

**REPRODUCTIVE BIOLOGY OF
FEMALE SPOTTED DOLPHINS, *STENELLA ATTENUATA*,
FROM THE EASTERN TROPICAL PACIFIC**

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ABSTRACT

Reproductive parameters were estimated from about 4,700 female spotted dolphins collected in the eastern tropical Pacific from 1973 to 1981. From this sample, specimens for which ages were estimated were divided into two subsets and were used to estimate age-specific rates for the northern offshore stock of this species. The youngest sexually mature individual was 10 years old; the oldest immature was 17 years; the youngest and oldest pregnant individuals were 10 and 35 years, respectively. There was high individual variability in the accumulation of corpora with age; the ovulation rate appears to slow abruptly after the eighth ovulation. Average age at attainment of sexual maturity (ASM) for all years ranged from 10.7 to 12.2 years (\bar{x} = 11.4 years) for two sets of age estimates; no significant temporal change in ASM was detected. Correlation between color phase and state of sexual maturity suggests that color phase may be a good indicator of maturity for this stock. The average annual pregnancy rate was about 0.33; this rate did not change significantly with age. The calving interval was 3.03 years (SE = 0.205). The lactation period was 1.66 years, but there was a significant increase noted in the percent lactating from 1973 to 1981. A low percentage of postreproductive females was found in the sample (0.4%) indicating that reproductive senescence is of little importance in reproductive rates of this stock.

Purse seine operations of the yellowfin tuna fishery in the eastern tropical Pacific Ocean (ETP) have caused high mortality of the spotted dolphin, *Stenella attenuata* (Perrin 1969a, 1970). Estimated incidental kills for the northern offshore stock of spotted dolphins were between 100,000 and 400,000 annually throughout the 1960's and early 1970's (Smith 1983). Since 1968, research efforts by the National Marine Fisheries Service (NMFS) have focused on assessing the biological consequences of the large incidental kill of this and other affected dolphins using specimens and data collected by NMFS observers aboard U.S. tuna seiners. Perrin et al. (1976) presented the first comprehensive description of spotted dolphin life history and reproduction for specimens from the ETP. The accumulation of thousands of additional specimens, the sharp decline in dolphin mortality (Smith 1983; Hammond and Tsai 1983), and the improvements made in estimating age since that study (Myrick et al. 1983) have made a new analysis necessary.

The purpose of this paper is to estimate the reproductive parameters of the female spotted dolphin, based on analyses which include more data and a better age estimating method than previous

studies. Reproductive features of the male spotted dolphin (Hohn et al. 1985) and temporal trends in reproduction in the northern offshore stock (Barlow 1985) are discussed in separate papers.

MATERIALS AND METHODS

Samples

The specimens were analyzed as three samples. The "overall" sample contained about 4,700 specimens that had been collected from 1973 through 1981. A second sample for which ages were estimated contained 580 specimens selected randomly from more than 3,500 specimens collected in 1973 through most of 1978 (the 1973-78 aged sample). The randomly chosen 1973-78 aged sample did not include any of the specimens studied by Perrin et al. (1976). The third sample (the 1981 aged sample) was composed of 226 specimens which had been collected in 1981 and for which ages were estimated. It included almost all specimens for which ovaries and teeth were collected in that year. The two aged samples, referred to collectively as the aged sample, are subsets of the overall sample. In several analyses the 1973-78 aged sample was divided into 1973-74 and 1975-78 subsamples in an effort to detect possible temporal changes in reproductive rates. Only the

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northern offshore stock of spotted dolphins (as defined by Smith 1983) is treated in this analysis. The geographic boundary used to divide it from a southern stock is lat. 1°S (Henderson et al. 1980).

Life History Data

Data and specimens were collected by biological technicians aboard tuna purse seine vessels in the ETP. Biological data used in this analysis are body length, color phase, reproductive condition (pregnant, lactating, or resting), and corpora counts for each specimen (see Perrin et al. [1976] for a description of collection and examination procedures). Although there is no certainty that all ovarian corpora persist for life in all delphinids (Perrin and Reilly 1984), corpora counts were used with age to estimate ovulation rates. Counts included corpora albicantia (CAs), corpora lutea (CLs), and in some cases corpora atretica (atretic follicles). Only specimens that had both ovaries examined were included in the ovulation rate analyses.

