GROWTH AND REPRODUCTION OF THE SPOTTED PORPOISE, *STENELLA ATTENUATA*, IN THE OFFSHORE EASTERN TROPICAL PACIFIC

WILLIAM F. PERRIN, JAMES M. COE, AND JAMES R. ZWEIFEL[1]

ABSTRACT

This study is based on data from several thousand specimens of spotted porpoise, *Stenella attenuata*, incidentally killed in the purse seine fishery for yellowfin tuna, *Thunnus albacares*. Average length at birth is 82.5 cm. Gestation is 11.5 mo. Average length at 1 yr is 138 cm. Length-weight equations are given for fetuses and postnatal males and females. Age was estimated from dentinal layers in thin sections of teeth. A two-phase Laird-Gompertz growth model was fitted to the layer-length data. Direct calibration of the dentinal layers beyond the first year (two layers) was not possible, and three alternative hypotheses were considered: 1) two layers per year, until pulp cavity occluded, 2) two layers per year in first year, and one per year thereafter, and 3) two layers per year until puberty, and one per year thereafter. The second alternative is most probably the correct one, but reproductive parameters were estimated in terms of layers. Breeding is diffusely seasonal, with prolonged calving seasons in spring and fall and a pronounced low in winter. A third calving season may exist in the summer. Average age at attainment of sexual maturity of males is approximately 12 layers (average length about 195 cm and average weight about 75 kg). Females attain sexual maturity on the average at about 9 layers and 181 cm. Ovarian changes in adult females are described. Apparently postreproductive females were encountered in the samples. It is concluded that corpora albicantia of ovulation and pregnancy persist indefinitely in the ovaries. It was not possible to distinguish between the two types of corpora. Ovulation rate changes with age, from about four per layer in very young adult females, to about one per layer in older females. The average calving interval is 26 mo long and consists of 11.5 mo of pregnancy, 11.2 mo of lactation, and 3.3 mo of resting and/or estrus. About 9.6% of lactating females are also pregnant. Pregnancy rate decreases with age, from about 0.6 per year at 8 to 10 layers, to about 0.3 at 16 layers. The overall sample contained 44.9% males and 55.1% females. Sex ratio changes with age, from near parity at birth, indicating higher mortality rates for males. Gross annual production of calves, based on age and sex structures of the sample and the estimated pregnancy rate, is 14.4% of the population per year. No evidence was found of age or sex segregation in schooling. The estimated parameters differ in a consistent way from those estimated for a population of *Stenella attenuata* in the western Pacific, possibly reflecting the exploitation in the eastern Pacific.

Porpoises of the genera *Stenella* and *Delphinus* are killed incidentally in the tuna seine fishery in the eastern tropical Pacific (Perrin 1969, 1970a; National Oceanic and Atmospheric Administration[2]). Since 1968, the National Marine Fisheries Service (NMFS) has conducted a program of research into the population biology of the major porpoise species to assess the impact of this fishing mortality on the porpoise stocks. The purpose of this paper is to describe the life history of the spotted porpoise, *Stenella attenuata*

(Gray),[3] the animal most frequently killed in the fishery.

Little information on life history of the spotted porpoise has been available until very recently. Harrison et al. (1972) examined the gonads of 6 specimens from Japan (5 males and 1 female) and 45 specimens of *S. attenuata* from the eastern tropical Pacific (19 males and 26 females), but did not separate their results and conclusions from

---

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92039.
[2]National Oceanic and Atmospheric Administration. 1972. Report of the NOAA Tuna-Porpoise Review Committee, September 8, 1972. Unpubl. rep. U.S. Dep. Commer., Wash., D.C., 63 p.

[3]The taxonomy of the spotted porpoise has long been confused. Recent morphological studies (Perrin in press) have shown that the spotted porpoise in the tuna fishery is conspecific with the spotted porpoise occurring around Hawaii. The name *S. attenuata* (Gray 1846, holotype from unknown locality) applied by True (1903) to the Hawaiian form is used here for the eastern Pacific form, taking priority over *S. graffmani* (Lönnberg 1934). This usage is strictly provisional, pending the completion of current taxonomic studies, when a different name, such as *S. dubia* (G. Cuvier 1812) or *S. frontalis* (G. Cuvier 1829) may take priority.

those for *S. longirostris*. Preliminary unpublished results of our studies indicate that these two species are probably disparate in such growth parameters as length at birth, length at maturity, and asymptotic length. Harrison et al. (1972) stated that lengths of the fetuses examined indicate that parturition occurs both in the spring and in the autumn. They described in detail the gross and microscopic histological appearances of several pairs of ovaries. A maximum of nine corpora albicantia were encountered. They concluded that if all the corpora albicantia in ovaries of specimens of this species do not represent past pregnancies, either the fertility is very low or the corpora are not permanent.

Nishiwaki et al. (1965) published length-frequency distributions of 34 fetuses (up to 106 cm long) and 194 postnatal animals (104 to 208 cm) from a school driven ashore in Japan. They estimated that gestation lasts 1 yr, length at birth is about 105 cm, juveniles reach 150 cm in 6 mo, and adult size (180 cm for females and 190 cm for males) is reached in 1 yr. They concluded that there are two seasons for mating and parturition, in the spring and in the autumn, and that there are fewer males than females among adults. Ontogenetic changes in coloration, external proportions, organ weights, the skeleton, parasite load, and feeding habits have been described (Perrin 1970b, in press; Perrin and Roberts 1972; Dailey and Perrin 1973; Perrin et al. 1973).

Kasuya et al. (1974) recently published results of a study of several hundred specimens caught in the Japanese fishery for *S. attenuata*. Their results are discussed and compared with ours in the body of this paper.

METHODS AND MATERIALS

Observer Program

Beginning in 1968, NMFS placed observers aboard U.S. tuna seiners to collect information on the incidental take of cetaceans in the eastern tropical Pacific. Observers were placed on 1 cruise in 1968, 5 in 1971, 12 in 1972, and 22 in 1973. Most of the cruises were 30 to 60 days long. In addition, biological data were collected during chartered cruises of commercial seiners: one in 1971, one in 1972, and two in 1973.

The data collecting had to be carried out in such a way as to not interfere with the fishing operation. Hence, the amount of information col-

lected on the animals killed in a net set varied widely, depending on the amount of time that was available before the next set was made. Following is the hierarchy of types of data that were collected (sample sizes were largest for the first and smallest for the last):
Animals killed were:

1. Counted (estimates were made in cases where counts were not possible), usually on the deck or in the net,
2. Identified to species (and race when possible),
3. (*S. attenuata* only) identified to developmental color pattern phase (Perrin 1970b), and sexed,
4. Measured (to nearest centimeter with 2-m calipers), and
5. Dissected to collect information on reproductive condition (for females, mammaries were examined and reproductive tract collected; for males, the right testis was collected) and age (a section of the left lower jaw at midlength was collected). The gonadal material and jaw sections were preserved in 10% Formalin.[4] Small fetuses (≤ 30 cm) were preserved in the uterus. Larger fetuses were removed from the uterus and frozen.

For each specimen that was at least measured (step 4 above), a field serial number was assigned, and a specimen data sheet was filled out. Data for specimens that were not at least measured were collected on a running tally.

The Study Area

One of us has described the distribution of *S. attenuata* in the eastern tropical Pacific (Perrin 1975). The known occurrence of mixed aggregations of cetaceans and tuna is strongly correlated with certain oceanographic conditions peculiar to that region. The porpoise-tuna association is known only in the eastern tropical portion of the Pacific. That area, which has been called the North Pacific Equatorial water mass (Seckel 1972), has an unusual oxygen-salinity-temperature structure. The reason for this is not

---

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

fully understood but certainly has to do with the latitude of the area, its position relative to the rest of the Pacific and to the American continents, and the shapes of the adjacent land masses. These factors interact with general global oceanic and atmospheric circulation to produce a water mass with relatively high surface temperature, low surface salinity, a strongly developed, shallow thermocline (usually within 100 m of the surface), and a pronounced, thick oxygen minimum layer just below the thermocline. The effect is to create a very extensive but shallow warm habitat with a sharp oxythermal floor. To the west, these conditions tail off along a divergence centered on lat. 10°N (Wyrtki 1964). The conditions must be causally interrelated, but one of the more striking correlations with the occurence of the mixed-species aggregation is in the thickness of the oxygen minimum layer (Figure 1).

The occurrence of the aggregation is not tightly correlated with the geographic distributions of the major prey species of the participating predators. Major shared prey items are the ommastrephid squid *Dosidicus gigas,* an unidentified ommastrephid (probably *Symplectoteuthis* sp.), a scombrid fish *Auxis* sp. (*A. thazard* or *A. rochei*), and the exocoetid fish *Oxyporhamphus micropterus* (Perrin et al. 1973). *Dosidicus gigas* is primarily equatorial but migrates sporadically as far as California and southern Chile, far beyond the limits of the distribution of the mixed-species aggregation (Clarke 1966; Young 1972). Species of *Symplectoteuthis* occur widely in the tropical Pacific and Indian oceans (Clarke 1966). *Auxis thazard* occurs in "tropical and subtropical waters of the Indo-Pacific and Atlantic oceans," and *A. rochei* in "tropical and subtropical waters of the Indo-Pacific and Atlantic oceans, including the Mediterranean Sea" (Richards and Klawe 1972). The genus *Oxyporhamphus* is also pantropical (Bruun 1935). At least some of the several myctophid fishes in the aggregate apparently are a mainstay of the diet of the spinner porpoise in mixed schools (Perrin et al. 1973) and are not restricted to the tropics but occur also in temperate waters of the eastern Pacific (Moser and Ahlstrom 1970) and elsewhere. These facts, combined with the pantropical distributions of the cetaceans, tunas, and birds, suggest that the multispecies aggregation does not have its roots in the distribution of the component species or their prey but rather in the peculiarities of the physical oceanography of the region.

The Sample

In 1971 and early 1972, when more specimens were decked than could be processed in the time available (the limit per net set was usually about 35 to 40 specimens), adult females were selected for measuring and dissection. The intention was to insure that sample sizes would be large enough to allow estimation of pregnancy rate with adequate precision. The information on age structure of the catch for that period is limited to the coloration phase data. The observer program subsequently expanded, and beginning in October 1972 no selection was practiced in determining which animals were to be dissected; the first 35 to 40 specimens of both sexes and all ages that came to hand were set aside for measuring and dissection and the remainder discarded. The length data for 1968 and for October 1972-December 1973 are presumably cross-sectional with respect to the kill.

The sample of animals at least measured included 3,504 postnatal animals and associated fetuses from known localities and 23 from imprecisely known localities (Figure 2). Coloration phase and sex data were collected for another 6,150 specimens. In addition, some data were available for 45 other specimens collected by other research agencies, museums, and private individuals. Because of the seasonal nature of the tuna fishery, the sample is heavily biased toward the early months of the year, with minimal coverage of the latter part of the year and practically no specimens from the summer months (Table 1).

Two races of *S. attenuata* exist in the eastern tropical Pacific — a large coastal form and a small offshore form (Perrin 1975, in press). This paper deals only with the offshore form. The estimates of life history parameters cannot be assumed to apply also to the coastal form.

TABLE 1.—Samples of postnatal spotted porpoise by month for all years.

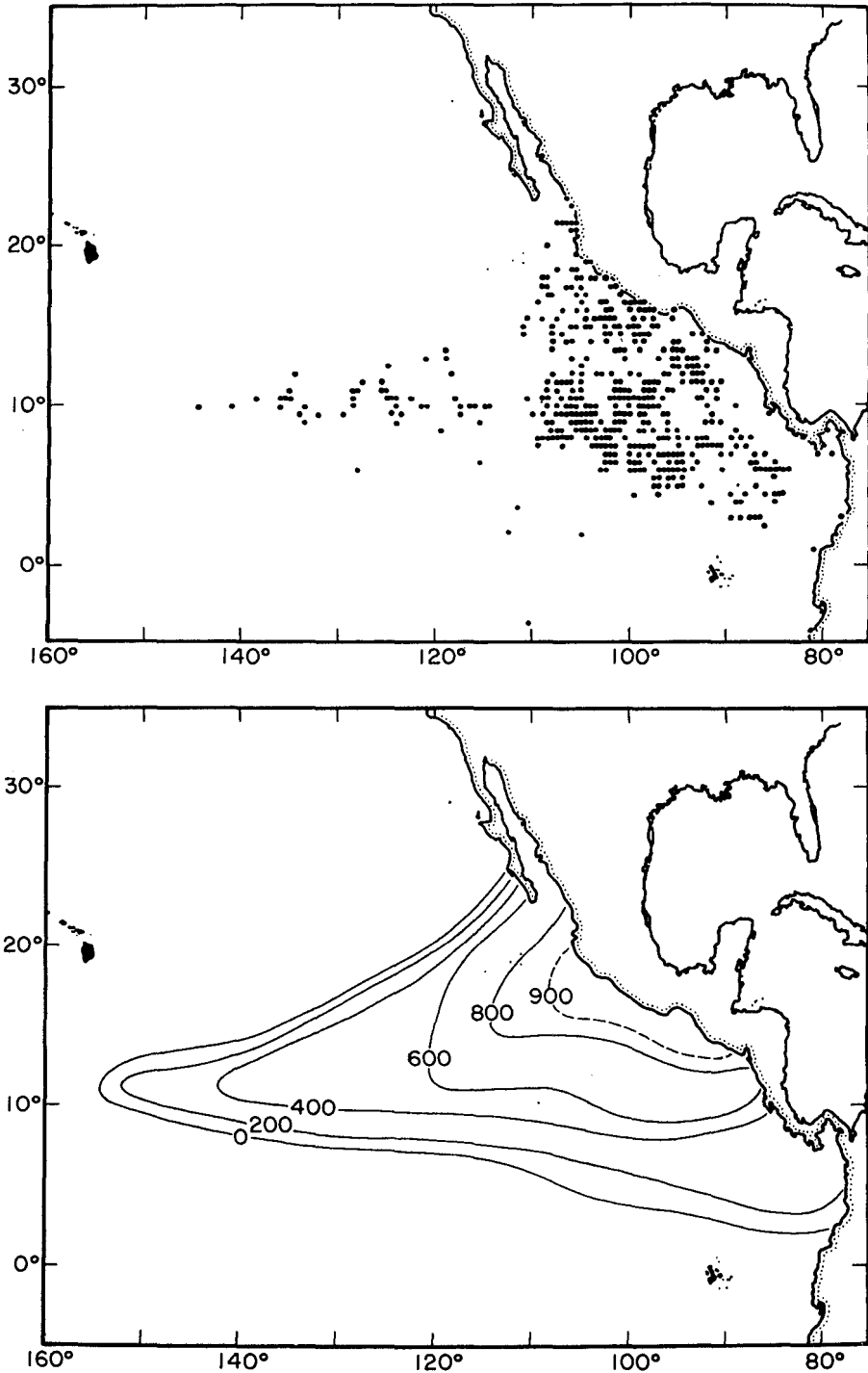| Month	Males	Females	Total
January	748	443	1,191
February	263	209	472
March	298	147	445
April	216	155	371
May	181	97	278
June	69	58	127
July	1	0	1
August	6	5	11
September	0	0	0
October	222	158	380
November	110	87	197
December	30	24	54
Total	2,144	1,383	3,527

FIGURE 1.—Comparison of the known occurrence of spotted porpoise in the eastern Pacific (above) with average thickness of the subsurface layer of water (contours in meters) in which the dissolved oxygen is less than 0.25 ml/liter (below, after Knauss 1963). The entire layer lies above 1,000 m.
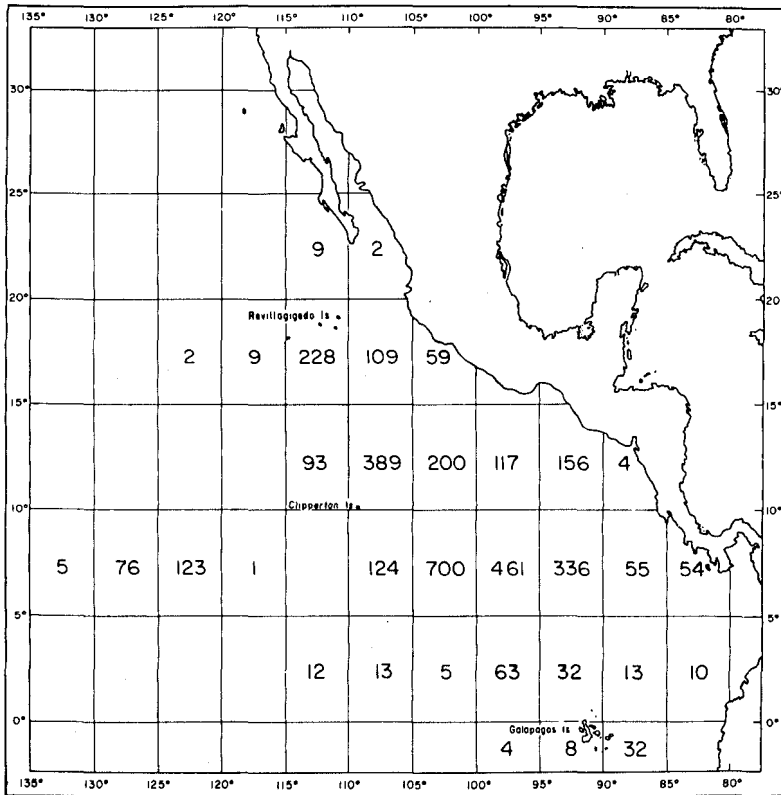
FIGURE 2.—Samples of spotted porpoise used in life history studies by 5° square. Does not include specimens that were not at least measured.

Because the field program is a continuing one, the sample sizes for the various analyses were different and depended on how much material was available at the time each analysis commenced. Restrictions on sample size are set out in the text below.

Laboratory Procedures

Fetuses were measured with dial calipers or with calipers mounted on a 1-m stick. Postnatal animals were weighed to the nearest pound on platform scales. Fetuses were weighed to the nearest gram on a triple beam balance. Testes were weighed to the nearest gram on a platform balance. A 1-cm^3 cube from the center of each testis[5] and a similarly sized sample of the epididymis from midlength of the testis were sectioned and stained with hematoxylin and eosin.

The mounted sections were subsequently examined under a compound microscope.

Ovaries were weighed to the nearest 0.1 g on a platform balance. They were then cut into transverse sections approximately 1 mm thick with a scalpel and the sections examined under a dissecting microscope. The corpora albicantia in each ovary were scored to eight categories based on size, color, vascularization, and gross appearance (categories described below). If a corpus luteum was present, it was measured with dial calipers to the nearest millimeter in its three largest dimensions. The diameter of the largest follicle was measured to the nearest 0.1 mm.

Age was estimated for 442 animals by examination of dentinal layers in the teeth. Three or four teeth were extracted from the lower right tooth row at approximately midlength and mounted on wooden blocks in dental wax or plastic resin. A longitudinal section 0.012 inch (0.31 mm) thick was cut from each tooth with a diamond saw. The sections were cleared for several days in a 1:1 mixture of glycerine and 95% ethanol, mounted under cover slips in balsam, and examined with transmitted light under a

---

[5]Some early samples were taken near the dorsal surface of the testis. Tubule diameter in these was subsequently found not to differ relative to length, weight, and age of the animal from that in those taken at the center of the testis, and the lots were therefore combined for analysis.

compound microscope at approximately 30 diameters. One postnatal layer was considered to consist of an opaque subunit and a translucent subunit (Figure 3). The layers in most of the teeth examined were not as well-defined or as regular in thickness as those illustrated by Kasuya (1972) for *Stenella coeruleoalba* or by Klevezal' and Kleinenberg (1969) for *Delphinus delphis*. Teeth from 39 of the 442 animals were completely unscorable, being heavily worn or showing no discrete layers in the sections examined. All the teeth were scored several times, over a period of several months, without referring to specimen numbers or to values obtained previously, until the scorer felt confident of the results. The values used in the analyses are those obtained in the final round of scoring. The teeth were scored to the nearest postnatal layer when possible, or a range, e.g., "8 to 10 layers," was estimated. Average accuracy is estimated at ±1 layer for teeth with 5 layers or less and ±2 layers for teeth with 5 to 12 layers. Convoluted secondary dentine was present in most of the teeth with more than 12 layers, making counts very difficult and of dubious reliability. We feel that the counts for many of these teeth are probably underestimates. Teeth in which the pulp cavity was entirely closed in all sections examined were scored as "occluded."

The NORMSEP computer program was used to define modes in the length-frequency distributions for fetuses. The program was written by Hasselblad (1966) and modified by Patrick K. Tomlinson, Inter-American Tropical Tuna Commission. The program separates the mixture of normal length distribution into its components, assuming that the lengths of individuals within age groups are normally distributed and that an unbiased sample of the length distribution was obtained.

GROWTH

Length at Birth

Average length at birth of 82.5 cm was obtained from a linear regression line based on 3-cm groupings of fetuses and neonatals (Figure 4). The largest fetus of the 461 examined was 904 mm long. The smallest neonatal animal was 780 mm long. Eighty-six calves and fetuses between 73 and 94 cm were measured in random samples. Assumptions inherent in the method used to arrive at this estimate are that pregnant females and

calves are 1) equally vulnerable to capture in the purse seine, 2) equally likely to die once captured, and 3) equally represented in the sample of dead animals measured. For example, if neonates were less likely to be included in the samples than were pregnant females, average length at birth would be overestimated. Other potential sources of error are differential rates of prenatal and postnatal natural mortality and premature births caused by stresses imposed by pursuit and by capture in the purse seine.

