growth rates may well reflect these changes. If this is the case, a two-cycle model may describe growth more accurately during this period. Such an approach was used by Perrin et al. (1976, 1977) in spotted and spinner dolphins, respectively, to describe a secondary surge in the growth of pre-adult animals.

CONCLUDING REMARKS

Our analyses have produced different estimates of growth rates and lengths-at-age from two different techniques. The reliability of fitting growth curves to series of means of identifiable distributions of length by month depends primarily upon being able to select a sample in which breeding is both seasonal and synchronous from year to year. The reliability of fitting growth curves to length-age data as determined by counting GLGs depends primarily upon the validity of the assumption that 1 GLG is equivalent to 1 yr. We believe that neither technique is sufficiently reliable to be labelled as the "best" method

or to try to calibrate the other. Rather, our analyses underline the need for the analysis of data collected from known-age animals of these populations. However, we do believe that the estimates of growth rates and lengths-at-age presented here are the best currently available for offshore spotted dolphins from the eastern tropical Pacific.

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