Age Estimates

Ages were estimated for about 800 specimens (from 1973 to 1978 and 1981 samples) by counting growth layer groups (GLGs, Perrin and Myrick 1980) in the dentine and cementum of decalcified and hematoxylin-stained thin sections (Myrick et al. 1983). Tooth readings were made independently by two readers (A. C. Myrick and A. A. Hohn), without referring to field or laboratory data on size or reproductive condition. For the 1973-78 sample, a tooth of each specimen was read at least three times by each reader. Age estimates by each reader were significantly different (Reilly et al. 1983). To minimize the differences, the mean of the multiple age esti-

mates by each reader was calculated and the average of the two means was used as the estimate of a specimen's age. For the 1981 sample a tooth from each specimen was read once by each reader after calibration tests showed that differences in estimates between readers were acceptably small (Reilly et al. 1983). An average of these two readings was used for specimen age.

We consider the method we used to estimate ages improved over that used by Perrin et al. (1976) because

- 1) the preparation technique we used provides superior resolution of GLGs (Myrick et al. 1983);
- 2) the new method of reading utilizes GLGs in the cementum as well as in dentine and allows a more accurate estimate of maximum age for adults (Myrick et al. 1983; see also Kasuya 1976);
- 3) calibration of GLGs in tetracycline-labeled teeth of Hawaiian spinner dolphins, *Stenella longirostris* (Myrick et al. 1984), has provided a basis for interpreting dental layering within an absolute-time framework (Myrick et al. 1983; Myrick et al. 1984). Perrin et al. (1976) used the term tooth layers in lieu of known time units.

RESULTS AND DISCUSSION

Composition of Samples

Chi-square (contingency) tests were used to evaluate whether fractions of mature, pregnant, and lactating females in the 1973-78 aged sample were a representative subset of the overall sample for those years. For all three tests, differences were not significant ($P > 0.05$).

Reproductive statistics showed some differences between years (Table 1). Chi-square tests were carried out for homogeneity between 1973-74 and

TABLE 1.—Number of sexually mature, pregnant only, lactating only, simultaneously pregnant and lactating, and "resting" female spotted dolphins, and the proportion of the sample pregnant or lactating in the aged and overall samples. The proportion pregnant and proportion lactating include the simultaneously pregnant and lactating specimens.

Years	Number				Proportion		
	Sexually mature	Pregnant only	Lactating only	Pregnant and lactating	Resting	Pregnant	Lactating
Aged							
1973-74	188	57	87	7	38	0.34	0.50
1975-78	205	48	100	13	44	0.30	0.55
1981	149	34	86	9	17	0.29	0.64
Total	542	139	273	29	99	0.31	0.56
Aged and unaged							
1973-81	2,979	780	1,480	151	568	0.31	0.55

constant, a semilog plot of the frequency distribution of corpora counts would be linear. The slope of this line would be negative, and its value would be determined by mortality and ovulation rates. The observed shape of the log-frequency distribution of corpora counts for spotted dolphins (Fig. 3) suggests that ovulation and/or mortality rates are not constant. After about eight ovulations, log-frequencies decrease monotonically and nearly linearly. For up to the first eight ovulations, the rate is apparently much higher (presuming, again, that mortality rates do not change with the number of ovulations and that all CAs persist for life [Perrin and Reilly 1984]) This supports the findings of Perrin et al. (1976) that ovulation rates decrease with reproductive age in spotted dolphins.

Sexual Maturity

The age at which a female first ovulates is considered the age at attainment of sexual maturity (DeMaster 1978, 1984). Using the aged samples, we estimated average age at sexual maturity (ASM) using two methods. For these estimates, ages were grouped by 1-yr intervals: age-class 1 included specimens 0-1.0 yr, age-class 2 from 1.1 to 2.0 yr, etc. The mean age of sexually mature females was 18.7 yr.

Method-One

ASM was estimated from both readers' age esti-

mates using a variation of the method described by DeMaster (1978). Age-specific maturation rates were used to calculate mean ASM as

$$ASM = \sum_{x=1}^w (x - 0.5) P_x$$

where x is age class, P_x is the probability of first ovulating in age class x , and w is the maximum age in the sample. The term $(x - 0.5)$ was substituted for DeMaster's (x) so that the mean age in an age-class interval would be represented by the midpoint of that interval. The terms P_x were estimated as

$$P_x = f(x + 1) - f(x),$$

where $f(x)$ is the probability of being mature at age x . The function $f(x)$ was estimated as the best least-squares fit of a curve (York 1983) to the observed values of percent mature by age class. A 3-parameter sigmoid curve based on a modification of the logistic equation was found to give an adequate fit of the data (Fig. 4).