Gestation Period and Fetal Growth

The most commonly used method for estimating the gestation time of cetaceans is that of Huggett and Widdas (1951). They showed that for a variety of mammals of widely different orders, a plot of the cube root of fetal weight on age is linear except during the first part of pregnancy, when growth is exponential. Their model can be expressed in the general formula $W^{1/3} = a(t - t_0)$, where W = weight, t = age, a = the "Specific Fetal Growth Velocity," and t_0 = "the intercept where the linear part of the plot, if produced backwards, cuts the time axis." Laws (1959) applied the method of Huggett and Widdas to fetal length/time data for three odontocetes (*Physeter catodon*, *Delphinapterus leucas*, and *Phocoena phocoena*) and obtained estimates of gestation periods (15, 14, and 11 mo, respectively). He assumed that weight is proportional to the cube of length and used the form $L = a(t_g - t_0)$, where L = length. This assumption is not entirely correct (see length-weight results below), but is a close enough approximation of the real relationship between length and weight to allow its use in estimating gestation period. Laws' estimates corresponded closely with other estimates obtained by more direct methods. Laws' version of Huggett and Widdas' method is used here.

A gestation period of 11.5 mo was obtained from an analysis based on 281 fetal and postpartum specimens collected in January, February, March, April, May, and October 1972 (Figure 5). The January-May samples comprised all of the fetuses of all of the females examined. The postpartum samples in these months were not random and are therefore not included. The October samples were random over all age-classes in the catch; therefore, all specimens less than 160 cm long, approximately the length at onset of puberty (Harrison et al. 1972), are included in the plot. Obvious modes are present in the length distributions (seasonal-
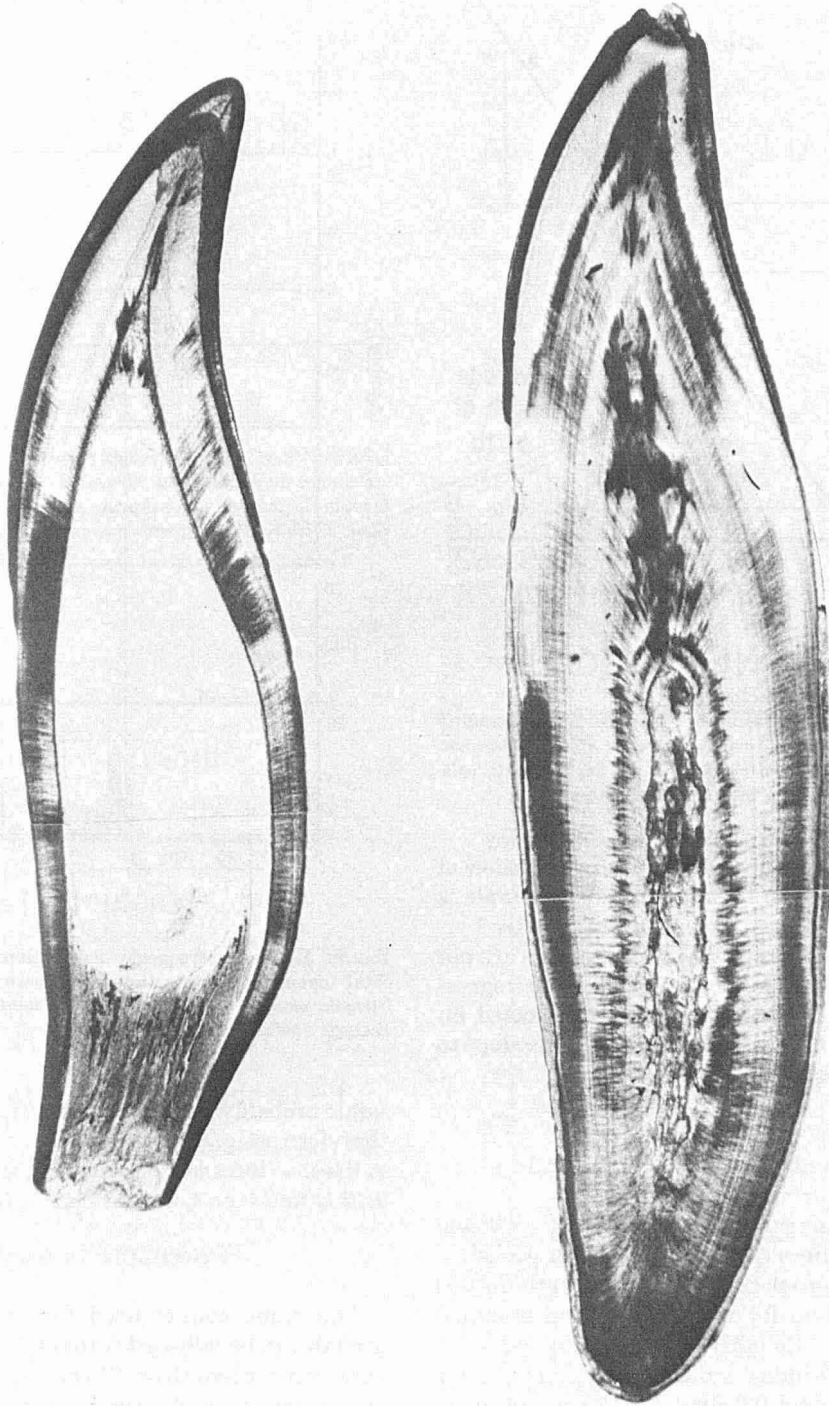
FIGURE 3.—Longitudinal thin sections of teeth from two specimens of *Stenella attenuata* from the offshore eastern tropical Pacific. (Left) field number CV300 male, 144 cm, with two postnatal dentinal layers; (right) number LR55 female, 191 cm, with 13 layers.
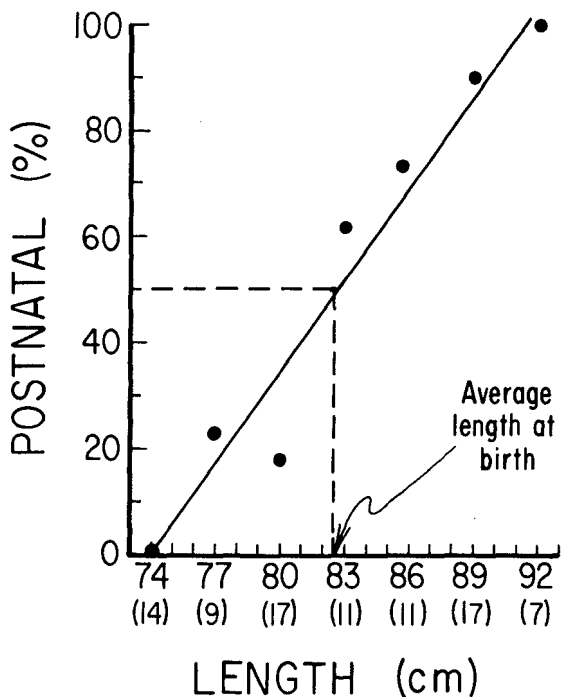
FIGURE 4.—Linear regression analysis of percent postnatality on body length for 86 fetuses and calves of *Stenella attenuata* from the offshore eastern Pacific grouped in 3-cm intervals. Sample size for each 3-cm interval in parentheses.
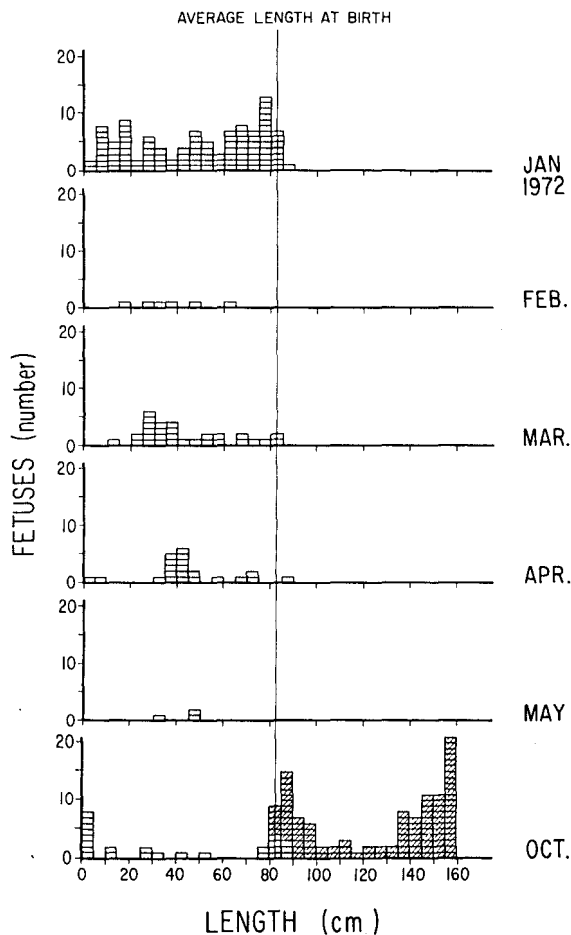

FIGURE 5.—Length-frequency distributions by month for 281 fetal (open) and young (hatched) postnatal specimens of *Stenella attenuata* captured by tuna seiners in the offshore eastern tropical Pacific in 1972.

ity is discussed below). Apparent progression of the smaller mode in the January 1972 sample is consistent with a gestation period of roughly 1 yr. Sample sizes for the other apparent modes are not large enough for similar analysis. Linear regression analysis of the modal lengths plotted on month (Figure 6) yields an estimate of the slope to use in Laws' equation:

$$L = 8.283 \, (t - t_0), \text{ or}$$
$$\text{length at birth} = 8.283 \, (t_g - t_0)$$

with $(t_g - t_0)$ (using months of 30.4 days) = 9.96 mo or 303 days, where t_g = total gestation period.

Laws (1959) proposed that t_0 for length data is slightly less than for weight data and assumed $t_{0_{Ln}} = 0.9 \, t_{0_{wt}}$. Roughly interpolating between Huggett and Widdas' values for $t_{0_{wt}}/t_g$ of 0.1 for $t_g > 400$ days and 0.2 for $t_g = 100$ to 400 days (using provisional $t_g \cong 330$ days to enter the iteration) (Figure 7) and applying Laws' correction, $t_{0_{Ln}}$ of $\cong 0.135 \, t_g$ is obtained. This value yields an estimate of gestation time of 11.5 mo (349 days). The estimate of t_0 (47 days) is crude, but the true

value probably lies between $0.12 \, t_g$ and $0.15 \, t_g$. We therefore estimate the gestation period to be 11.5 ± 0.2 mo (interval between estimates using $t_0 = 0.12 \, t_g$ and $0.15 \, t_g$), or 11.3 to 11.7 mo.

Postnatal Growth

The same cohort used for analysis of fetal growth can be followed through the samples until approximate length of 125 cm (Figure 8) at the age of approximately 8.5 mo. In order to optimize resolution, 4-cm intervals were used, and the samples for April, May, and June were combined. Modes were estimated with NORMSEP.

A linear regression line through the modal lengths yields the postnatal growth equation
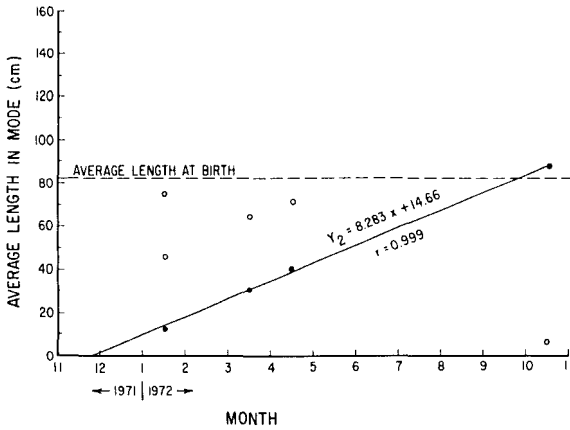
FIGURE 6.—Linear regression analysis of modal lengths of fetal and neonatal specimens of *Stenella attenuata* (from Figure 4). Open circles are modes not included in the analysis. Modal lengths defined with computer program NORMSEP (see Materials and Methods).
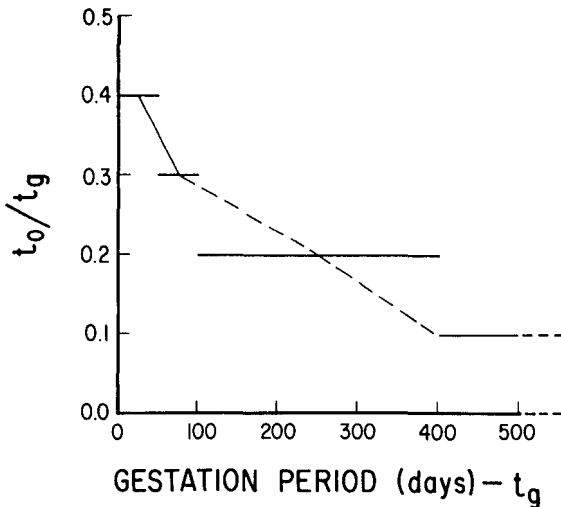

FIGURE 7.—Ratio t_0/t_g interpolated between empirical estimates of Huggett and Widdas (1951)—"...for gestation times up to 50 days $t_0 \hat{=} 0.4 \times$ (gestation time), from 50-100 days $t_0 \hat{=} 0.3 \times$ (gestation time), from 100-400 days $t_0 \hat{=} 0.2 \times$ (gestation time), over 400 days $t_0 \hat{=} 0.1 \times$ (gestation time)."

$$L = 82.5 + 5.42\,t,$$

where L = length in centimeters
t = postnatal age in months.

Analysis Based on Analogy with Other Cetaceans

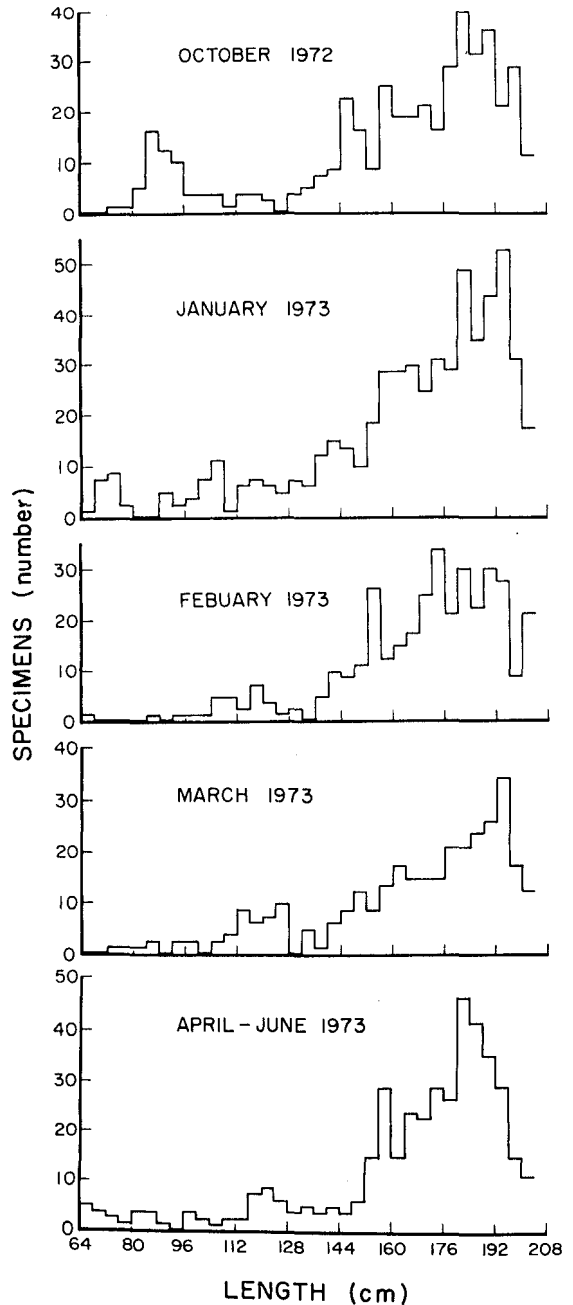Fetal growth in length of cetaceans, except for

FIGURE 8.—Length frequencies of fetuses and postnatal specimens of *Stenella attenuata* between 64 and 204 cm long, of both sexes, by month.

an initial slow phase (t_0), is nearly linear. Postnatal growth during at least a period equivalent in length to the gestation period is also nearly linear, but at a lower rate. The difference between the
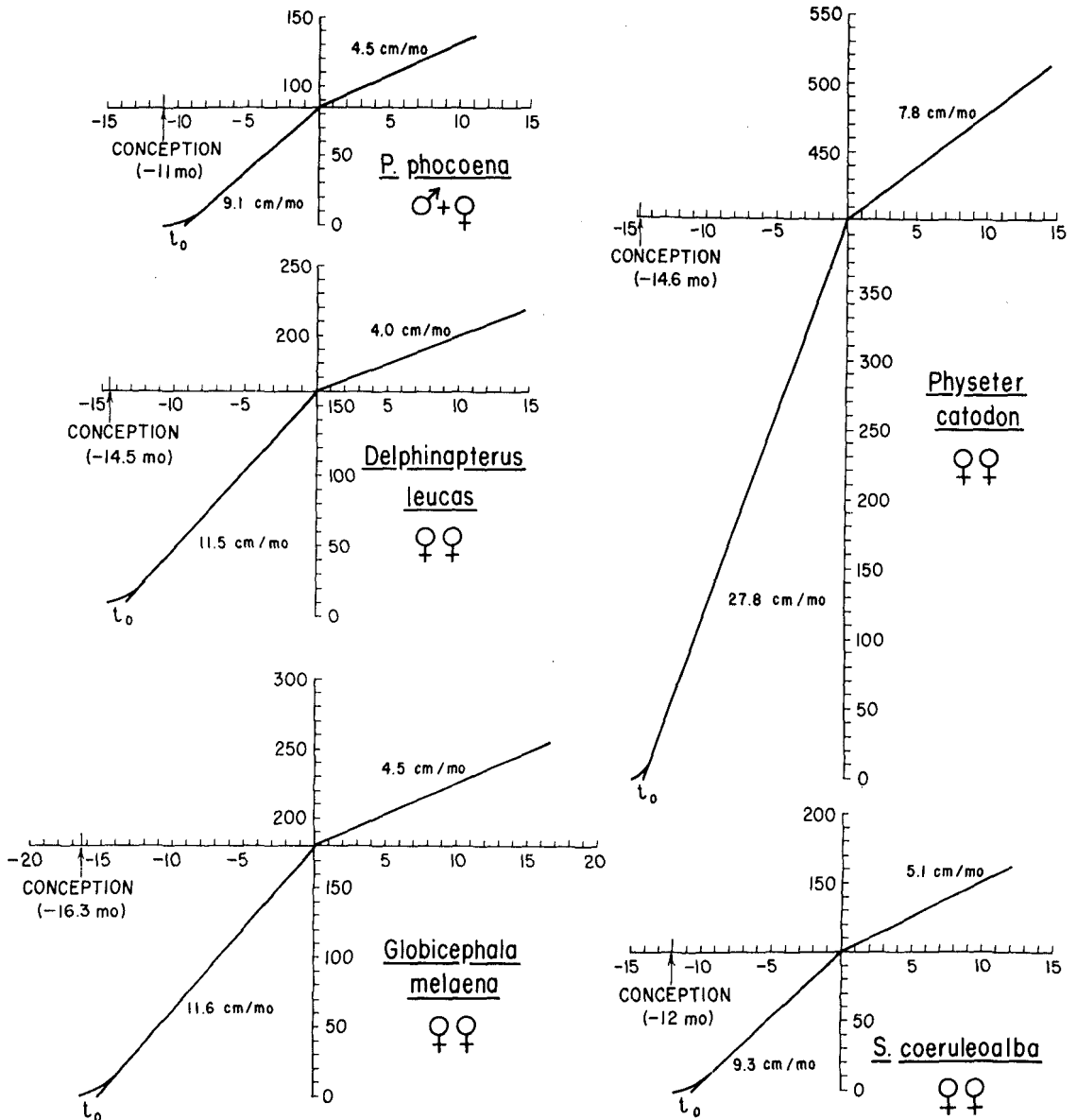
237

FIGURE 9.—Fetal growth and average postnatal growth during a period equal to the gestation period in five odontocete cetaceans: *Phocoena phocoena* (gestation period and postnatal growth from Møhl-Hansen 1954; t_0 from Laws 1959; length at birth from Fisher and Harrison 1970); *Delphinapterus leucas* (from Brodie 1971); *Globicephala melaena* (from Sergeant 1962); *Physeter catodon* (from Best 1968, 1970); and *Stenella coeruleoalba* (from Kasuya 1972).

fetal rate and the average rate during a postnatal period equal to the gestation period differs among the five odontocete species for which sufficient data exist (Figure 9) and is correlated with length at birth (Figure 10). The least-squares line for log of the difference between fetal and postnatal

growth rates (Y) on log of length at birth (X) yields $Y = -1.33 + 0.997X$, from which a predicted Y of 3.75 cm/mo is estimated for *S. attenuata* and an average growth rate in the first year of 4.66 cm/mo is estimated. This average rate is close to those for the other three delphinids (5.1 for *S. coeruleoalba*,
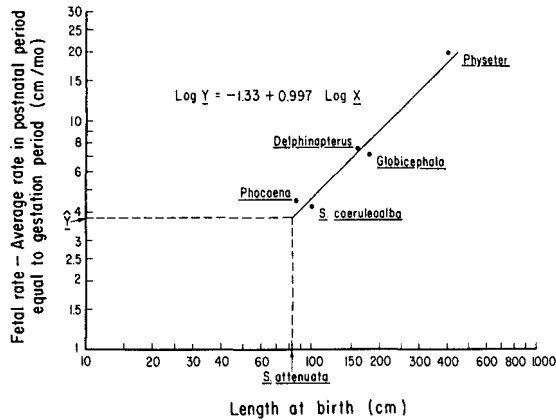
FIGURE 10.—Relationship of difference between fetal growth rate during linear phase and average growth rate during postnatal period equal to gestation period to length at birth in five odontocete cetaceans. Line is linear regression line of log difference on log length. Data from Figure 11. $\hat{Y}$ is predicted difference for *Stenella attenuata* from the offshore eastern tropical Pacific.