ASMs were calculated separately for the aged samples, 1973-74, 1975-78, and 1981. There were no significant differences among these samples ($P > 0.05$). The ASM for all samples combined was 10.7 (var. = 0.03) to 12.2 (var. = 0.05) yr for the two readers. The average of these two ASM estimates was 11.4 yr. The precision between readers in age estimates of the 1981 specimens was greater than

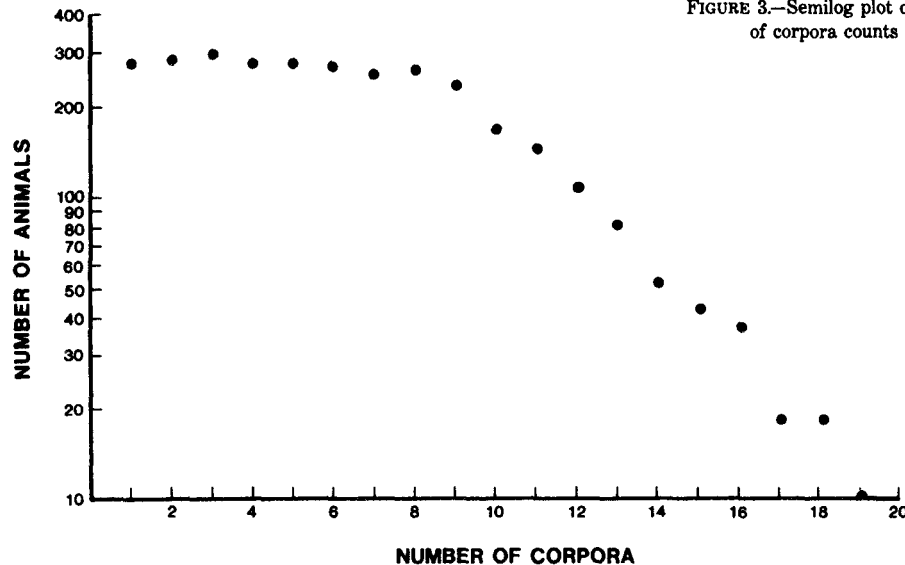


FIGURE 3.—Semilog plot of the frequency distribution of corpora counts for female spotted dolphins.

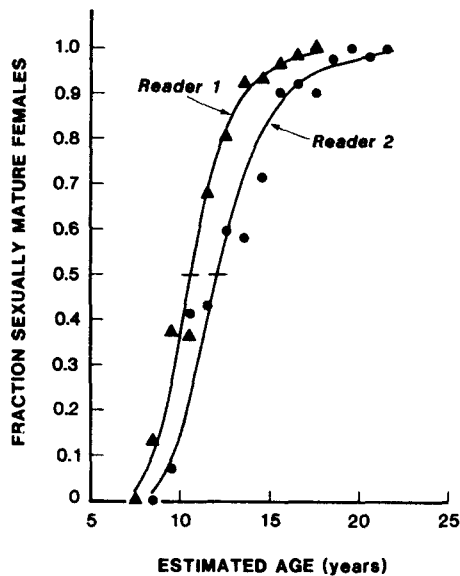


FIGURE 4.—Fraction of sexually mature female spotted dolphins versus age based on estimates of two readers. Logistic curves are fitted to the data. Bars predict ages at which 50% are sexually mature.

for the 1973-78 specimens (Reilly et al. 1983); the mean ASM range for the 1981 sample was 11.6-11.7 yr.

Method Two

The second method we used for estimating ASM was to interpolate, from a maturation curve, the age at which 50% of the specimens were mature. Again, sigmoid curve fits of the percent of mature specimens as a function of age were used for the maturation curves. For all aged samples combined, the method predicts an ASM of 10.6-12.0 yr (for the two readers), with an average of 11.3 yr.

Our overall estimates of ASM (11.3 or 11.4 yr) differ markedly from the ASM estimated for ETP spotted dolphins by Perrin et al. (1976) which was 9 tooth layers, "5.1 to 8.3 yr, depending on [which] layering hypothesis is used" (p. 250). Our estimates also differ from the ASM estimate for spotted dolphins off the Japanese coast by Kasuya (1976) which was 9 yr.

Biases in ASM

All of the above estimates of ASM are dependent on two important assumptions. First, we assume that counts of dentinal and cemental GLGs give precise

and unbiased estimates of age. Second, we assume that our samples are unbiased with respect to the maturity of the specimens collected. Potential biases would result if the assumptions were invalid. Because age estimates of the two readers differ significantly (Reilly et al. 1983), the difference in ASM estimates for the readers (1.5 yr) should be taken as a minimum range in the ASM estimates.

Color Pattern and Maturity

Perrin (1969b) described the ontogenetic development of color pattern in spotted dolphins in the ETP: he divided the development into five sequential phases (neonatal, two-tone, speckled, mottled, and fused) based on patterns of ventral and dorsal spots. Kasuya et al. (1974) described color-phase changes in western Pacific spotted dolphins using somewhat different definitions than those of Perrin (1969b), although the description indicated that the ontogenetic changes were similar to those observed by Perrin. Perrin (1969b) found a close correlation between size and color pattern and (for a smaller sample) between sexual maturity and color pattern. Kasuya et al. (1974) found that the development of the adult color pattern in spotted dolphins from the western Pacific coincides with the attainment of sexual maturity.

In our sample of spotted dolphins, there was considerable overlap in age and length between animals with different color patterns, but a correlation between color pattern and state of maturity was evident. In females from the aged sample, speckled animals ranged from 3 to 18 yr, mottled from 6 to 32 yr, and fused from 10 to 38 yr. A similar overlap occurred in body-length distribution from the overall sample of females, 135-200 cm ($n = 166$), 140-210 cm ($n = 179$), and 155-220 cm ($n = 188$) for speckled, mottled, and fused specimens, respectively. However, 96% of fused animals ($n = 2,764$), 50% of mottled animals ($n = 857$), and only 4% of speckled animals ($n = 559$) were sexually mature.

In addition, for a given length or age class, females with a fused color pattern appeared to have been mature for a longer time than animals with a mottled pattern. For females of similar lengths, mature specimens with a fused color pattern had more corpora than those with a mottled color pattern (Fig. 5). Similarly for the aged sample, the fused specimens within a given length group tended to have more total corpora than mottled specimens, and when specimens in the same body length categories were of similar ages, fused animals had more total corpora.