4.5 for *Globicephala*, and 4.5 for *P. phocoena*)[6]; and yields a predicted length at 1 yr of 138 cm.

Length Relative to Tooth Layers

Total length was plotted on number of postnatal layers for 115 males and 306 females (Figure 11). The teeth of five males and three females had completely filled pulp cavities. These are included in the plots in a separate category "occluded."

The plots of means for 2-layer intervals (the points in Figure 12; the curves were fitted as explained below) very closely resemble the growth curve obtained by Sergeant (1962) for *Globicephala*. Asymptotic length (L_∞) for females is approximately 190 cm and for males approximately 200 cm. There appears to be a secondary surge in growth at about 6 layers. With the restriction that the curves must pass through birth length of 82.5 cm and asymptotic lengths of 190 and 200 cm, it is not possible to fit any continuous equation to the data satisfactorily. Continuous curves that fit well at the upper and lower ranges of layer count seriously underestimate length at 5

---

[6]Fisher and Harrison (1970) stated that their data suggest that *Phocoena* in Canadian waters grows approximately 30 cm during the first year of life, or at an average rate of about 2.5 cm/mo, as opposed to the 4.5 cm/mo hypothesized by Møhl-Hansen (1954). However, they also suggested, and their figure 2 showed, an average rate of at least 5 cm/mo during the first 4 mo. It seems unlikely that the rate would drop to an average of ~ 1.25 cm/mo in the remaining 8 mo of the first year.

to 7 layers. Kasuya (1972) also encountered difficulty in attempting to fit a continuous model to growth of a delphinid, *S. coeruleoalba*. Good fits can be obtained, however, by assuming a dynamic growth function. A two-phase version of Laird's (1969) growth model was fitted to the 2-cm means for all males and females, using an iterative least-squares method. The occluded specimens were assigned to the 16+ interval.

Laird's model is

$$L(t) = L_0 \exp \left\{ \frac{a}{\alpha} \Big[1 - \exp\left(-\alpha t\right) \Big] \right\},$$

where

$L(t)$	=	length at time t
L_0	=	length at birth (82.5 cm in this case)
t	=	time (layers in this case)
a	=	specific rate of exponential growth
α	=	rate of decay of exponential growth.

This model assumes that an organism's growth pattern is determined at conception. The fitted parameters a and α express the premise that "growth is fundamentally exponential (implied by the normal binary fission of cells), and it also undergoes exponential retardation by some as yet unknown physiological mechanism" (Laird 1969).

In the two-phase approach, separate equations were simultaneously fitted to the upper and lower range of means. The assumptions were made that juvenile growth is the same for males and females (supported by the data) and that the growth discontinuity comes at about the same age for males and females. The only fixed point was 82.5 cm at 0 layers (birth). The convergence point (inflection in the growth curve) was allowed to float to the position that gave the best fit, with males and females considered jointly for lesser ages. The equations converged at 5.59 layers (rounded off to 6 below) at which predicted length is 159.9 cm. The fit is excellent for females (Figures 11, 12). Asymptotic length is 190 cm at predicted age of 18 layers. Average length of adult females (those with ovarian scars) is 187.3 cm, based on a sample of 555 (Perrin 1975). The largest female of 2,138 measured was 220 cm long. The equation for juvenile growth to less than 6 layers is

$$L = 82.5 \exp \left\{ \frac{0.4817}{0.7172} \Big[1 - \exp\left(-0.7172t\right) \Big] \right\},$$

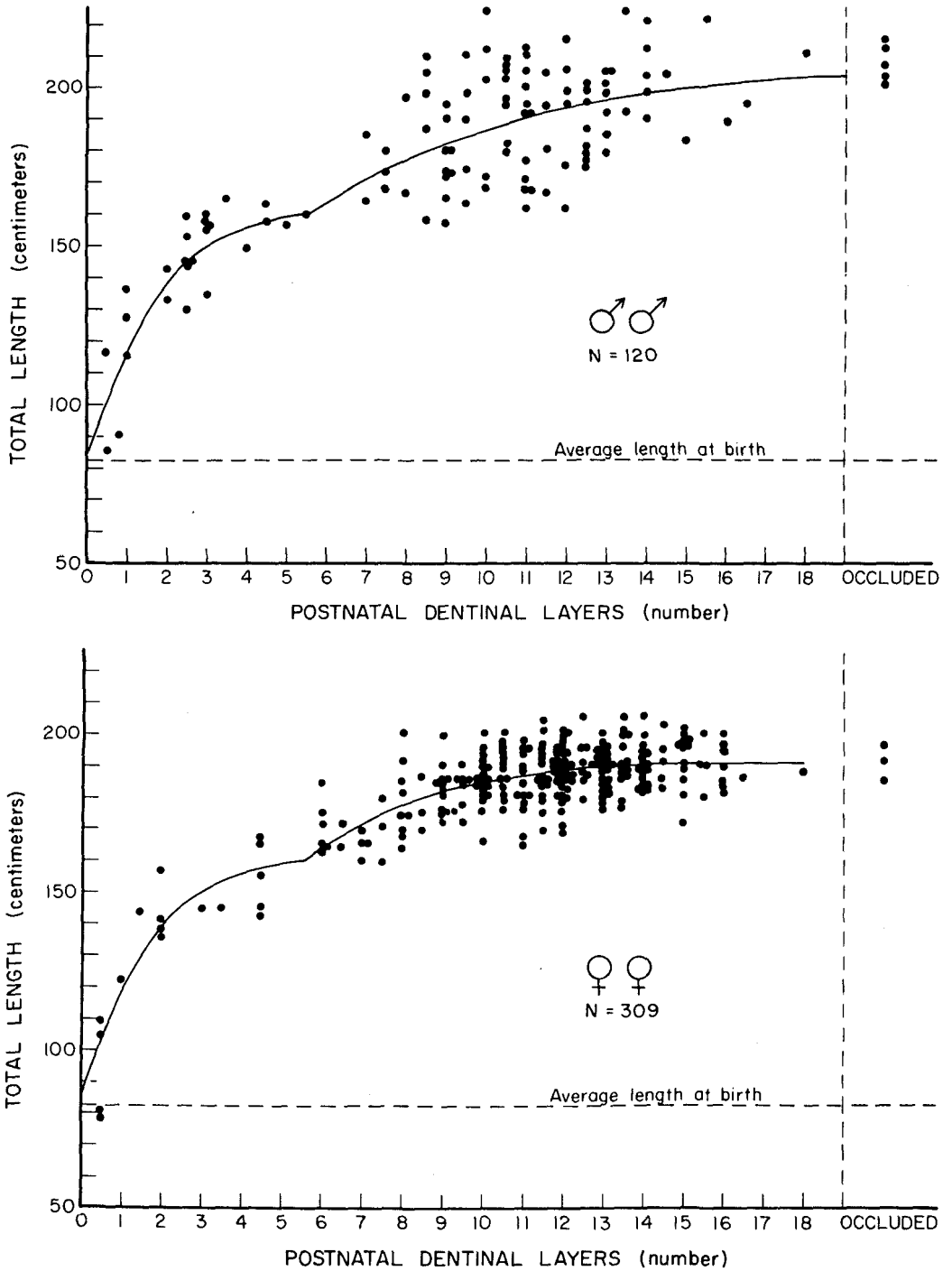where L = length, in centimeters
t = age in layers.

239

FIGURE 11.—Scatterplots of body length on number of postnatal dentinal layers from males (top) and females (bottom) of *Stenella attenuata* from the offshore eastern Pacific. Lines are fit to the growth model (see text).
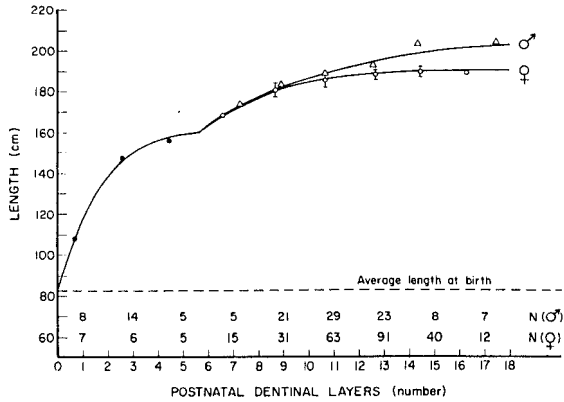
FIGURE 12.—Fit of the double Laird growth model (see text) to 2-cm mean values of body length on number of postnatal dentinal layers for males and females of *Stenella attenuata* from the offshore eastern Pacific. For samples greater than 30, ± standard errors indicated as vertical line.

For females with 6 or more layers, the growth equation is

$$L = 159 \exp \left\{ \frac{0.0657}{0.3707} \left[1 - \exp(-0.3707(t - 5.588)) \right] \right\}.$$

In this case, both the growth rate and the rate of decay of growth are sharply lower than for juveniles.

The fit for males is not as good (Figures 11, 12) as it is for females, probably due to greater variability and to inadequate sample sizes for the two oldest strata (the tooth-reading effort was concentrated on females because of their importance in population dynamics). Another possible explanation for the relatively poorer fit for males is that growth (real, or as inferred from tooth layers) in adult males is more complex than in adult females, and a model more complex than the Laird model is called for. Inferred asymptotic length is 206 cm, achieved at predicted age of 26 layers. Average length of adult males (defined as those having testes weighing 200 g or more) is 200.7 cm, based on a sample of 253 (Perrin 1975). The largest male of 1,083 measured was 226 cm long. The growth equation for males with 6 or more layers is

$$L = 159.5 \exp \left\{ \frac{0.0524}{0.2032} \left[1 - \exp(-0.2032(t - 5.588)) \right] \right\}.$$

The secondary growth rate (a, 0.0524) is very slightly smaller than for females, but the rate of decay (α, 0.2032) is sharply smaller, reflecting the attainment of greater size in males. The equations rearranged and reduced for estimating age (in terms of layers) from length are

$$t(\text{M and F} < 160 \text{ cm}) = -1.394 \ln (7.531 - 1.48 \ln L)$$

$$t(\text{F} \geqslant 160 \text{ cm}) = 5.588 - 2.698 \ln (29.606 - 5.64 \ln L)$$

$$t(\text{M} \geqslant 160 \text{ cm}) = 5.588 - 4.921 \ln (20.669 - 3.878 \ln L).$$

Note: These equations should not be used to estimate age from length except for grouped samples of smaller animals (about 180 cm or less), for which growth rate is still large compared to individual variation in length.

The juvenile growth curve based on tooth layers can be calibrated for the first year by comparison with the growth curve derived from analysis of modal progression (above) and by deduction from what is known about juvenile growth of other odontocetes (the fetal-postnatal growth argument above). Estimated average length at 8 mo based on analysis of modal progression is 125.5 cm. The predicted number of layers at that length (Figure 12) is 1.53. If the average growth rate during the first year is assumed to be the same as the average during the first 8 mo, the predicted number of layers at 1 yr (1.53 · 12 ÷ 8) is 2.3. This extrapolation, however, is a slight overestimate, because while growth during the first year in delphinids is approximately linear, there is some decay of rate. The predicted number of tooth layers (using Figure 12) at 138 cm, the above-predicted length at 1 yr based on camparison with other odontocetes, is 2.0. It seems safe to assume that about 2 layers are laid down during the first year of life.

Calibration of the remainder of the tooth-layer curve is more difficult. Kasuya et al. (1974) examined the innermost layer in teeth of *S. attenuata* and related type and thickness of layer to season of capture. They concluded that one layer (one transparent plus one opaque subunit) represents 1 yr of growth. We found no correlation between thickness of the innermost layer and season of capture. Almost all of the samples for which teeth were sectioned, however, were collected in the first few months of the year. Lacking such direct calibration, several alternative possibilities can be examined. The results, however,

241

must remain tentative and inconclusive until growth has been monitored directly in one or more captive or free-ranging, tagged individuals.

Some alternatives that can be considered are:

1. Two layers per year until the teeth are occluded.
2. Two layers in the first year and one per year thereafter until the teeth are occluded.
3. Two layers per year until puberty (about nine layers in males and seven in females; see section below on age at puberty), and one per year thereafter.

This list of alternatives can be extended to great length by making assumptions such as that layers are laid down at irregular intervals, males and females lay down layers at different rates, layers disappear with age, etc., but the above are probably the main possibilities that should be considered. All references below to age are in terms of layers, with the above alternative possibilities considered or implied. None of the alternatives can be eliminated with certainty. One tooth layer deposited per year has been inferred for the western Pacific population of *S. attenuata* by Kasuya et al. (1974). One layer per year has also been suggested for other closely related delphinids, including *S. coeruleoalba* (Kasuya 1972) and *Tursiops truncatus* (Sergeant et al. 1973). Two tooth layers per year have been found in *Delphinapterus leucas* (Sergeant 1973), but this form is less closely related to *Stenella*. Thus, there is more support in the literature for the one-layer-per-year model (number 2 above) than for the others.

Length-Weight Relationships

Length-weight relationships were determined for 218 fetuses, 66 postnatal males, and 33 nonpregnant, postnatal females by using linear regressions of log weight on log length.

Fetuses

The fetuses ranged from 20 to 897 mm long and weighed from 2 to 7,588 g. Ten fetuses less than 20 mm long were not included. The regression equation is

$$\log W = 3.5532 + 2.501 \log L,$$

where W = weight in grams
L = length in millimeters.

In exponential form, the relationship is

$$W = 2.79 \times 10^{-4} \ L^{2.501}.$$

Females

The females ranged from 100 to 200 cm and weighed from 12.0 to 69.1 kg. The regression equation is

$$\log W = -4.1576 + 2.6120 \log L,$$

where W = weight in kilograms
L = length in centimeters, or in exponential form, $W = 6.95 \times 10^{-4} \ L^{2.612}$.

Males

The males ranged from 86 to 218 cm and weighed from 6.8 to 90.0 kg. The regression equation is

$$\log W = -4.7135 + 2.873 \log L,$$

where W = weight in kilograms
L = length in centimeters, or in exponential form, $W = 1.93 \times 10^{-5} \ L^{2.873}$.

The slopes of the regression equations are statistically different (*t*-test at $\alpha = 0.05$) for males and females. Males are lighter for their length at birth, and heavier for their length after about 135 cm has been attained.

Color Pattern

Perrin (1970b) has previously described the development of the color pattern of *S. attenuata* in the offshore eastern Pacific. The animal begins life unspotted, develops dark spots ventrally that later coalesce, as light spots develop dorsally. The ontogenetic continuum can be divided into five stages as defined below and as shown in Figures 13 and 14:

1. *Newborn stage.* Dark purplish-gray dorsal surfaces and lateral blazes, with white ventral surfaces and no spots; about 80 to 160 cm.
2. *Two-tone stage.* General two-tone pattern with dark-gray surfaces above, lighter gray lower surfaces, and a well-defined pattern in varying shades of gray about the head and flippers; no spots; about 95 to 175 cm.

The division between this and the previous category is somewhat subjective and arbitrary.

3. *Speckled stage.* Same as two-tone but with discrete, very dark-gray spots on the ventral surfaces; discrete light-gray spots on the upper, darker surfaces present on some animals but lacking on others; about 140 to 190 cm.
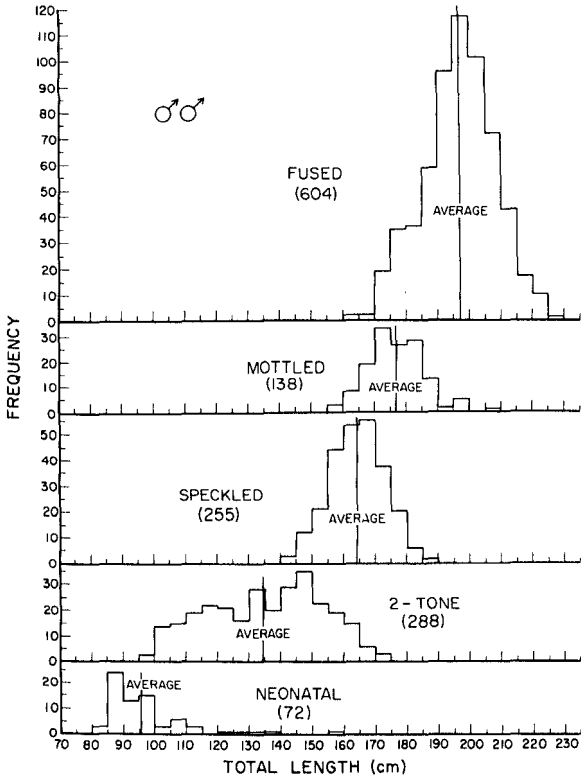

FIGURE 13.—Length-frequency distributions of males of *Stenella attenuata* from the offshore eastern Pacific, by color pattern phase.

4. *Mottled stage.* Ventral spots converging and overlapping in places, but patches of the lighter gray background still visible, yielding a mottled effect; discrete or merging light-gray spots present on the upper surfaces; about 155 to 210 cm.

5. *Fused stage.* Ventral spots completely convergent, to give the effect of a uniform, medium-gray to dark-gray surface; on close inspection, the individual overlapping spots still discernible; about 160 to 230 cm.

REPRODUCTION

Seasonality

Nishiwaki et al. (1965) suggested that *S. attenuata* in Japanese waters breeds in the spring and in the autumn. Harrison et al. (1972) stated that lengths of fetuses indicate that parturition in the eastern tropical Pacific (of *S. graffmani = S. attenuata*) also occurs both in the autumn and in the spring. The postnatal length-frequency data for large samples (Figures 15, 16; April 1968 and October 1972, for example) support the thesis of major reproductive seasons in spring and autumn but also suggest that there is a reproductive peak in summer as well. There is year-to-year variation in the timing of reproductive peaks, and there is some reproduction occurring throughout most of the year. It is difficult to define the reproductive seasons with precision because most of the sampling effort was in the early (January-April) and late (October-December) parts of the calendar year. The sampling intersected obvious calving seasons in April 1968, January 1972, October 1972, January 1973, and June 1973 (Figures 15, 16). Calving peaks were probably also present in some of the other sampling months, but the samples were too small to detect them or were biased in some fashion. A summary of predicted birth dates for 373 fetuses more than 15 cm long collected in 1971, 1972, and 1973, however, indicates that there may have been three calving peaks in each of the 3 yr (Figure 17). In each year there was a definite calving low in winter. The synchrony was diffuse, and some peaks were much sharper than others. The statistical evidence for three annual peaks in calving is weak, and when the data for all years are combined, all that can be said with certainty is that the calving season is prolonged, with a low point in winter and a tendency for high points in spring and fall.

The Male

Sexual development of the male was examined under three criteria: 1) weight of testes, 2) average diameter of seminiferous tubules, and 3) amount of sperm in the epididymis. Each of these was examined relative to total length, weight, and age (number of postnatal dentinal layers).