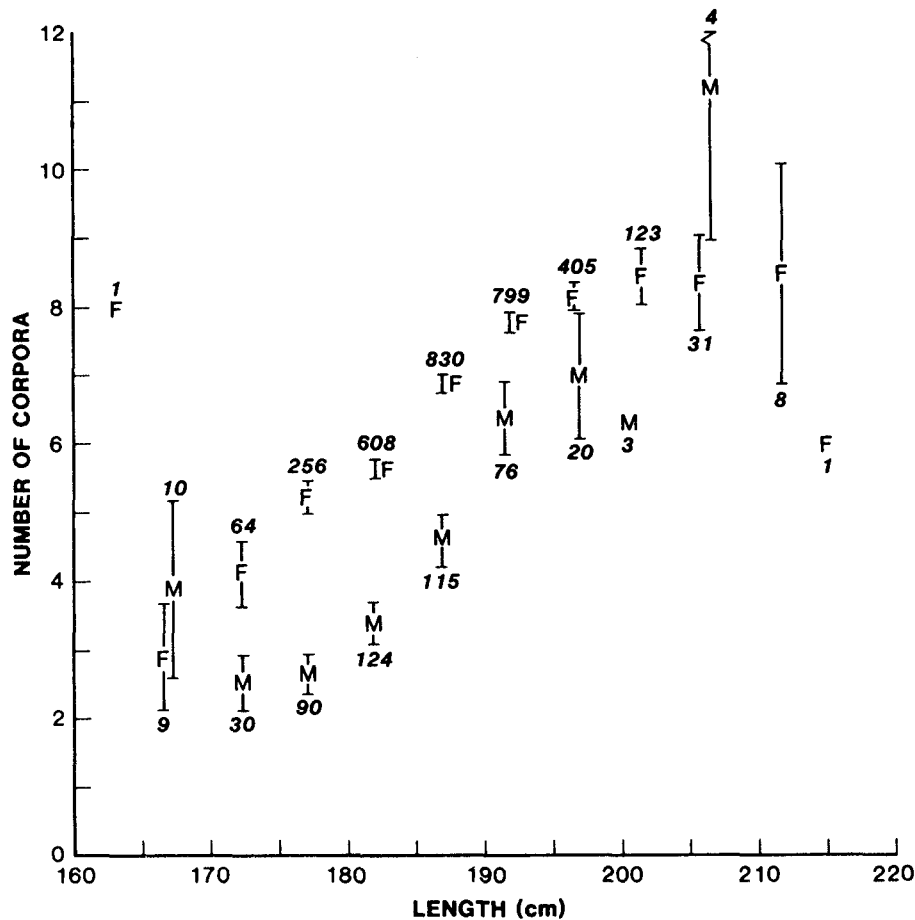


FIGURE 5.—Average number of corpora for mottled (M) and fused (F) color-phase specimens within each 5 cm length grouping for the overall sample of female spotted dolphins. Bars represent one standard error from the mean. Sample sizes are shown.

These results suggest that color phase may indicate sexual maturity more accurately than either age or length. Perrin (1969b) found 0% speckled ($n = 5$), 60% mottled ($n = 16$), and 100% fused ($n = 33$) females to be sexually mature. Using color phases that roughly correspond to the late mottled and fused stages of Perrin (1969b), Kasuya et al. (1974) found that 93% ($n = 30$) of the spotted dolphins in the third stage and 100% in the last (fourth) stage of dorsal spotting were sexually mature. A similar relationship between maturity and color pattern exists in male spotted dolphins in the ETP (Hohn et al. 1985). Assuming that the proportion of mature specimens in a given color phase does not change within a population, it would be possible to estimate the percentage of sexually mature specimens in a sample without having to examine the ovaries for corpora.

Pregnancy Rate

The annual pregnancy rate (APR) of a population is the fraction of mature females that would be expected to give birth in any given year. APR can be estimated as the average fraction of mature females that are pregnant divided by the gestation time in years. The variance of this estimate is approximated by

$$\text{var}(\text{APR}) = (-P/T_G)^2 \text{var}(T_G) + (1/T_G^2) P(1 - P)/n_p$$

where P is the proportion pregnant, T_G is the gestation time, and n_p is the sample size used to estimate P (Perrin and Reilly 1984). We use 0.958 yr (11.5 mo) as the gestation period for spotted

dolphins (Perrin et al. 1976). The variance in gestation time has not been calculated. We can, however, reasonably estimate that 95% confidence limits would span 0.1 yr. From this we estimate the var (T_G) to be 0.000625.

For the aged sample, 31.1% of the sexually mature specimens ($n = 542$) were pregnant. For the overall sample during the same years, 31.6% of the sexually mature specimens ($n = 2,458$) were pregnant and for all aged and unaged mature specimens from 1973 through 1981 inclusive ($n = 2,979$), 31.3% were pregnant (Table 1). By dividing the fraction of pregnant females by the gestation period (0.958), annual pregnancy rates of 0.325 and 0.330 were obtained for the aged and overall samples, respectively. The var(APR) for the overall sample is 0.0005.

To determine whether pregnancy rates changed with age, we estimated percent pregnant for four age-class intervals using the 1973-78 and 1981 samples combined. Sample size was small for estimating age-specific rates with much precision. Nevertheless, we detected neither a sustained increase nor a sustained decrease in the percent of pregnant females with age (Fig. 6); the variability in the percent of pregnant females with age can be accounted for by random sampling ($\chi^2_3 = 4.6$, $P > 0.50$). This result differs from that of Perrin et al. (1976) which indicated a significant reduction in pregnancy rate with age.

Calving Interval

Calving interval is an estimate of the mean period between births for mature females. Typically, it is estimated as the inverse of the annual pregnancy rate (Perrin and Reilly 1984). The principal requirements for calculating the calving interval are unbiased estimates of gestation time and of the fraction of mature females that are pregnant. The standard error in an estimate of calving interval (CI) by these methods is approximated by

$$SE(CI) = (APR^{-4}) \text{var}(APR)$$

(Perrin and Reilly 1984).