Weight of the testes (Figure 18) increases precipitously at body length of about 175 to 190 cm,
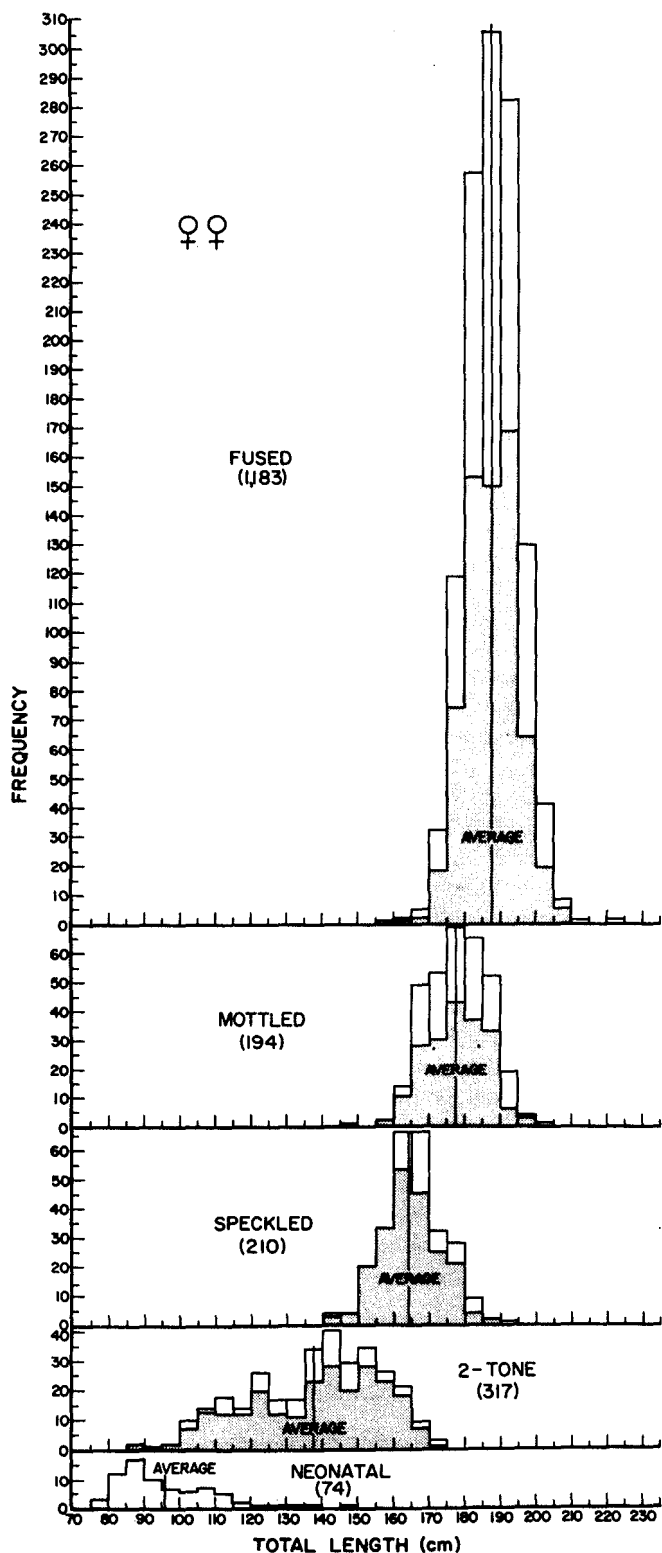
243

FIGURE 14.—Length-frequency distributions of females of *Stenella attenuata* from the offshore eastern Pacific, by color pattern phases. On cruises between January 1971 and October 1972, adult females (≥160 cm) were selected for measuring and dissection. Earlier and later samples were nonselective. Average lengths for neonatal, two-tone, and fused are based on all the samples (no length bias), and averages for speckled and mottled are based on the nonselective samples (shaded). The analyses of coloration transition are based on all the samples for neonatal-to-two-tone and on the nonselective samples for the remaining three transitions. Size of sample used for calculation of average is given in parentheses.
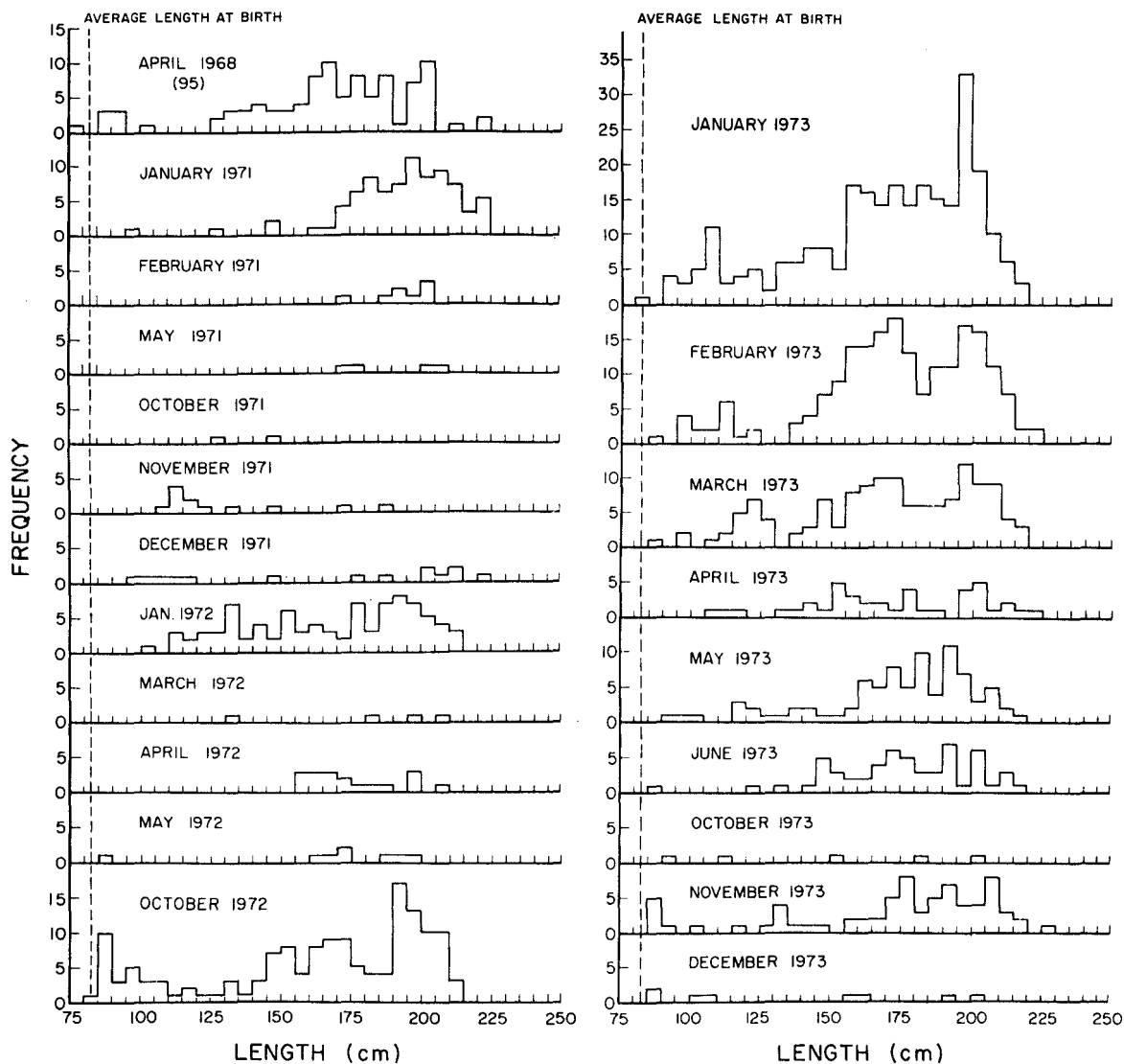
FIGURE 15.—Length-frequency distributions of postnatal male specimens of *Stenella attenuata*, 1968-73, by month.

but in animals larger than about 200 cm, there is little correlation with length. The largest testes encountered weighed 2,400 g and were possessed by a male 196 cm long. However, some males more than 210 cm long had testes weighing less than 300 g. Testes weight begins to increase sharply at 50- to 55-kg body weight and is strongly correlated with weight in larger animals. Males in the sample that weighed more than 70 kg (eight animals) had testes weighing more than a kilogram. The male with the third heaviest testes (2,017 g—heaviest testes for which body weight also available) weighed 80 kg;

the heaviest male in the sample weighed 91 kg and had testes weighing 1,348 g. A rapid increase in testes weight (Figure 19) occurs at age 7 to 13 layers, with maximum size increasing until 12 to 16 layers. All animals with more than 14 layers had testes weighing 500 g or more. Again, there is wide variation in testes size relative to age. Part of the variation is ascribable to the considerable error in the estimate of number of dentinal layers (±2 layers for animals with more than 5 to 12 layers, more for older), but it must be concluded that there is probably about a 5-layer period during which the onset of puberty may
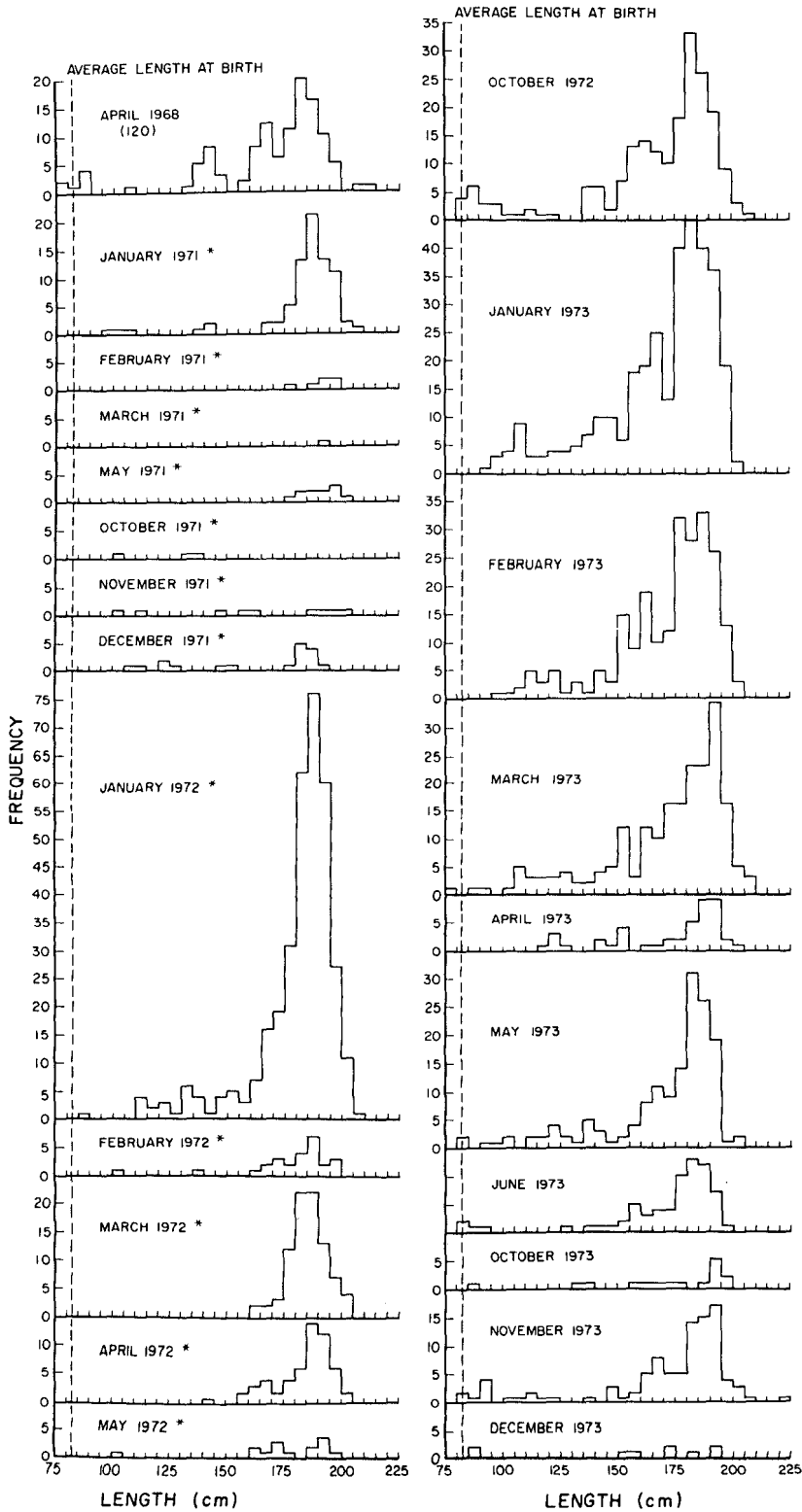
245

FIGURE 16.—Length-frequency distributions of postnatal female specimens of *Stenella attenuata*, 1968-73, by month.

take place (age about 7 to 12 layers) and that about 2 to 4 layers are required to attain "adult"
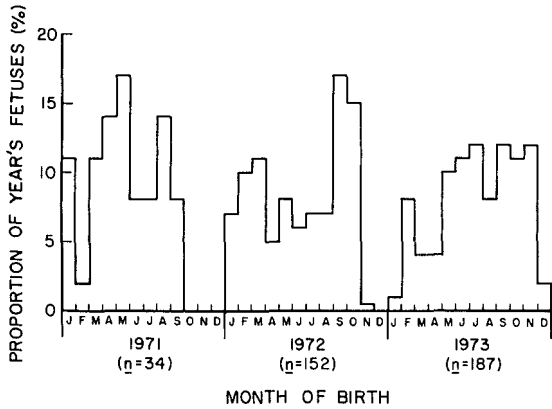

FIGURE 17.—Predicted month of birth for 373 fetuses of *Stenella attenuata*, based on fetal growth curve.

testes size (500 to 2,000 g). The third largest testes were possessed by an animal (202 cm long, 80 kg, discussed above) that had nonreadable teeth that were worn to the gum in all four tooth rows. Such tooth wear may be a correlate of relatively great age.

The diameter of the seminiferous tubules begins to increase rapidly at body length of about 155 to 170 cm (Figure 20), or at lengths about 15 cm shorter than those at which testes weight begins to increase. Tubule diameter is definitely correlated with body length until at least about 200 cm. The heaviest male (91 kg) had the largest tubules. The plot of tubule diameter on layers (Figure 21) indicates that the tubules enter a rapid development stage at 6 to 11 layers, before the onset of a rapid increase in testes weight (Figure 19). Asymptotic diameter is about $170 \mu m$ and appears to be attained by 10 to 14 layers.
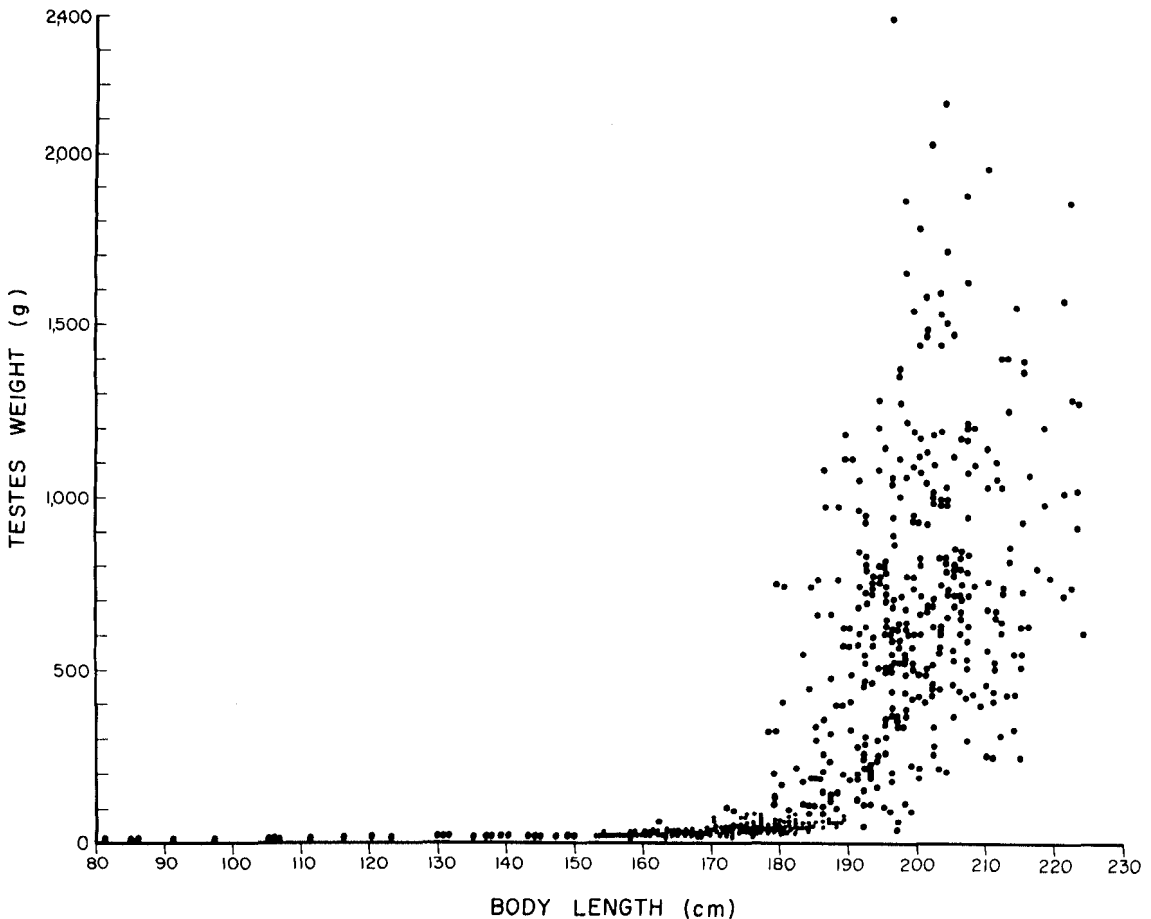

FIGURE 18.—Scatterplot of testes weight on body length in *Stenella attenuata*.
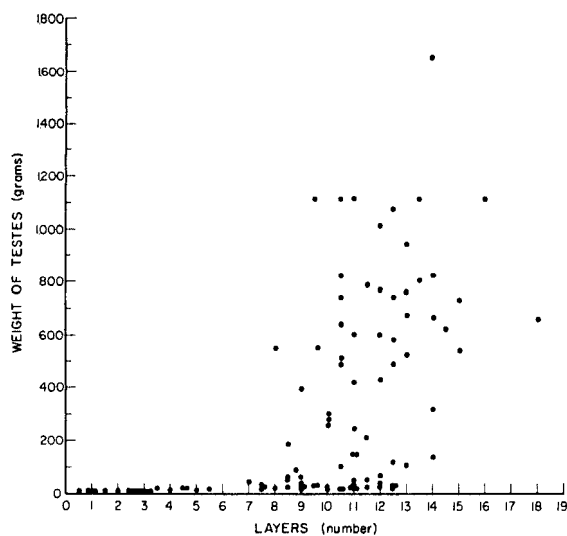
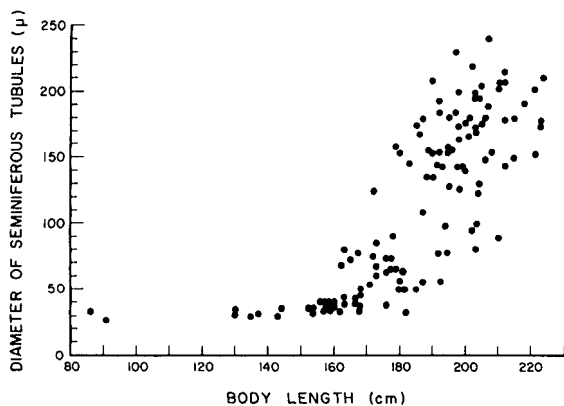FIGURE 19.—Scatterplot of testes weight on number of postnatal dentinal layers in *Stenella attenuata*.

FIGURE 20.—Scatterplot of average diameter of seminiferous tubules on body length in *Stenella attenuata*.
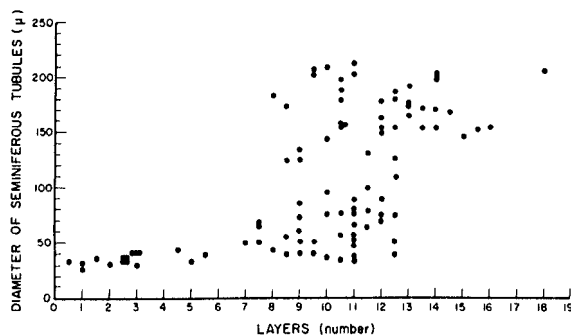

FIGURE 21.—Scatterplot of average diameter of seminiferous tubules on number of postnatal dentinal layers in *Stenella attenuata*.

Sperm in the epididymis were scored as "absent," "present in small numbers," or "copious" (easily seen in the histological sample without searching). The shortest individual with large numbers of sperm in the epididymis was 179 cm long. This animal weighed 62 kg. In animals larger than 180 cm and heavier than 58 kg, presence or absence of sperm in the epididymis bears little relationship to total length. Thirty-six large adults (>200 cm) were equally distributed among the three categories of no sperm, some sperm, and copious sperm.

The smallest testes bearing epididymis with sperm weighed 200 g, and the smallest testes with copious sperm weighed about twice as much. Some animals with testes heavier than 1.5 kg, however, had no sperm in the epididymis. The same pattern of wide variation is apparent in the relationship between epididymis code and layers. The youngest male with sperm in the epididymis had 9 layers. The youngest animal with copious sperm had 10 layers. After about 10 layers, there appears to be no relationship between age and presence or absence of large numbers of sperm.

In summary, the onset of puberty, as indicated by a rapid increase in diameter of seminiferous tubules and increase in testes weight, is at 7 to 12 layers (average ~9 layers; an estimate of ages at puberty) and at lengths of 155 to 170 cm and weights of 40 to 50 kg. Sexual maturity is attained about 2 to 4 layers later, at 10 to 14 layers, ≥180 cm, and ≥58 kg. The midpoint of the range of 10 to 14 layers, or 12 layers, may be taken as an approximation of average age at attainment of sexual maturity. Whether or not males at this point are "socially mature" (sense of Best 1969) can be determined only through behavioral studies. Average length of males 12 layers old is about 195 cm, and average weight is about 75 kg.

The Female

Attainment of Sexual Maturity

Harrison et al. (1972) described and figured the ovaries of *S. attenuata* (as *S. graffmani*). The ovaries weigh less than 0.5 g each at birth. Weight increases gradually to about 1.5 g at about age 6 to 8 layers (average ~7 layers; an estimate of age at puberty), when there is a sudden increase in average ovary size and weight due to presence of corpora of ovulation and/or pregnancy (Figure 22). This change comes at an
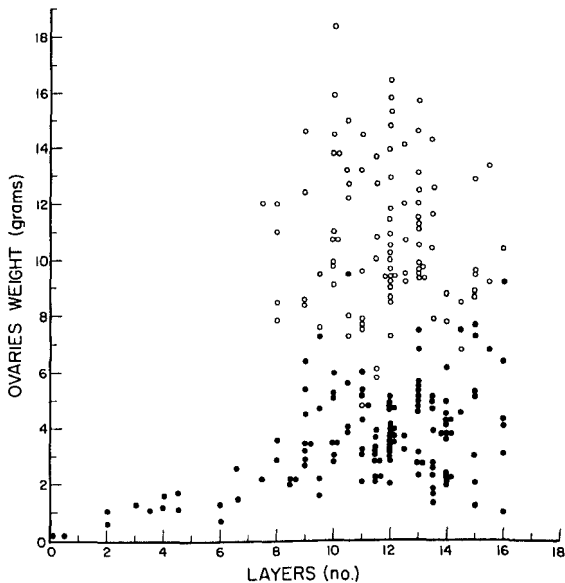
FIGURE 22.—Relationship between weight of ovaries and number of postnatal dentinal layers in *Stenella attenuata*. Open dots are females with a corpus luteum.

average total length of about 170 to 180 cm and weight of 50 to 60 kg (Figure 23).

Analysis of lengths of females with and without ovarian scars yields a more precise estimate of length at attainment of sexual maturity. The smallest of 1,410 specimens (160 cm long or longer) that possessed scars were two that were 167 cm long (one with a corpus luteum only and one with a corpus luteum and four corpora albicantia). The largest female with no scars was 193 cm long. The length-maturity curve is slightly asymmetrical, but a linear regression line through the nearly linear central portion ($M = 5.76L - 960.95$) estimates that average length at which scarring is first evident is 175.4 cm. This analysis probably underestimates length at attainment of maturity, because some of the small adults (170 to 180 cm) with many scars are those that have stopped growing at a shorter-than-average length. In other words, the left-hand portion of the frequency distribution of physically mature adults to an unknown extent artificially elevates the central portion of the length-maturity curve, making it asymmetrical.

An estimate of age and length at attainment of sexual maturity can also be derived directly from the smaller sample of females for which the number of tooth layers was determined. The youngest specimen exhibiting ovarian scarring

had 7.5 layers. The oldest with no scarring had 12 layers. The estimated age at which 50% have scars is 9.14 layers ($M = 19.5t - 128.25$). Predicted length at this age is 181.6 cm (based on growth equation above). This estimate is less biased than the others above but based on much smaller samples, especially at the lower end of the layer-maturity curve.

Another estimate of length and age at first ovulation can be made by back extrapolation of a relationship between body length and number of corpora (including corpora lutea) in the ovaries (Figure 24). Length increases with corpora count until at least six to eight corpora have been accumulated, at about 183 to 190 cm. A fit of the data to the Laird growth model (above) yields the equation

$$L = 180.17 \text{ cm} \exp\{0.0541[1 - \exp(-0.2815C)]\},$$

where L = length in centimeters
C = number of corpora.

Back extrapolation of the curve to zero corpora yields an estimate of 180.2 cm. Predicted age from the growth equation is 8.74 layers.

An estimate of length at first conception can be made by calculating the average length of pregnant females with a corpus luteum only (indicating first pregnancy) and subtracting the growth that they can be assumed to have undergone during pregnancy. Fifty-four primiparous females averaged 181.7 cm in length (range 167 to 193 cm). Predicted age at that length is 9.17 layers. The average length of their fetuses was 372 mm. This length is attained by about the beginning of the sixth month of gestation. Using the growth equations above to predict growth during 6 mo for the various tooth-layering models and substracting the growth increment from 181.7 cm yields estimates of length at first conception ranging from 177.7 to 180.0 cm (number 4 in Table 2). The primiparous females in this sample, however, are only those that became pregnant at the first ovulation. This may cause the estimate to be an underestimate, because many females ovulate several times, and presumably continue to grow, before becoming pregnant the first time (see Ovarian Changes below).

The various methods of estimating age and length at attainment of sexual maturity yield estimates of varying accuracy (Table 2). The estimates based on tooth layers and length at first
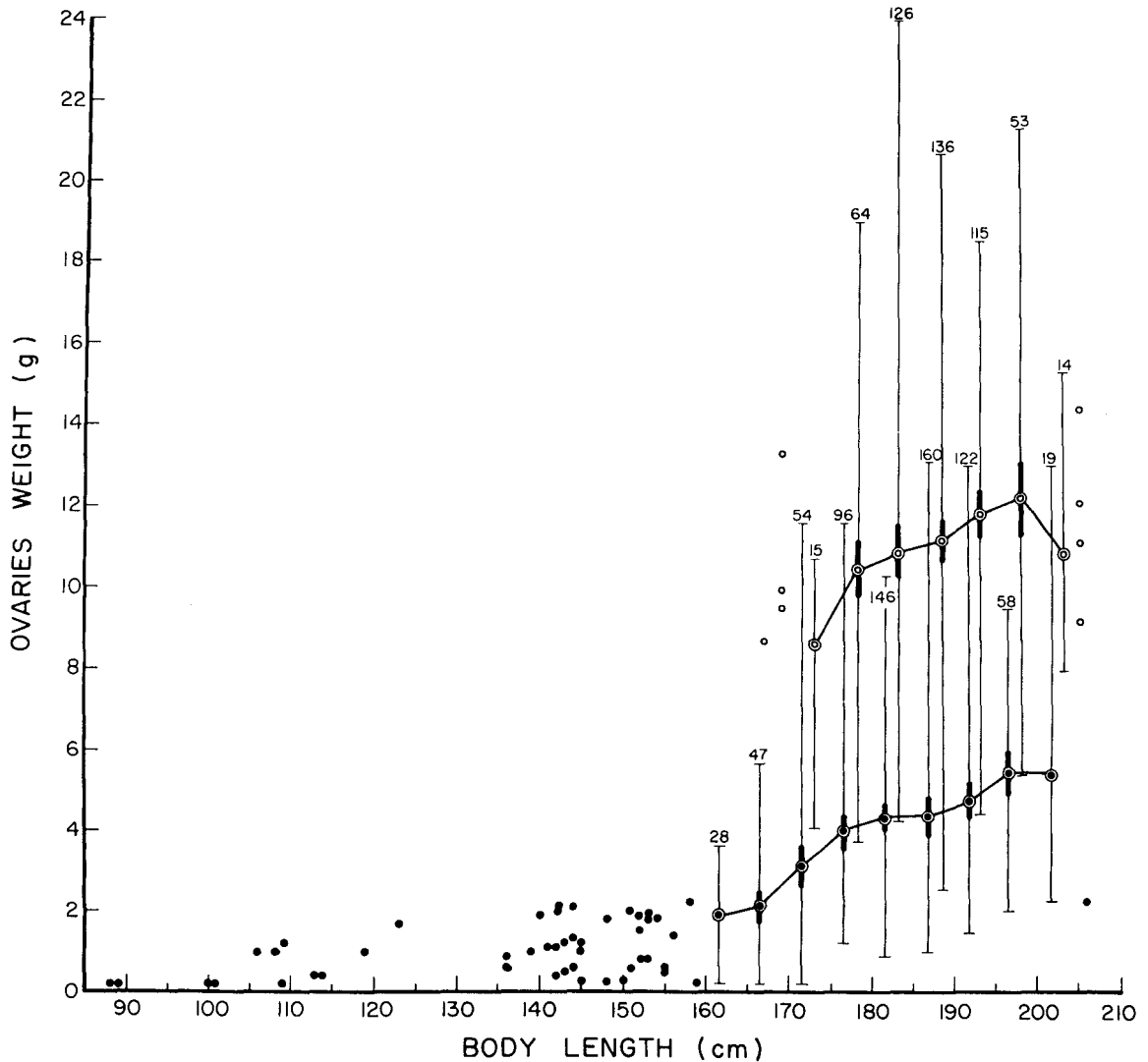
FIGURE 23.—Scatterplot of weight of both ovaries on body length in *Stenella attenuata*. Open dots represent females with a corpus luteum. For animals 160 cm or longer, where sample for 5-cm interval is 10 or more, means (circled symbols) and ranges are graphed and points are not plotted. Where the sample is ≥30, ± two standard errors are indicated by bars.

conception are the best of the four and probably bracket the true values. Under method number 3, age hypotheses numbers II and III are more probably correct than number I. Accordingly, we estimate that sexual maturity is, on the average, attained at 181 ± 1 cm and 9.0 (8.6 to 9.3) layers (5.1 to 8.3 yr, depending on the alternative layering hypothesis used).

An increase in size of Graafian follicles is another criterion of approaching sexual maturity. Diameter of the largest follicle also shows a sharp increase after 160 cm total length (Figure 25), con-

current with the increase in ovary weight (Figure 23). The largest follicle in immature females usually is less than 1 mm in diameter. The largest follicles in most ovaries containing scars are between 1 and 8 mm in diameter, but a few follicles (possibly cystic) as large as 10 to 16 mm in diameter were encountered.

Ovarian Changes in Adults

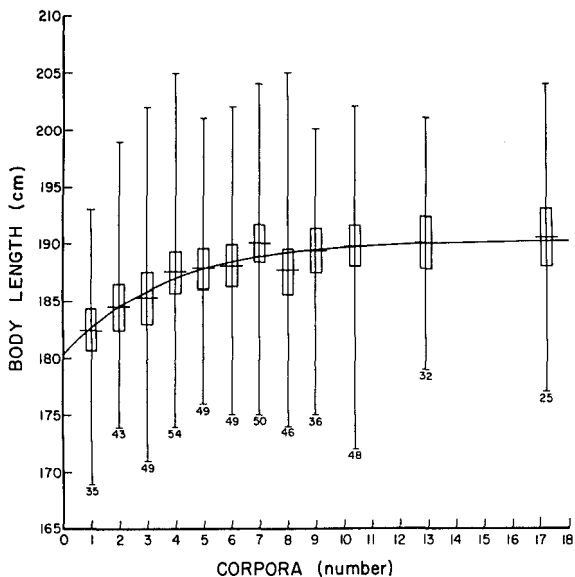The analyses of ovarian changes are based on material collected through 1972. The corpus

FIGURE 24.—Relationship between body length and number of corpora in *Stenella attenuata*. Average (bar), ± two standard errors (box), range (vertical line), and sample size shown.

TABLE 2.—Results of analyses of length and age at attainment of sexual maturity in *Stenella attenuata*, with comments (in parentheses) on pros and cons of the methods. Lengths and layer counts predicted with the growth equations are in parentheses.

Analysis	Length (cm)	Layers (no.)	Age (yr), under hypothesis		
			I	II	III
1. Length at which 50% have corpora (probable underestimate).	175.4	(7.66)	3.8	6.7	4.3
2. Number of tooth layers at which 50% have corpora (interpolation, but small sample sizes).	(181.6)	9.14	4.6	8.1	5.6
3. Back-extrapolation of corpora-length curve (large samples, but extrapolation).	180.2	(8.74)	4.4	7.7	5.2
4. Length at first conception under hypothesis: I	177.7	(8.17)	(4.1)	—	—
II	180.0	(8.57)	—	7.6	—
III	180.0	(8.57)	—	—	5.1
(includes only those that become pregnant at first ovulation; probable underestimate).					

luteum of pregnancy arises from the ruptured follicle and has an important secretory function in maintaining early pregnancy in all mammals and full gestation in most (Amoroso and Finn 1962). The gross and microscopic structures of corpora lutea in various delphinids, including *S. attenuata,* have been described by Harrison et al. (1972).

The corpus luteum decreases in size during gestation (Figure 26). Of 242 females with corpora lutea, 229 were pregnant. Eleven with fetuses less than 20 mm long (range 1 to 20 mm) had
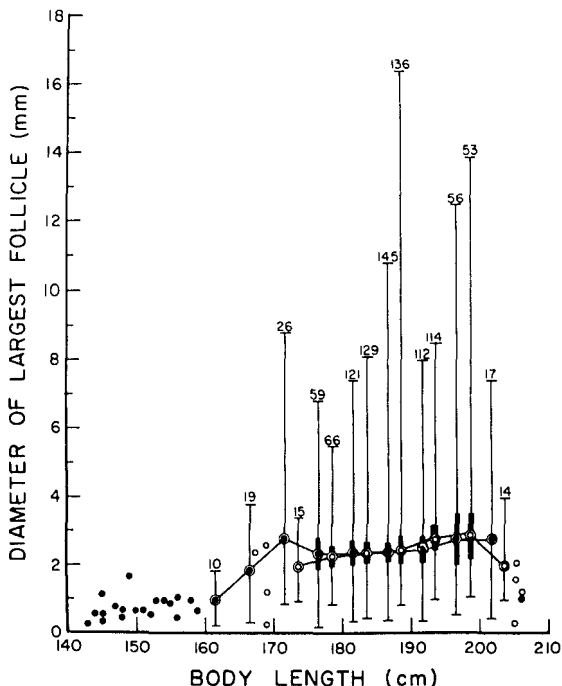

FIGURE 25.—Relationship between body length and diameter of the largest Graafian follicle in *Stenella attenuata*. Open dots represent females with corpus luteum. For length ≥160 and $n \geq 10$, means (circled symbols) and ranges shown. For $n \geq 30$, ± two standard errors are shown. Not included are 27 "senile" specimens with follicles <0.1 mm and five juveniles 88 to 122 cm with 0- to 1-mm follicles.

corpora with diameters of 23 to 29 mm (average 26.0 mm, SD 2.90). The mean diameter dropped sharply to 23.6 mm (range 21 to 27 mm, SD 2.27) in 17 females with fetuses between 20 and 100 mm (using Student's *t*, means are significantly different at $\alpha = 0.01$). This amounts to about a 32% decrease in luteal volume. Size of the corpus luteum continues to decrease at a slower rate, to 22.2 mm (range 19 to 28 mm, SD 1.79) in females with fetuses 700 to 825 mm (average length at birth is 825 mm) long, a further decrease in volume of about 15%. Luteal volume in females with near-term fetuses is only about half of that shortly after conception. Mean diameter in 10 females with fetuses longer than average birth length (825 mm) was 24.0 mm (range 20 to 26 mm, SD 2.21, greater than mean for 700 to 825 mm at $\alpha = 0.01$), a volume difference of about 38% more than for fetuses 700 to 825 mm long. Delayed regression (or re-enlargement) of the corpus luteum is apparently correlated with greater-than-average length at birth.
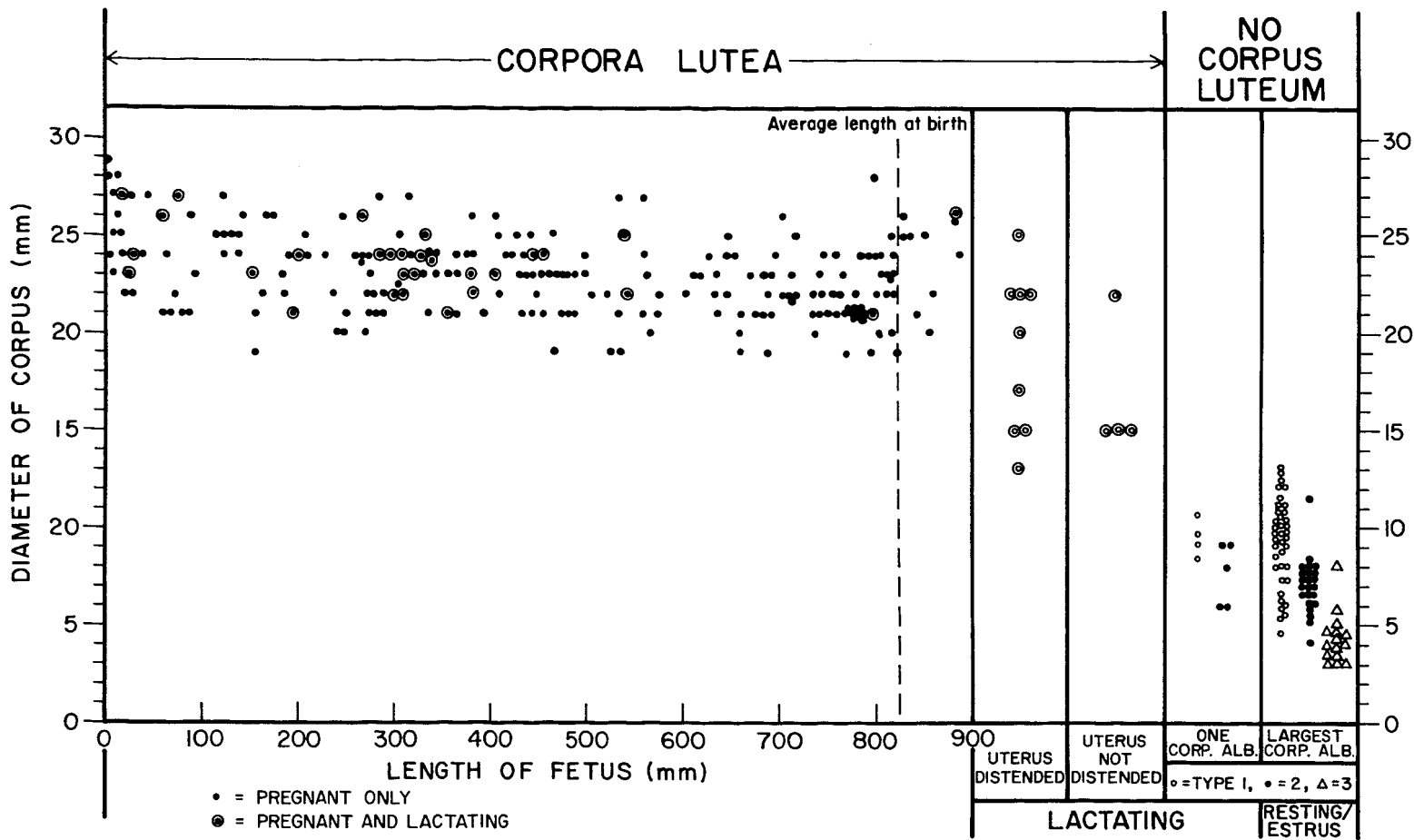
251

FIGURE 26.—Average diameter of corpus luteum in pregnant, lactating, and resting females of *Stenella attenuata*. Aberrant corpora (cystic, double, etc.) are not included.

Nine obviously postpartum females had corpora lutea 13 to 25 mm in diameter (Figure 26). Four lactating females with uteri not obviously distended had corpora lutea in the same size range. Average luteal volume in these lactating animals was less than half of that in animals at parturition. Some of these 13 cases may represent miscarriages.

The corpus luteum of pregnancy shrinks still further during the suckling period, losing its glandular appearance and becoming a corpus albicans. Nine of 197 lactating females without corpora lutea each had a single corpus albicans, which must represent the regressed corpus luteum of the first pregnancy. These corpora (Figure 26) were approximately spherical and 5.9 to 10.6 mm in diameter (average 8.5 mm). The lower end of this range—about 6 mm—must approximate the limit of regression during the suckling period (about 11.2 mo; see below). The small number of lactating females with corpora lutea (13) compared to the number with only copora albicantia (197) indicates that initial regression following parturition must be very rapid, perhaps occurring in less than 15 days. Still further regression in size and histological structure of the corpus albicans of pregnancy probably occurs. Many adult females have a large corpus albicans (in most cases, one of several) between 3 and 6 mm in diameter (Figure 26) with greatly degenerated structure. Unless these corpora all represent ovarian events not resulting in pregnancy, i.e., the females are all completely barren, the corpus albicans of pregnancy must decrease in diameter during a resting period following a pregnancy, to possibly as little as 3 mm.

Multiple corpora lutea are uncommon in *S. attenuata*. They were encountered in only 2 out of 258 females with corpora lutea. One of these was pregnant with twin fetuses (males, 83 and 86 mm) in the left horn of the uterus. The left ovary contained two corpora lutea of approximately equal size, each possessing a surface scar of ovulation, together with seven corpora albicantia visible on the surface. The right ovary was devoid of scars. Another female with two corpora lutea had a 592-mm fetus (male) in the left horn of the uterus. The left ovary looked very much like that of the specimen with twin fetuses, having two corpora lutea of approximately equal size and eight corpora albicantia on the surface. Neither corpus luteum bore a discernible surface scar. The right ovary was unscarred. There are two possible

explanations for the presence of two corpora lutea in this specimen: 1) one of them was an accessory corpus, or 2) one of a pair of twin fetuses was aborted during early pregnancy. In any case, the incidence of multiple corpora lutea is very low in *S. attenuata*, less than 1% in the sample examined. This is in sharp contrast to some other cetaceans, in which rates of presence of accessory corpora range to 15.6% (*Delphinapterus leucas* —Brodie 1972). The contribution of double and accessory corpora lutea to the accumulation of corpora albicantia can be considered to be negligible in *S. attenuata*.

Corpora albicantia in *S. attenuata* represent both regressed corpora lutea of pregnancy and regressed corpora of ovulations that do not result in pregnancy. This conclusion is based on the accumulation rate of corpora albicantia and on the estimate of the mean length of the calving interval (see below). We were not, however, able to differentiate between small regressed corpora lutea and regressed corpora of ovulation. This impasse, also encountered by workers dealing with other cetaceans (Harrison et al. 1972) is caused by the wide and largely discordant variation in size, shape, surface texture, and internal structure and color of the corpora albicantia. If one looks at enough corpora, it is possible to find corpora with these characters in almost any combination of expressions.

Harrison et al. (1972) found no more than six corpora albicantia in the ovaries of any *Stenella* female. In the present sample, however, nearly half (44%) of the females had more than six corpora, including the corpus luteum. Fifty-five females of 1,131 had 15 or more corpora; one had 28 (Figure 27). Three thousand five hundred and two corpora from ovaries of 530 females were scored to six categories. These categories are somewhat arbitrary in view of the continuity of regression and the wide variation discussed above, but, nonetheless, they are useful in analyzing the course of regression. The numbers and proportion of total corpora complement represented by each of these categories varies with the total number of corpora (Table 3, Figure 28). The categories were defined as follows:

Type 1. Surface raised, smooth or slightly wrinkled. Looks externally like a small corpus luteum. Cortex white or yellow, with obvious remnants of vascularization. Center solid or loosely constructed, consisting mainly of white
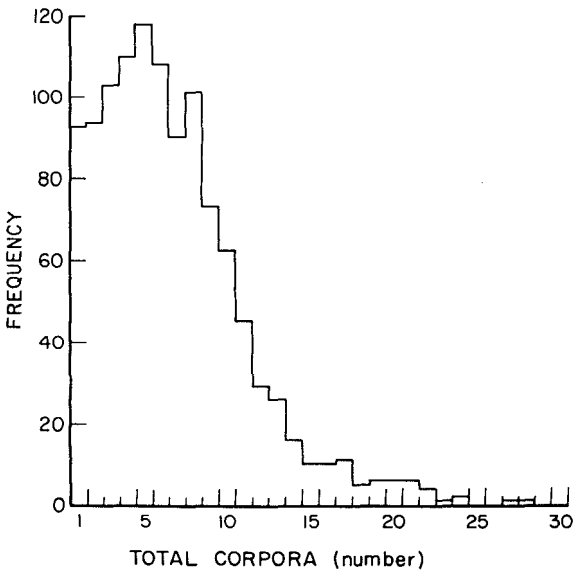
FIGURE 27.—Frequency distribution of corpora count in 1,131 females of *Stenella attenuata*.

TABLE 3.—Types of corpora present in ovaries of *S. attenuata* in relation to total corpora. Averages in Figure 28.

Total number of corpora (including corpora lutea)	Sample size (no.)	Range of number of each type of corpus albicans—Type:					
		1	2	3	4	5	6
1	35	0-1	0-1	0	0	0	0
2	42	0-2	0-2	0-1	0-1	0-1	0
3	48	0-3	0-3	0-2	0-1	0	0
4	53	0-3	0-4	0-3	0-1	0-2	0
5	49	0-5	0-4	0-5	0-2	0-2	0
6	49	0-5	0-4	0-6	0-3	0-1	0
7	50	0-5	0-5	0-6	0-3	0-2	0-1
8	46	0-5	0-6	0-7	0-2	0-4	0
9	36	0-2	0-5	2-9	0-4	0-3	0-1
10-11 (average 10.4)	48	0-4	0-5	3-10	0-2	0-2	0-1
12-14 (average 12.9)	32	0-2	0-5	3-14	0-3	0-4	0-3
15-27 (average 17.2)	25	0-4	0-5	7-19	0-2	0-9	0-1
Total	513	0-5	0-6	0-19	0-4	0-9	0-3

connective tissue, 3.5 to 15.5 mm in diameter, average 7 mm. These corpora almost certainly are nearly all regressed corpora lutea. Four hundred fifty-six were encountered (13.2%). Females with two or more corpora have, on the average, about one Type 1 corpus (Figure 28), although as many as five may be present (Table 3).

Type 2. Surface raised and wrinkled. Interior white to yellow, often with traces of luteal cortex and vascularization. Center solid or loosely constructed, consisting mainly of white connective tissue. Definitely less integrated in structure than Type 1 (above). Diameter 3.0 to 12.0 mm, average 6 mm. The evidence on accumulation rate (below) suggests that these corpora are probably a mixture of regressed corpora lutea and corpora of ovulation. We found 787 of this type (22.5%). The number of Type 2 corpora is relatively constant in females with three or more corpora, at about one and one-half (Figure 28) with a
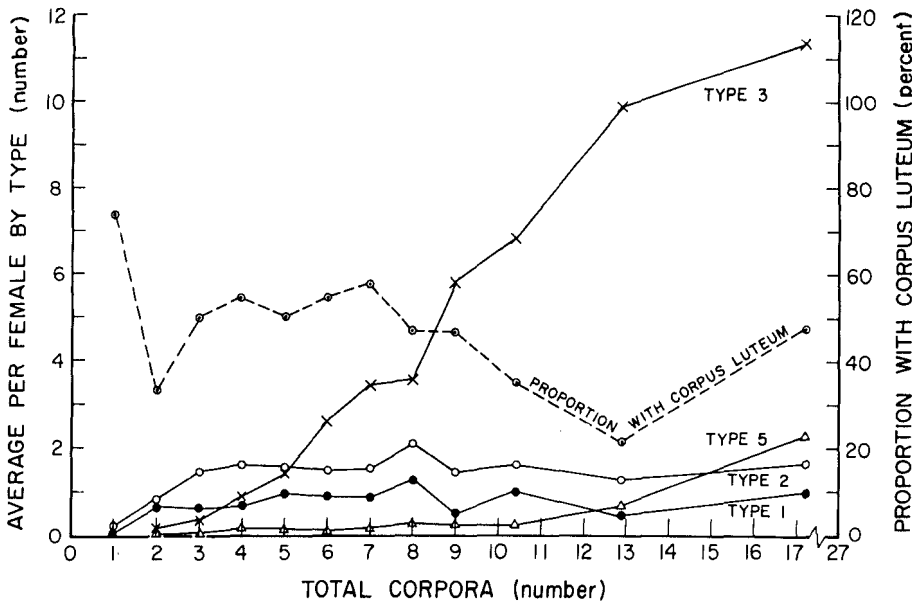

FIGURE 28.—Relationships between numbers of corpora of various types and total number of corpora in ovaries of females of *Stenella attenuata*. Ranges and sample sizes in Table 4.

range of 0 to 6 (Table 3). This number is tightly correlated with the number of Type 1 corpora (Figure 28), indicating that there may be some overlap in the classification criteria for these categories.

Type 3. Surface usually not raised; scar usually smaller than Type 2 and heavily wrinkled. May be pedunculate and flattened. May be flattened against the surface or may run deep into the ovary. Interior consists of white connective tissue. May have yellow "stains" around the white center. When many corpora are present, some of this type may be present but not apparent at the surface. Diameter 2.0 to 8.5 mm, average 3.5 mm. This is a catch-all category for all small compact corpora with surface scars and internal structure. It probably includes both regressed corpora lutea and corpora representing ovulation and other events. We found 1,999 corpora of this type (57.1%). The number increases steadily with total corpora number (Table 3, Figure 28), while the numbers of Types 1 and 2 corpora remain constant, indicating that Types 1 and 2 corpora regress into and accumulate as Type 3 corpora. This is assuming, of course, that total corpora count is related to age (see below).

Type 4. Thin, flattened against the surface of a new corpus luteum. Two to 15 mm in diameter. These are Types 2 and 3 corpora that cannot be allocated to those categories because of distortion caused by the corpus luteum. One hundred were encountered (2.9%).

Type 5. Surface trace very slight or apparently absent. Interior deep yellow or orange, with no concentrated connective tissue or apparent internal structure. Diameter 0.5 to 5.5 mm, average 2 mm. Harrison et al. (1972) have suggested that this type of corpus is the end result of regression of an atretic lutealized follicle. We encountered 149 (4.3%).

Type 6. A small surface scar with no discernible internal structure. Two to 5 mm in diameter. Only 11 corpora of this type were encountered (0.3%). They may represent extremely regressed corpora of other types or may originate from different ovarian events.

Types 1, 2, and 3 comprise a series of increasing regression and/or decreasing complexity of original structure, and it is probable that regressing corpora lutea pass through these types or stages. The shapes of the diameter frequency distributions (Figure 29) suggest that corpora albicantia regress to an average size of about 3 mm in diameter and then persist and accumulate at that size for at least part of the remainder of the life of the female. The skewness of the aggregate distribution (sum Types 1, 2, and 3 in Figure 29) becomes even more significant when one considers that the volume of the corpus decreases as the cube of the diameter. On a volume scale, the left
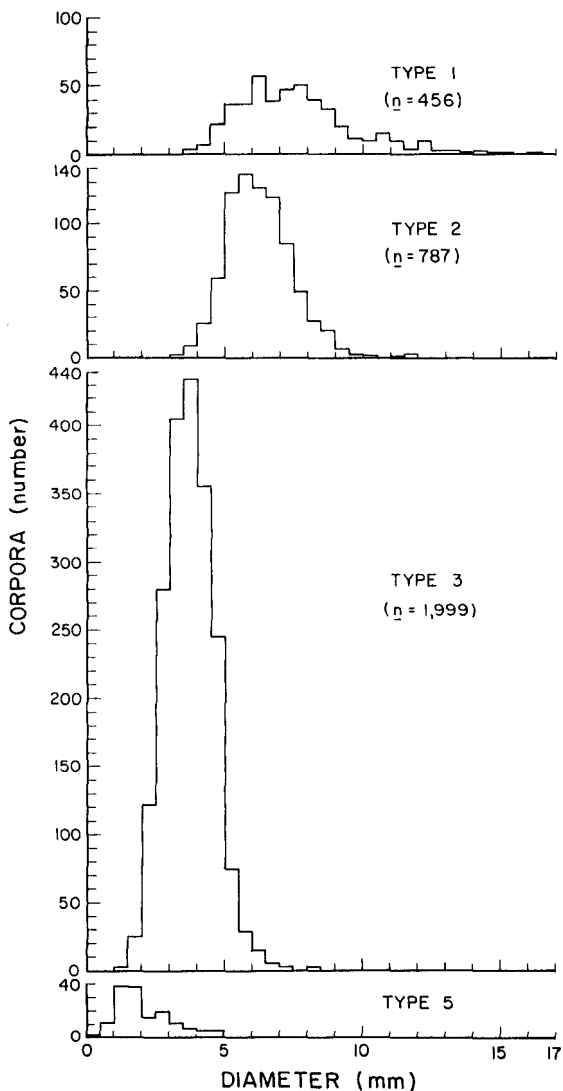

FIGURE 29.—Frequency distribution of diameter of Types 1, 2, 3, and 5 corpora albicantia in *Stenella attenuata*.

255

side of the curve would be steeper and the right side less steep.

Consideration of the relative rates of deposition of corpora in the left and right ovaries is important to the question of persistence of corpora. The distribution of corpora between left and right ovaries is related to the number of corpora present (Table 4). The first corpus occurs in the left ovary about 94% of the time. Subsequent corpora occur in the same ovary as preceding ones at about the same rate (~95%), causing a gradually increasing percentage of animals with corpora in both ovaries, until about 10 to 11 corpora have been deposited, when emphasis switches sharply to the opposite ovary (left or right). All females with 15 or more corpora (27 specimens) had corpora in both ovaries.

A group of 15 seemingly postreproductive

TABLE 4.—Location of corpora (corpora lutea and corpora albicantia) in ovaries of 488 specimens of Stenella attenuata.

Corpora (no.)	Sample size (no.)	Location of corpora		
		Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	31	93.6	6.4	—
2	40	85.0	7.5	7.5
3	44	86.5	4.5	9.0
4	53	88.7	1.9	9.4
5	47	78.8	2.1	19.1
6	48	75.0	4.2	20.8
7	45	73.4	2.2	24.4
8	41	61.0	2.4	36.6
9	34	70.6	2.9	26.5
10-11	47	46.8	2.1	51.1
12-14	31	6.5	0.0	93.5
15-27	27	0.0	0.0	100.0
Total	488			

females was encountered. These specimens had very small, obviously regressed ovaries with 10 to 15 Type 3 or smaller corpora albicantia (Figure 30). They had no corpora lutea or Type 1 corpora

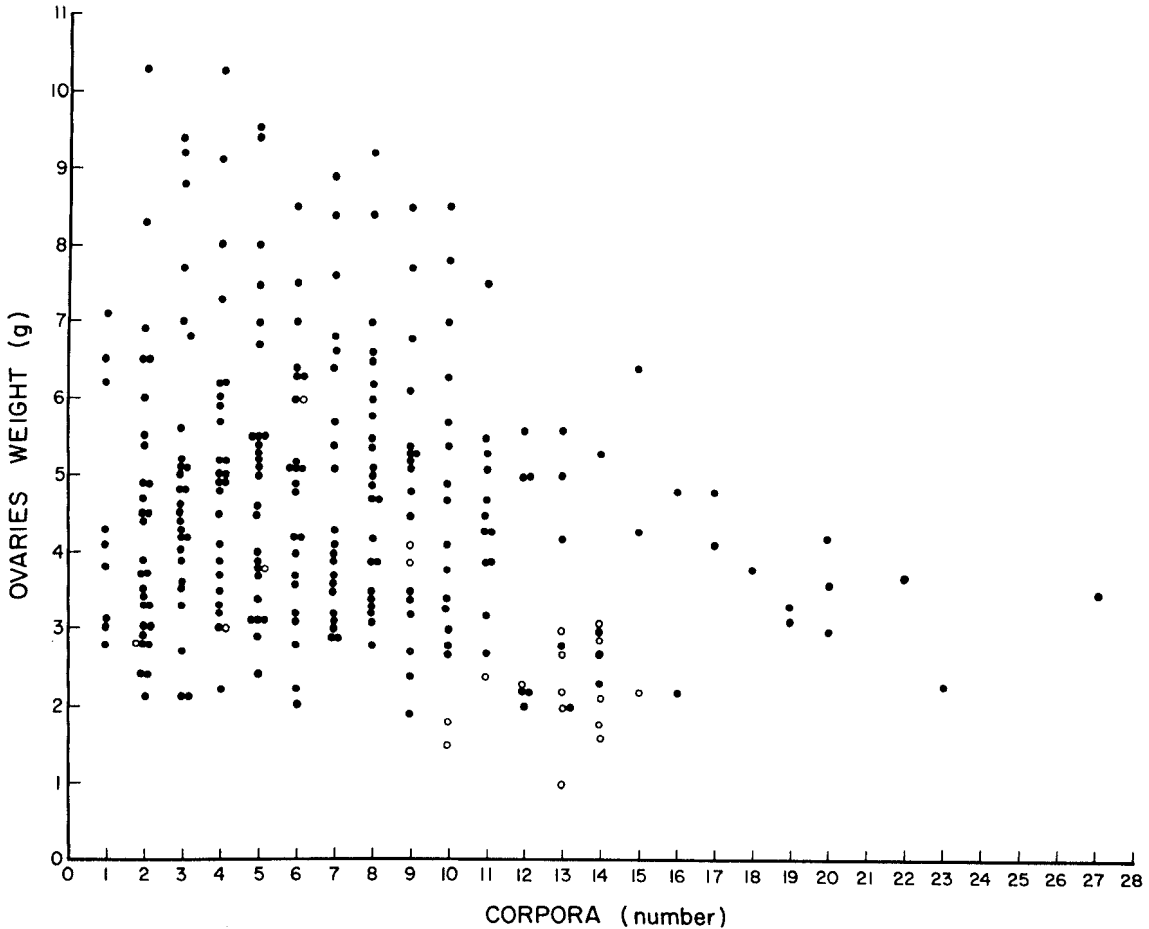FIGURE 30.—Scatterplot of ovaries weight on number of corpora in Stenella attenuata. Females with corpus luteum not included. Open dots are females with no Type 1 or 2 corpora albicantia.
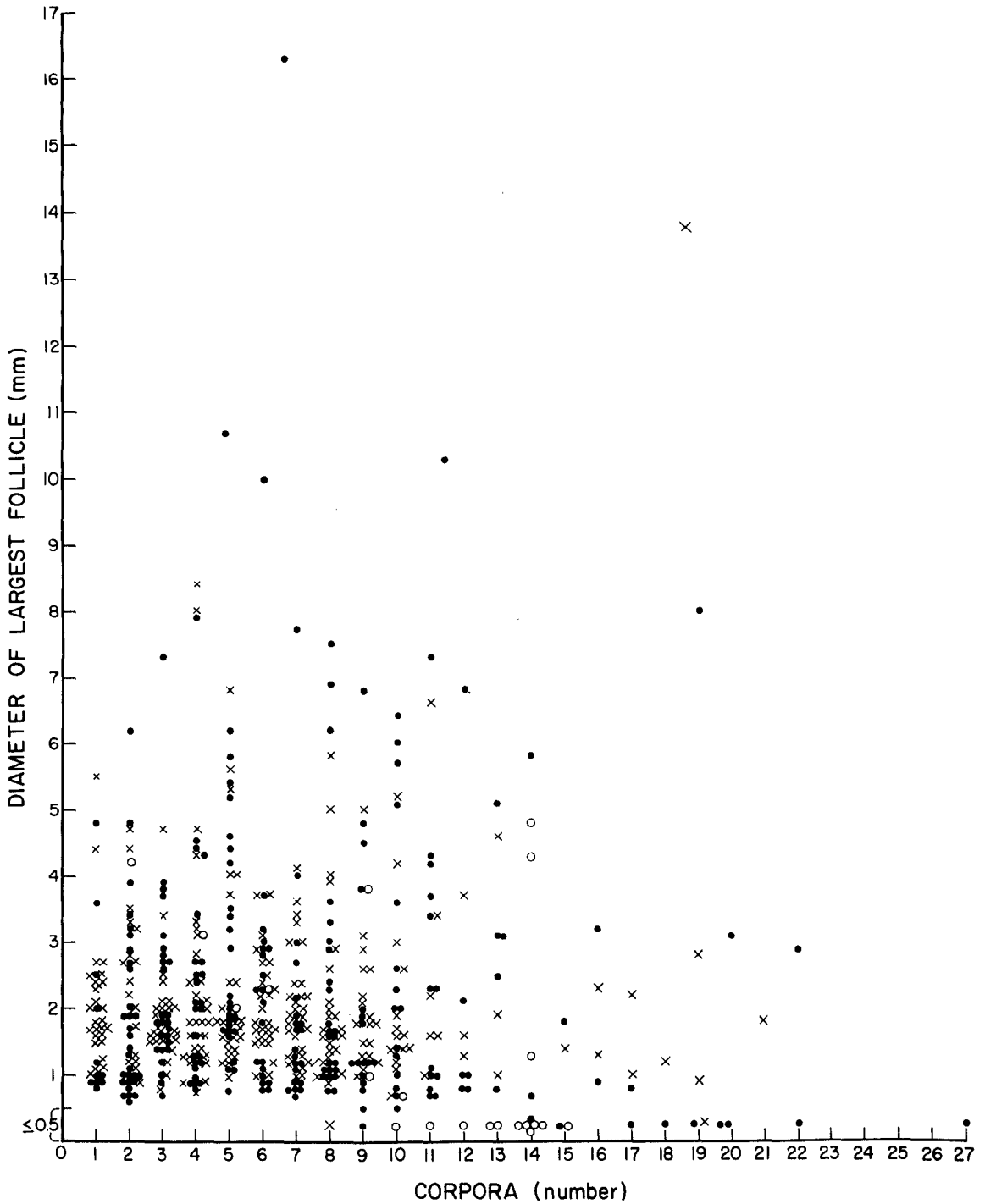
FIGURE 31.—Scatterplot of diameter of largest follicle on number of corpora in *Stenella attenuata*. Females with corpus luteum indicated with ×. Open dots are females with nor corpus luteum or Type 1 or 2 corpora albicantia.

albicantia. They also typically had very small Graafian follicles (Figure 31). A consideration of these females bears on the question of persistence of corpora albicantia. Sergeant (1962) encountered similar females in *Globicephala*. They comprised about 5% of adult females. He called them "senile" and concluded that the ovarian scars in these animals represent some residual subset of the maximum complement of corpora of pregnancy, ovulation, and other events. He implied that they probably are the corpora of pregnancy, since those corpora are larger at the outset and presumably less likely to regress to the point of macroscopic disappearance. The ovarian data for *S. attenuata* do not support this hypothesis of disappearance of some corpora in regressed ovaries. The regressed ovaries have 10 to 15 corpora (Figures 30 and 31). The ovaries of other, still reproductive females are larger and have 16 to 27 corpora, although follicles are typically smaller than in reproductive females with fewer corpora (Figure 31). Three alternative hypotheses explain this apparent dichotomy in females with 10 or more corpora:

1. The usual maximum number of corpora is about 21, and some corpora disappear in postreproductive females, i.e., the "senile" group in Figure 30 properly belongs at the far right side of the plot at the end of a downward trend in ovary weight (the hypothesis of Sergeant 1962).
2. Corpora are laid down at about the same rate in all individuals, but some become postreproductive at about 10 to 15 corpora while others continue to accumulate corpora (16 to 27) until a greater age, i.e., the corpora scale in Figure 30 is effectively an age scale. Under this hypothesis, corpora do not disappear.
3. Corpora are accumulated at rates varying widely among individuals, but the typical maximum complement is 10 to 15 corpora, i.e., the reproductive females with more than 15 corpora in Figure 30 properly belong in the body of the distribution in the left two-thirds of the plot. A possible explanation for widely varying rates of accumulation is that some females are more fecund and the senile period is reached with some maximum number of pregnancies, so that the varying ratios of corpora of pregnancy to corpora of ovulation may produce the appar-

ent dichotomy. Sergeant (1973) found greatly varying individual rates of ovulation in the white whale, *Delphinapterus leucas*.

In order to examine these alternative hypotheses, the females in Figure 30 and 31 with 10 or more corpora were examined in three groups—A, B, and C:

A. 10 to 15 corpora, reproductively active (corpus luteum and/or Types 1 and 2 corpora albicantia).
B. 16 or more corpora, reproductively active.
C. 10 to 15 corpora, postreproductive (ovaries regressed, no corpus luteum or Types 1 or 2 corpora albicantia).

The three groups were compared in terms of corpora count, weight of ovaries, size of largest follicle, number of dentinal layers, total length, and relative corpora counts in left and right ovaries (Table 5). Only nonpregnant females were included in the sample for ovary weight. Follicle size was examined separately for pregnant and nonpregnant animals.

Ovary weight and follicle size for nonpregnant animals decline progressively from A to C. This is

TABLE 5.—Characteristics of females of *Stenella attenuata* in groups A, B, and C (see text).

Item	A	B	C
Corpora (no.)			
Sample size	67	24	15
Average	11.2	18.9	12.9
Range	10-15	16-27	10-15
SD	1.41	2.56	—
Ovary weight (g) (nonpregnant)			
Sample size	44	13	15
Average	4.4	3.6	2.2
Range	2.0-8.5	2.2-4.8	1.0-3.1
SD	1.61	0.81	0.59
Largest follicle (mm) (nonpregnant)			
Sample size	27	13	<14
Average	2.9	1.5	<0.5
Range	<0.5-10.3	<0.5-8.0	0.5-4.3
SD	2.53	2.35	—
Layers (no.)			
Sample size	30	18	7
Average	13.1	13.1	13.2
Range	10.0-16.0	11.0-15.0	11.5-16.0
SD	1.39	1.31	1.52
Length (cm)			
Sample size	67	24	15
Average	190.1	190.3	187.0
Range	172-202	177-204	179-192
SD	6.43	6.78	3.54
Left/right ovary			
Sample size	65	23	15
Average in right (%)	24	33	29
Left/right (no./no.)	548/178	291/144	—

a requirement of hypothesis 1, above, but does not eliminate hypotheses 2 and 3.

The three groups do not differ in average estimated number of tooth layers. This may, in part, be due to the difficulty of accurately counting the innermost layers in teeth with more than 12 layers (the number of layers is probably underestimated by as much as one-third in teeth with large amounts of convoluted secondary dentine), but careful comparison of the teeth of the three groups in terms of other features presumably correlated with age, such as tip wear, degree of closure of the pulp cavity, and amount of secondary dentine does not indicate that any group is older than any other. This evidence is against hypothesis 1, which requires that group C be older than A, and hypothesis 2, which requires that B be older than A and C.

Groups A and B have reached asymptotic length (~190 cm). The animals in group C averaged about 3 cm less. A statistical comparison of A with B using Student's t indicates that the difference is significant at $\alpha = 0.05$. These results do not eliminate or support directly any of the hypotheses. Since A, B, and C are about the same age, the length data indicate that asymptotic length may be less for females that become senile with 10 to 15 corpora. This indirectly supports the idea of considerable individual variation in life history.

The most convincing evidence against hypothesis 1 has to do with number of corpora in right versus left ovaries. If the emphasis in corpus deposition shifts from left to right at about 10 corpora, and if group C regresses from group B (animals with about 20 corpora) losing about 6 corpora in the process, then group C should have about equal numbers of corpora in the right and left ovaries. If most corpora of ovulation come in early reproductive life (as data analyzed below indicate) and, as suggested by Sergeant (1962), are more likely to disappear than corpora of pregnancy because of smaller initial size, then the regressed group C should have, on the average, more corpora on the right than on the left, because most of the corpora of pregnancy would be in the right ovary. Forty-one percent of the corpora in 14 individuals having 18 to 22 corpora (average 19) were on the right. Only 29% of the corpora in group C were on the right. The difference between C and A (29 and 24%) can be accounted for simply by the difference in average total corpora count (12.9 and 11.2). These re-

sults eliminate the hypothesis (number 1 above) of loss of corpora with regression of ovaries.

The various lines of evidence largely speak against hypotheses 1 and 2 and support hypothesis 3, that of great individual variation in life history and of persistence of corpora albicantia. This is in line with findings by some other workers in small cetaceans (Sergeant 1962, 1973; Brodie 1971).

The data on the relationship of percent occurrence of corpora lutea to number of corpora (Figure 28) also support the hypothesis of widely varying rate of accumulation of corpora albicantia. After stabilization at about 50% at 3 to 4 corpora, the rate declines after 8 to 9 corpora to 20% at 13 corpora; but the rate for females with 17 to 27 corpora is again 50%. Assuming that fecundity is inversely related to age, this pattern suggests that the females in the 17 to 27 group are about the same age as those in the 3 to 9 group.

Ovulation Rate

Even assuming that corpora albicantia persist and represent various ovarian events, estimating average rates of accumulation is difficult because of 1) the above-mentioned unreliability of age estimates based on more than 12 tooth layers, 2) the evident individual variation in accumulation rate, and 3) change in ovulation rate during the reproductive span. All of these factors must contribute to the scatter in a plot of corpora number (including corpus luteum) on estimated age (Figure 32). Several workers have pointed out that cetacean ovaries often contain two or more corpora of the same size and same stage of regression. It has been suggested that these are the result of multiple infertile ovulations or lutealization of atretic follicles in newly mature animals (Harrison et al. 1972). Many in the present series of ovaries had two or more corpora (of Type 1 or 2) that were very similar in size and structure and must have resulted from nearly contemporaneous events. One probable multiple ovulation is apparent in Figure 32. This female, field number CWOR8, possessed 7 or 8 well-defined layers in its teeth. In spite of its extreme youth, it had a small corpus luteum, three Type 1 corpora, two Type 2 corpora, one Type 3 corpus, and one Type 4 corpus. The uterus was empty, and there was no milk in the mammaries. The animal could not have been reproductively active for more than about a year, but had already experienced eight
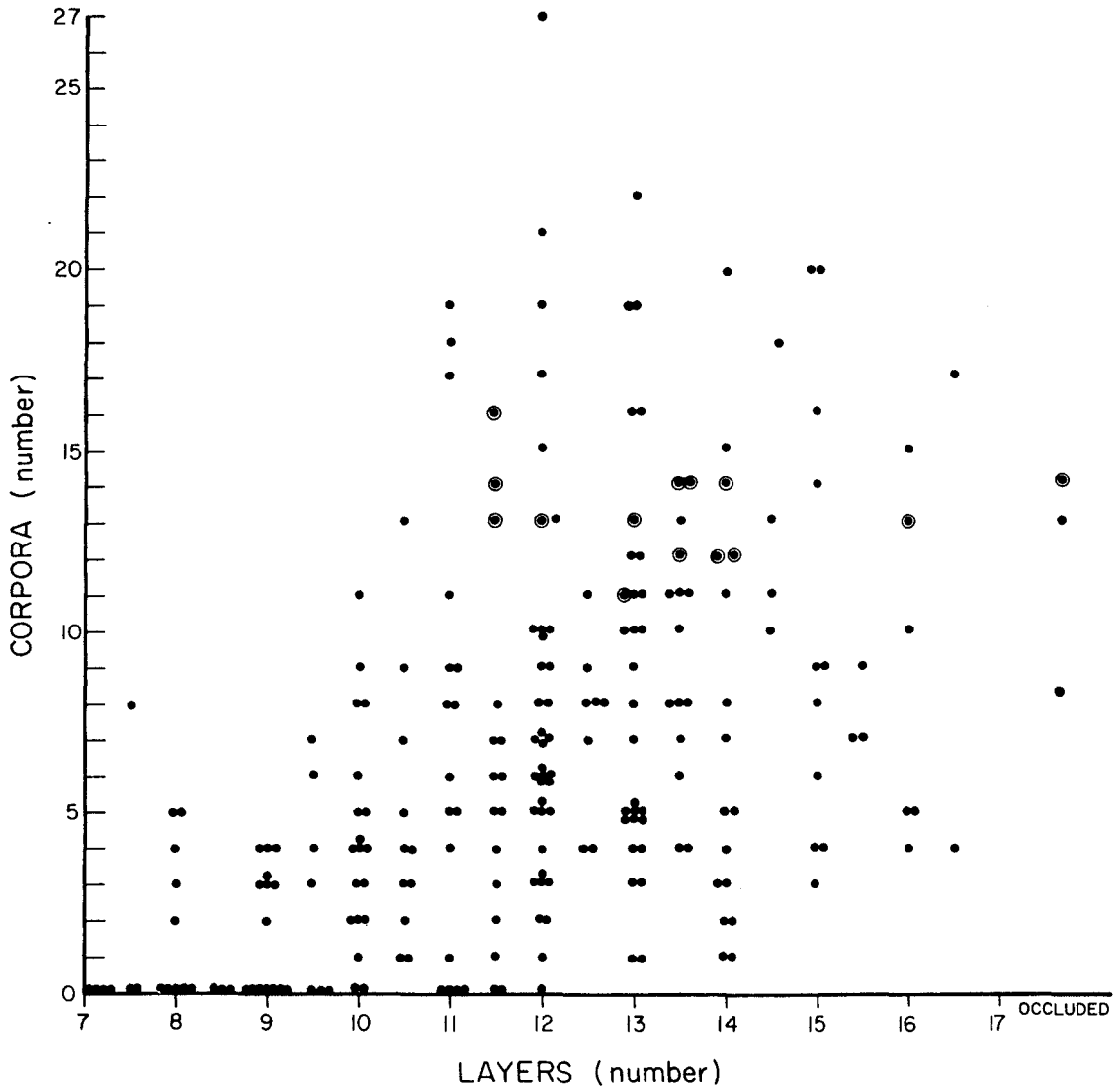
FIGURE 32.—Scatterplot of number of corpora on number of postnatal dentinal layers in *Stenella attenuata*. Circled symbols are senile females [shriveled ovaries with no corpus luteum or Type 1 or 2 corpora albicantia].

apparently nonreproductive ovarian events that resulted in corpora belonging to all of the types through which a corpus luteum must pass during regression to a small corpus albicans.

Calculation of average ovulation rates from the data in Figure 32 must take into account individual variation in age at first ovulation. The females in Figure 32 were grouped into 10 one-layer intervals beginning with 7.5 layers (Table 6). The average reproductive age in interval p was calculated as

$$\bar{A} = \left(\sum_{i=1}^{p} a_i b_i \right) \div c,$$

where a_i = % maturing in ith interval (% mature in i minus % mature in i - 1)

b_i = average reproductive age in interval p of females mature in i

c = % mature in interval p.

Average reproductive age in the ith interval of

TABLE 6.—Average reproductive ages and corpora counts of females of *Stenella attenuata* used in estimating ovulation rate based on corpora and tooth layers.

Layers (no.)	Sample (no.)	Proportion mature (%)	Average reproductive age of mature (layers)		Average corpora (no.)	
7.5- 8	13	46.2	0.50 ⎫		4.50 ⎫	
8.5- 9	18	44.4	1.56 ⎬ 1.43		3.25 ⎬ 4.21	
9.5-10	24	79.2	1.67 ⎭		4.53 ⎭	
10.5-11	25	84.0	2.56		6.42	
11.5-12	52	94.2	3.25		8.35	
12.5-13	36	100.0	4.05		8.92	
13.5-14	31	100.0	5.06		8.71	
14.5-15	15	100.0	6.07 ⎫		10.87 ⎫	
15.5-16	7	100.0	7.08 ⎬ 6.60		9.86 ⎬ 10.45	
>16	3	100.0	8.09 ⎭		9.75 ⎭	
Total	224					

Note: Teeth of all available females with more than 12 corpora were sectioned, while only a nonselective subsample of females with fewer corpora were included. The effect on estimate of average reproductive age is negligible, since nearly all had 11 or more layers.

females maturing in i was set at 0.50 layers. Because of small sample sizes, the first three intervals and the last three were pooled. The results show an increase in average corpora count (number of ovulations) with reproductive age (Figure 33). A curvilinear fit to the interval means, using a power model forced through the origin, fits well and indicates that ovulation rate is higher in animals of reproductive age 0-2 layers than in older animals. The breaking point seems to come at about 12 layers, when about 6 corpora have been accumulated and rate appears to become nearly constant. Average ovulation rates estimated from the curve are about four during the first layer, two during the second, and about one per layer thereafter.
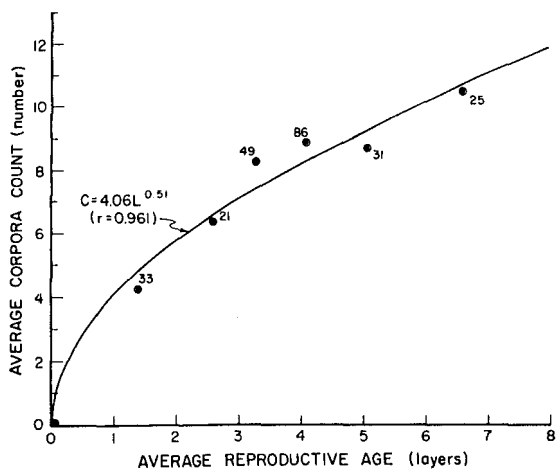

FIGURE 33.—Relationship between average number of corpora and average reproductive age (in layers) in *Stenella attenuata*.

Calving Interval

The pattern of reproduction definable with the methods used here consists of three phases: pregnancy, lactation, and a period of inactivity and/or estrus called here "resting/estrus." The length of pregnancy was estimated above as 11.5 ± 0.2 mo. We estimated length of lactation in three ways, based on 1) stomach contents of calves, 2) numbers of lactating females and calves, and 3) ratio between numbers of lactating and pregnant females.

The forestomachs of 45 calves less than 150 cm long were opened and examined by eye for presence of milk. Twenty-one were empty. The stomachs of four calves 120 to 130 cm long contained both milk and solid food (fish and/or squid). Stomachs of 8 smaller calves (80 to 115 cm) contained only milk, and 12 of the larger calves (130 to 150 cm) apparently contained only solid food. About 130 cm appears to be the length at which effective weaning occurs. The estimated time required to grow to 130 cm is 9.4 mo (based on growth curve above). This estimate is not very reliable for two reasons: the sample is small, and small amounts of milk could be present and undetectable by eye, i.e., suckling could continue at a low level after the effective shift to solid food. The estimate can, however, be considered to be a probable lower bound on length of lactation.

A second estimate is based on the assumptions that 1) a suckling calf exists for each lactating female and 2) the samples of specimens are unbiased with respect to suckling calves and lactating females. Given these assumptions, the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length at weaning. This length in eight variously sized, 1-mo "random" samples of calves and females ranged from 125 to 145 cm (Table 7). The aggregate estimate for the eight samples pooled (320 lactating females) is 137 cm. Average age at 137 cm is estimated at 1.94 tooth layers, or (assuming two layers accumulated during first year) 11.6 mo. If calves were overrepresented in the samples, this would be an underestimate. If they were underrepresented, it would be an overestimate. It would be an overestimate if the assumption that the number of lactating females equals the number of nursing calves were not valid. The assumption is not valid if the mortality of nursing calves is

TABLE 7.—Length at which cumulative frequency of calves equals the number of lactating females in eight 1-mo samples of *Stenella attenuata*.

Sample (mo)	Lactating females (no.)	Length (cm) at which cumulative frequency of calves = no lactating females
Oct. 1972	51	132
Jan. 1973	65	125
Feb. 1973	50	144
Mar. 1973	48	136
Apr. 1973	13	142
May 1973	32	142
June 1973	18	145
Nov. 1973 (Oct. 28-Dec. 11)	43	142
Total	320	137

higher than that of lactating females and lactation continues after death of a nursing calf.

A third estimate of length of lactation was derived from the ratio of lactating to pregnant females. This analysis included all the material from 1971 and 1972, when only adult females were sampled, as well as the material included in the calf-lactating female analysis above. Females both lactating and pregnant were included in both categories. The assumption is made that samples were unbiased with respect to relative representativeness for lactating and pregnant females. The ratio was 0.95 in the 1971 sample (86 adult females), 1.00 in 1972 (455), 0.96 in 1973 (573), and 0.97 for the pooled samples ($n = 1,114$; Table 8). The ratio of lactating to pregnant should equal the ratio of the lactation period to the gestation period. Gestation is 11.5 mo, therefore lactation is by this method estimated at 0.97 times 11.5 mo, or 11.2 mo. Estimated length at this age is 135.5 cm.

The three estimates of 9.6, 11.6, and 11.2 mo are based on largely independent assumptions and are close enough to each other to indicate that length of lactation is almost certainly between 9 and 12 mo. Of the three, the central estimate, 11.2

mo, is best in terms of sample size and probable validity of assumptions and is used below in estimating length of the calving interval.

The basic data used for estimating average length of calving interval were the relative frequencies of adult females in several reproductive conditions (Table 8). Adult females were defined as those with at least one corpus luteum or corpus albicans. Senile females were those with 10 or more corpora albicantia, no corpus luteum or Type 1 or 2 corpora albicantia and ovaries weighing less than 3.5 g. Resting/estrus females were those nonsenile adults that were neither pregnant nor lactating. Many of these (16 to 31%) had a corpus luteum. The corpus luteum may have represented an undetected very early pregnancy, a very recently aborted pregnancy, loss of a calf shortly after birth (resulting in cessation of lactation), or may have been a corpus luteum of ovulation. All of these alternatives may be represented in the samples.

In calculating the proportions of females in the three phases of pregnant, lactating, and resting (Table 9), senile females were excluded. One-half of the animals simultaneously pregnant and lactating were assigned to the pregnant category and one-half to the lactating category.

The average length of calving interval was estimated by two methods — 1) using the estimates of gestation and lactation periods and 2) using the percentage of females pregnant. The data for the 3 yr are comparable (Table 9), with the exception of possible existence of a trend in proportion resting; therefore, length of calving interval was estimated from the pooled data. Eighty-four and one-half percent of reproductive females were pregnant or lactating. Pregnancy (11.5 mo) plus lactation (11.2 mo) total 22.7 mo. If the proportion in a phase is equal to the proportion of the total

TABLE 8.—Reproductive condition of 1,114 adult female specimens of *Stenella attenuata*, collected 1973.[1]

	1971		1972		1973		Total	
	No.	%	No.	%	No.	%	No.	%
Pregnant only (P)	31	36.0	180	39.7	233	40.7	444	39.6
Lactating only (L)	29	33.7	180	39.7	223	38.9	432	38.8
Pregnant and lactating (PL)	13	15.1	16	3.5	17	3.0	46	4.1
Resting/estrus $\left(\frac{A}{B}\right)$ (R)	11 $\left(\frac{3}{8}\right)$	12.8	64 $\left(\frac{10}{54}\right)$	14.1	94 $\left(\frac{29}{65}\right)$	16.4	169 $\left(\frac{42}{127}\right)$	15.2
Senile[2]	2	2.3	15	3.3	6	1.0	23	2.1
Total	86	100	455	100	573	100	1,114	100

[1]In the resting/estrus category, subcategories A and B (in parentheses) are specimens with and without a corpus luteum, respectively.
[2]≥10 corpora, no Type 1 or 2 corpora, and ovaries ⩽3.5 g.

TABLE 9.—Proportions of 1,091 adult reproductive females of *Stenella attenuata* in pregnant, lactating, and resting/estrus phases.

	1971		1972		1973		Total	
	No.	%	No.	%	No.	%	No.	%
Pregnant (P + ½PL in Table 8)	37.5	44.6	188	42.8	241.5	42.6	467	42.8
Lactating (L + ½PL)	35.5	42.3	188	42.8	231.5	40.8	455	41.7
"Resting" (R)	11	13.1	64	14.4	94	16.6	169	15.5
Total reproductive females	84	100	440	100	567	100	1,091	100

calving interval spent in that phase, then total length of the interval cycle is 22.7 mo divided by 0.845, or 26.9 mo.

A second estimate was obtained directly from the proportion of females pregnant. In calculating this proportion, all pregnant animals were included (P + PL in Table 8): 490 of 1,091 reproductive females were pregnant, or 44.9%. Division by length of pregnancy, 0.958 yr (11.5 mo), yields an estimate of annual pregnancy rate, 0.469. The reciprocal of pregnancy rate, 2.133 yr, or 25.6 mo, is an estimate of average length of calving interval.

Both estimates of length of calving interval, 26.9 and 25.6 mo, are overestimates to the extent that the "resting" females with corpora lutea represented uncounted pregnancies, but the effect can be at most very minor. For example, if all these females represented undetected pregnancies or pregnancies aborted during capture, the unlikely extreme case, the estimates would be 25.7 and 24.7 mo respectively, an average difference of about 1 mo. Since the "resting" females with corpora lutea probably represent a mixture of causes and conditions, including nonfertile ovulations, the probable effect on the estimates is less than 1 mo. Considering this factor and the closeness of the two estimates to each other, it seems certain that the true length of the interval is between 24 and 27 mo. The lower of the two estimates, which is based on fewer assumptions and calculations, was rounded off to 26 mo and is used below in further analysis of life history. The average pattern of events then, consists of 11.5 mo of pregnancy, 11.2 mo of lactation, and 3.3 mo of resting and/or estrus.

Overlapping Lactation and Pregnancy

About 9.6% of lactating females were also pregnant (Table 8). Most had fetuses less than 35 to 40 cm long (Figure 26), about halfway through the gestation period. This suggests that overlap when it occurs is usually about 5 to 6 mo long, i.e., conception occurs about halfway through the lactation period of about 11 mo, making the calving interval about 20 mo long instead of 26. The very few lactating females with near-term fetuses may have conceived during postpartum estrus or may have begun to lactate shortly before parturition.

The data on Graafian follicles are consistent with the theory that postpartum estrus occurs during lactation (Figure 34). The largest follicle in the ovaries of resting/estrus females (including those presumably about to ovulate) is on the average 3 to 4 mm in diameter. After ovulation and conception, the remaining large follicles regress rapidly to about 2 mm (or become lutealized or atretic). There is a further net decline during gestation to about 1.5 mm, and during lactation the main modal diameter is about 1.0 mm. During both pregnancy and lactation, however, about 10% of the females (excluding senile individuals, as defined above) have follicles that are within the size range (≥ 3.0 mm) of the presumably ripe follicles present during the resting/estrus phase. This is most clear-cut during lactation. Most of the larger follicles during pregnancy occur in females having fetuses 400 to 500 mm long, or about halfway through the gestation period (Figure 34).

Decrease in Reproductive Rate with Age

Reproductive rate decreases with age. Age-specific estimates of pregnancy rates and lactation rate were calculated from a random sample of the data for specimens for which teeth were sectioned (stratified to insure representation of corpora-number strata in about the proportions as in the entire sample). The analysis shows decline of pregnancy rate from about 0.6 at 8 to 9 layers to about 0.3 at 16 to 17 layers (Figure 35). The weighted rate for the pooled sample of 138 used in the calculation was 0.51, comparable to the rate of 0.47 obtained for 1,091 animals (above). The specimens for which teeth were sectioned were about one-third from 1971 and two-thirds from 1972, with a few specimens from earlier years. Lactation rate
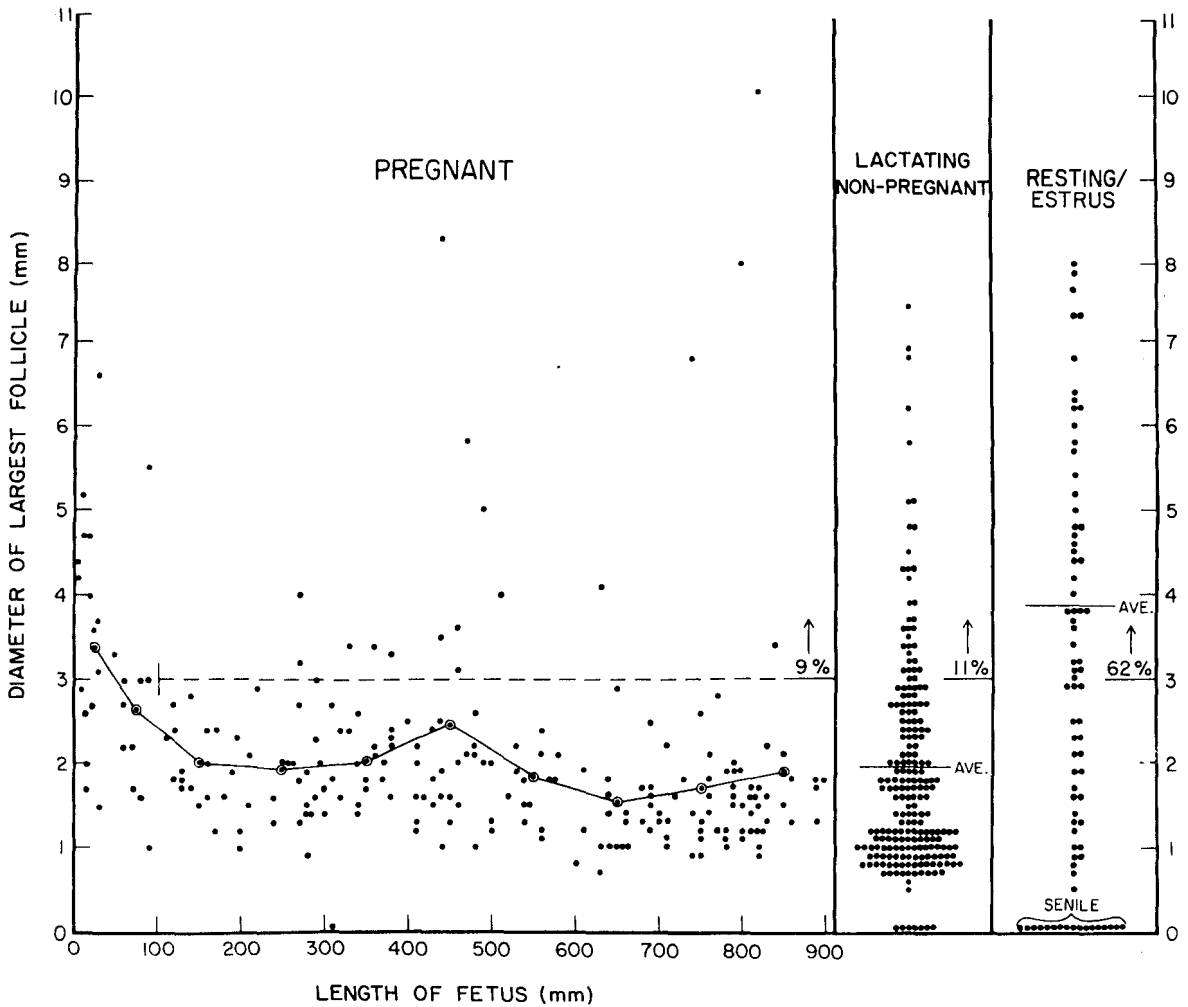
263

FIGURE 34.—Diameter of largest follicle in pregnant, lactating, and resting females of *Stenella attenuata*.

(Figure 35) increases from about 0.1 at 8 layers to about 0.6 at 12 layers and then again decreases to about 0.5.

The initial very low lactation rate compared to pregnancy rate, of course, reflects the fact that a very high percentage of the young females are pregnant for the first time and thus cannot be lactating. The lactation rate climbs rapidly to a level about equal to the pregnancy rate (at about 12 layers) and behaves like the pregnancy rate thereafter. The apparent decline of reproductive rates in older females may be related to the physiological or social mechanisms that cause the appearance of postreproductive females in this age group (see above; not included here).

Sex Ratios

The overall sex ratio was 44.9% males and 55.1% females (Figure 36). Many large samples examined were predominantly female. Fourteen of 32 single-school samples of 50 or more specimens were more than 60% female, whereas none was more than 60% male. The largest single-school sample examined (342) was almost half and half males and females.

Sex ratio changes with age (Table 10). This is, of course, making the assumption that the samples examined were representative of the population. Neonates and two-tone animals were almost equally divided between the sexes, but only about
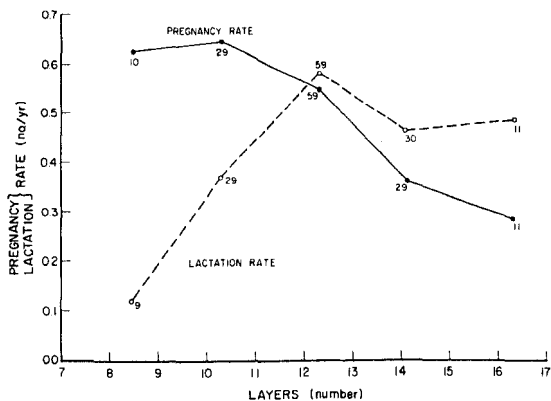
FIGURE 35.—Age-related changes in pregnancy (solid line) and lactation rates (dashed line) in *Stenella attenuata*, based on tooth layer data. Postreproductive females not included.
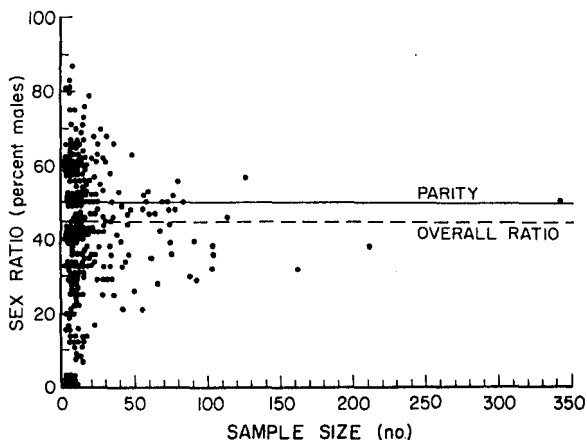

FIGURE 36.—Scatterplot of sex ratio (percent males) on sample size in single-school samples of five or more specimens of *Stenella attenuata*. Overall ratio (dashed line) from Table 12.

TABLE 10.—Sex ratio, by color pattern stage, in 9,371 specimens of *Stenella attenuata*, 1971-73.

Color pattern stage	Males		Females		Total
	No.	%	No.	%	
Neonate	205	49.8	207	50.2	412
Two-tone	666	48.7	701	51.3	1,367
Speckled	609	47.8	666	52.2	1,275
Mottled	569	43.8	729	56.2	1,298
Fused	2,154	42.9	2,865	57.1	5,019
Total	4,203	44.9	5,168	55.1	9,371

43% of the adults examined were males. The greatest change in ratio, from 48.0 to 43.5% male, comes about during the transition to mottled coloration between 7 and 8 layers of age. Assuming random sampling of the population, male and

female mortality rates must diverge sharply at this point.

Gross Annual Production

An estimate of average gross annual production of calves for 1971 to 1973 was calculated based on the estimate of annual pregnancy rate, the color pattern phase data, and the proportions of mottled and fused females found to be sexually mature (Table 11).

Seven hundred and twenty-nine of 9,371 animals were mottled females (7.8%) and 2,865 were fused females (30.6%). Of 127 mottled and 1,141 fused females, 47.4 and 88.4% were sexually mature, respectively (Table 11). Average pregnancy rate was 0.469. Production = [(0.078 × 0.474) + (0.306 × 0.884)] 0.469 = 0.144 of the population per year.

TABLE 11.—Sexual maturity (presence of ovarian corpora) in mottled and fused females of *Stenella attenuata*, 1971-73.

Year	Mottled			Fused		
		Mature			Mature	
	N	No.	%	N	No.	%
1971	6	5	(—)	99	82	(82.8)
1972	92	37	(40.2)	473	417	(88.2)
1973	170	85	(50.0)	569	510	(89.6)
Total	268	127	(47.4)	1,141	1,009	(88.4)

Schooling in Relation to Reproduction

Kasuya (1972) reported changes in structure and size of schools of *S. coeruleoalba* correlated with breeding condition and breeding activities. Kasuya et al. (1974) proposed a complex hypothetical system of school formation and breakdown determined by reproductive activities in the Japanese population of *S. attenuata*. They suggested that juveniles of *S. attenuata* in Japanese waters leave breeding schools and school separately, rejoining the breeding schools at puberty. There is nothing to indicate that this happens in the eastern Pacific. We examined the coloration structure (= age structure) of single-school samples. Of 324 single-school samples of seven or more animals, only 1 (of 17 animals) contained no adults (or neonatal calves, which would indicate presence of adult lactating females in the school). This sample (8 two-tone, 2 speckled, and 7 mottled) was from a school of about 600 spotted porpoise, *S. attenuata*, congregated with about 600 spinner porpoise, *S. longirostris*. Given that about half the animals examined were adults, the probability of

a single-school sample of seven containing no "fused" individuals is about 0.01 (= 0.5[7]). If schools consisting only of juveniles were common, many more all-juvenile samples would have been encountered. Conversely, juveniles (two-tone, speckled, and/or mottled) occurred in all but 3 of the 324 samples. It must be concluded that juveniles probably do not school separately in the eastern Pacific. Another possibility, albeit unlikely, is that all-juvenile schools exist but are not captured by tuna seiners.

COMPARISON WITH THE JAPANESE POPULATION

Many of the estimates of life history parameters presented here differ from those published by Kasuya et al. (1974) for the relatively unexploited population of *S. attenuata* in Japanese waters (Table 12). The differences could be caused by 1) differential procedures or analytical methods, 2) intrinsic racial differences between the populations, or 3) differential population status, e.g., exploited versus unexploited. The comparisons below of similarly calculated average estimates, of course, rest on the assumption that the overall samples in both cases were not biased with respect to age or sex. The major sampling differences between the two studies is that the Japanese sample consisted mostly of large samples from a few schools, whereas our sample consisted mainly of aggregated, small samples from many schools. Both studies assume no sampling bias. Comparison of large, single-month samples in the present study with large, single-school samples in the Japanese study (e.g., the October 1972 sample in Figures 15 and 16 with sample number 2 in Figure 2 of Kasuya et al. 1974) indicate very similar length-frequency distributions and support the idea that the aggregated samples are probably not biased, or, if biased, are biased in the same way. This inference is, of course, based on the assumption that the underlying population structures are about the same in the two populations.

The estimate of Kasuya et al. (1974) of length at birth was based on only 5 full-term fetuses and newborn calves versus 86 in the present study. Our estimate can, therefore, be considered more reliable, although the possibility does exist that length at birth is greater in the Japanese population. The difference between the estimated lengths at 1 yr for the two populations is about the same as the difference between the estimates of length at birth. Estimated length at attainment of sexual maturity and maximum length (for males) are also greater for the Japanese samples. The estimate of length at maturity of males is greater in spite of the fact that Kasuya et al. used a lower testis-weight criterion than we did (68 versus 100 g). The average lengths of both adult males and

TABLE 12.—Comparison of estimates of average life history parameters of *Stenella attenuata* by Kasuya et al. (1974) and in present paper.

Parameter (average)	Kasuya et al.	Perrin et al.
1. Length at birth	89 cm	82.5 cm
2. Growth rate in 1st year	4.5 cm per mo	4.6 cm per mo
3. Length at 1 yr	143 cm	138 cm
4. Length at onset of sexual maturity:		
Males	197 cm	~195 cm
Females	187 cm	181 ± 1 cm
5. Age at onset of sexual maturity:		
Males	10.3 layers (10.3 yr)	12 layers (6-11 yr)
Females	8.2 layers (8.2 yr)	9 layers (4.5-8 yr)
6. Average length of sexually mature adults:		
Males	204-207 cm	200.7 cm
Females	192-195 cm	187.3 cm
7. Maximum length:		
Males	234 cm	226 cm
Females	220 cm	220 cm
8. Maximum number of consistently readable tooth layers	~13	12-13
9. Average ovulation rate (based on layers)	0.8 per layer	~1 per layer
	(0.8 per yr)	(1 or 2 per yr) in fully mature, more in younger
10. Pregnancy rate (overall)	0.27 per yr	0.47 per yr
11. Breeding seasons	3 per yr	multiple
12. Gestation	11.2 mo	11.5 ± 0.2 mo
13. Lactation	29.3 mo	11.2 mo
14. Resting	9.8 mo	3.3 mo
15. Length of calving interval	4.19 yr	2.17 yr
16. Sex ratio:		
Overall	0.76 male:1 female	0.81 male:1 female
At birth	1.3-1.5:1	1.00:1
Adults	0.58:1	0.75:1

females are also greater in the Japanese population, and in this case, all four of the estimates are based on large and certainly adequate samples. These differences all suggest that the Japanese form is about 6 to 8 cm larger than the eastern Pacific form.

The estimates of Kasuya et al. (1974) of age at attainment of sexual maturity are based on their conclusion that one tooth layer corresponds to 1 yr of growth. It appears from comparisons of their first-year growth curve with ours (note rate in first year and length at 1 yr) that our first two layers correspond to their first layer. Kasuya (1972) in his paper on growth of *S. coeruleoalba* mentioned observing "one or two faint translucent layers in the thick opaque layer accumulated just after the birth" that were "not used for age determination because it was not expected to show the annual accumulation cycle," and Kasuya et al. (1974) stated that the "dentinal growth layers of this species [*S. attenuata*] does not differ so much from that of *S. coeruleoalba*." After the first year, our hypothesis 2 corresponds to the assumption of Kasuya et al. of one layer per year, e.g., nine layers of Perrin et al. (1973) = eight layers of Kasuya et al. = 8 yr.

The average length of calving interval in both studies was estimated by several methods that converged on the respective central estimates. One minor difference between the two analyses is that Kasuya et al. (1974) did not exclude postreproductive females from the "resting/estrus" group. Thus, their estimate of the average resting/estrus period of 9.8 mo may be a slight overestimate. The probable effect of this on the estimate of length of total calving interval is very small, however, and it therefore seems that the estimates are analytically comparable and that the difference between them is real. Kasuya et al. estimated that individual intervals in the Japanese population vary from 23 to 60 mo, with modes at 28 to 30, 36 to 38, and 54 to 56 mo. The potential thus probably exists for a shift in average length from 50 mo (4.17 yr) to 26 mo (2.17 yr) under exploitation.

Kasuya et al. (1974) used the same methods used here to estimate length of the lactation period and arrived at a "best" estimate of 29.3 mo, some 18 mo longer than our estimate of 11.2 mo. They found that the major shift from milk to solid food occurs at body length of about 133 cm, about the same as in our sample, but that some suckling and lactation of the mother continues for an average additional 20 mo. The prolonged suckling is prob-ably nutritionally a largely nonfunctional aspect of general prolonged parental care. It has been suggested on the basis of comparison of the life histories and behavior of mysticetes and odontocetes that this period in odontocetes may allow for "sophisticated" communicational-navigational training (Brodie 1969). Thus the apparent shorter lactation period in the eastern Pacific, and the concomitant shorter calving interval and higher pregnancy rate, does not necessarily mean earlier effective weaning, but may reflect a truncated parental care period.

The apparent overall sex ratios are almost the same for the two populations, but the proportion of males was higher at birth and lower at maturity in the Japanese samples than in the eastern Pacific samples. A lower proportion of males at birth could be a response to exploitation. Kasuya et al. (1974) suggested that the very low proportions of males in mature age-classes in the Japanese catches could be partially caused by segregation of adult males or by differential catchability but are largely due to differential mortality rates. If the decrease in proportion of males with age is caused by differential mortality, the apparent faster decrease in the Japanese population must mean that the disparity in mortality rates between the sexes is greater there than in the eastern Pacific.

In summary, the two sets of estimates differ in a consistent way, and the differences are real. It seems possible that the differences in some way reflect exploitation in the eastern Pacific.

ACKNOWLEDGMENTS

LITERATURE CITED

AMOROSO, E. C., AND C. A. FINN.
1962. Ovarian activity during gestation, ovum transport and implantation. In S. Zuckerman (editor), The ovary. Vol. 1, p. 451-537. Academic Press, N.Y.

BEST, P. B.
1968. The sperm whale (Physeter catodon) off the west coast of South Africa. 2. Reproduction in the female. S. Afr. Div. Sea Fish., Invest. Rep. 66, 32 p.
1969. The sperm whale (Physeter catodon) off the west coast of South Africa. 3. Reproduction in the male. S. Afr. Div. Sea Fish., Invest. Rep. 72, 20 p.
1970. The sperm whale (Physeter catodon) off the west coast of South Africa. 5. Age, growth and mortality. S. Afr. Div. Sea Fish., Invest. Rep. 79, 27 p.

BRODIE, P. F.
1969. Duration of lactation in Cetacea: An indicator of required learning? Am. Midl. Nat. 82:312-314.
1971. A reconsideration of aspects of growth, reproduction, and behavior of the white whale (Delphinapterus leucas), with reference to the Cumberland Sound, Baffin Island, population. J. Fish. Res. Board Can. 28:1309-1318.
1972. Significance of accessory corpora lutea in odontocetes with reference to Delphinapterus leucas. J. Mammal. 53:614-616.

BRUNN, A.
1935. Flying-fishes (Exocoetidae) of the Atlantic. Systematic and biological studies. Dana Rep. 2(6), 106 p.

CLARKE, M. R.
1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol. 4:91-300.

DAILEY, M. D., AND W. F. PERRIN.
1973. Helminth parasites of porpoises of the genus Stenella in the eastern tropical Pacific, with descriptions of two new species: Mastigonema stenellae gen. et sp. n. (Nematoda: Spiruroidea) and Zalophotrema pacificum sp. n. (Trematoda: Digenea). Fish. Bull., U.S. 71:455-471.

FISHER, H. D., AND R. J. HARRISON.
1970. Reproduction in the common porpose (Phocoena

phocoena) of the North Atlantic. J. Zool. (Lond.) 161:471-486.

HARRISON, R. J., R. L. BROWNELL, JR., AND R. C. BOICE.
1972. Reproduction and gonadal appearances in some odontocetes. In R. J. Harrison (editor), Functional anatomy of marine mammals. Vol. 1, p. 361-429. Academic Press, N.Y.

HASSELBLAD, V.
1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431-444.

HUGGETT, A. ST. G., AND W. F. WIDDAS.
1951. The relationship between mammalian foetal weight and conception age. J. Physiol. 114:306-317.

KASUYA, T.
1972. Growth and reproduction of Stennella caeruleoalba based on the age determination by means of dentinal growth layers. Sci. Rep. Whales Res. Inst. (Tokyo) 24:57-79.

KASUYA, T., N. MIYAZAKI, AND W. H. DAWBIN.
1974. Growth and reproduction of Stenella attenuata in the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. (Tokyo) 26:157-226.

KLEVEZAL', G. A., AND S. E. KLEINENBERG.
1969. Age determination of mammals from annual layers in teeth and bones. Izdatel'stvo "Nauka," Mosc., 1967. (Translated by Israel Program Sci. Transl., Jerus., 128 p.)

KNAUSS, J. A.
1963. Equatorial current systems. In M. N. Hill (editor), The sea. Vol. 2, p. 235-252. Interscience Publ., N.Y.

LAIRD, A. K.
1969. The dynamics of growth. Res./Dev. 20(8):28-31.

LAWS, R. M.
1959. The foetal growth rates of whales with special reference to the fin whale, Balaenoptera physalus Linn. Discovery Rep. 29:281-307.

MØHL-HANSEN, U.
1954. Investigations on reproduction and growth of the porpoise (Phocaena phocaena (L.)) from the Baltic. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 116:369-396.

MOSER, H. G., AND E. H. AHLSTROM.
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.

NISHIWAKI, M., M. NAKAJIMA, AND T. KAMIYA.
1965. A rare species of dolphin (Stenella attenuata) from Arari, Japan. Sci. Rep. Whales Res. Inst. (Tokyo) 19:53-64.

PERRIN, W. F.
1969. Using porpoise to catch tuna. World Fishing 18(6):42-45.
1970a. The problem of porpoise mortality in the U.S. tropical tuna fishery. Proc. 6th Annu. Conf. Biol. Sonar Diving Mammals, Stanford Res. Inst., Menlo Park, Calif., p. 45-48.
1970b. Color pattern of the eastern Pacific spotted porpoise Stenella graffmani Lönnberg (Cetacea, Delphinidae). Zoologica (N.Y.) 54:135-149.
1975. Distribution and differentiation of populations of dolphins of the genus Stenella in the eastern tropical Pacific. J. Fish. Res. Board Can. 32:1059-1067.
In press. Variation of spotted and spinner porpoises (genus Stenella) of the eastern tropical Pacific and Hawaii. Bull. Scripps Inst. Oceanogr., Univ. Calif.

PERRIN, W. F., AND E. L. ROBERTS.
    1972. Organ weights of non-captive porpoise (*Stenella* spp.). Bull. South. Calif. Acad. Sci. 71:19-32.
PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
    1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares,* in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.
RICHARDS, W. J., AND W. L. KLAWE.
    1972. Indexed bibliography of the eggs and young of tunas and other scombrids (Pisces, Scombridae), 1880-1970. U.S. Dep. Commer., NOAA Tech. Rep., NMFS SSRF-652, 107 p.
SECKEL, G. R.
    1972. Hawaiian-caught skipjack tuna and their physical environment. Fish. Bull., U.S. 70:763-787.
SERGEANT, D. E.
    1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Fish. Res. Board Can. Bull. 132, 84 p.

    1973. Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. J. Fish. Res. Board Can. 30:1065-1090.
SERGEANT, D. E., D. K. CALDWELL, AND M. C. CALDWELL.
    1973. Age, growth, and maturity of bottlenosed dolphin (*Tursiops truncatus*) from northeast Florida. J. Fish. Res. Board Can. 30:1009-1011.
TRUE, F. W.
    1906. Notes on a porpoise of the genus *Prodelphinus* from the Hawaiian Islands. Bull. U.S. Fish Comm. 23:811-815.
WYRTKI, K.
    1964. The thermal structure of the eastern Pacific Ocean. Ergänzungsh. Dtsch. Hydrogr. Z. Reihe A 8(6), 84 p.
YOUNG, R. E.
    1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithson. Contrib. Zool. 97, 159 p.

269