Given our calculated APR estimate of 0.330 for the overall sample, the calving interval is 3.03 yr. The standard error of this estimate is about 0.205. Although it is difficult to prove that our estimates of the percent of pregnant females are unbiased, support for such a position is given by Barlow's finding that the percent of pregnant females varies little with sampling conditions (including sampling season, geographic area, dolphin school size, and dolphin kill-per-set) (Barlow 1985). However, if annual variability in the percent of pregnant females is important, binomial sampling theory is likely to underestimate our certainty in estimating the percent of pregnant females, APR, and calving interval. Because no significant trends were detected in the percentage

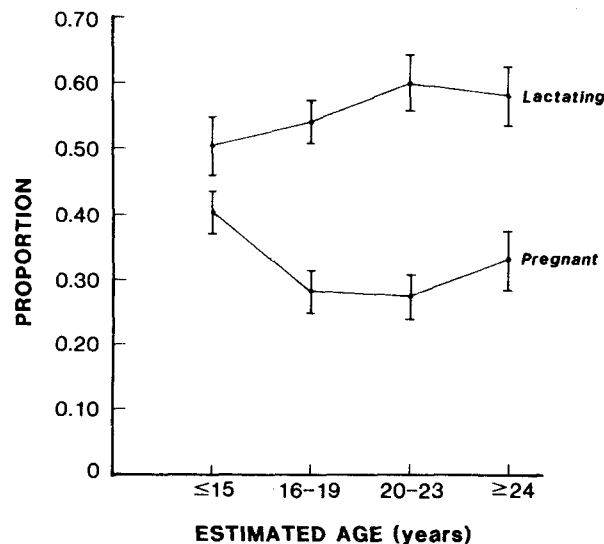


FIGURE 6.—Proportion lactating and proportion pregnant as a function of age for sexually mature female spotted dolphins, in 1973-78 and 1981. Bars represent one standard error from the mean ($n = 542$).

1981 aged samples and between 1975-78 and 1981 aged samples for numbers of specimens pregnant, lactating, and resting. These tests revealed significant differences (1973-74 vs. 1981: $\chi^2_2 = 7.46$, $P = 0.024$; 75-78 vs. 1981: $\chi^2_2 = 6.16$, $P = 0.046$). These differences are the result of an increase in the relative frequency of lactating females (see section on Lactation Period). There were no differences in percent pregnant during this time (see also Barlow 1985).

Ovulation Rate

Individual Variability

Perrin et al. (1976) found high variability in the number of corpora (corpora atretica included) for a given age (in tooth layers). Nevertheless, by fitting a power curve to the average number of corpora as a function of average reproductive age, they determined that the average ovulation rate slowed abruptly from about "four during the first layer, [to] two during the second, and about one per layer thereafter" (Perrin et al. 1976, p. 261).

The sexually mature specimens in the combined aged samples were used in our study to plot average frequency of corpora (corpora atretica excluded) on estimated age (Fig. 1). Regressions for the 1973-74 sample and for the 1981 sample are not significantly different; when the samples are pooled, the resulting slope is 0.61 corpora/yr. A plot of number of corpora on age for all individuals ($n = 542$) in

mature age classes (10 through 38 yr old) for all aged specimens (Fig. 2) showed a significant slope ($P < 0.0001$) but a low correlation ($r^2 = 0.397$), indicating high individual variability. For example, the sample included 12- and 13-yr-olds with 7 or 8 corpora, and 21-yr-olds with 4 or fewer corpora. A 38-yr-old had only 11 corpora (Table 2). These results support those of Sergeant (1962), Brodie (1971), Kasuya et al. (1974), and Perrin et al. (1976), that great individual variation occurs in ovulation rates among odontocetes.

TABLE 2.—Summary of age-related reproductive statistics for female spotted dolphins taken in 1973-78 and 1981.

Variable	Estimated age (years)
Range of ages with no corpora	0-17
Oldest with one corpus	23
Youngest with one corpus	10
Youngest pregnant	10
Oldest pregnant	35
Average age pregnant	18
Oldest simultaneously pregnant and lactating	29
Oldest lactating	36
Youngest lactating	10
Oldest	38

Changes in Rate

Ovulation rate apparently decreases with reproductive age. If ovulation and mortality rates were

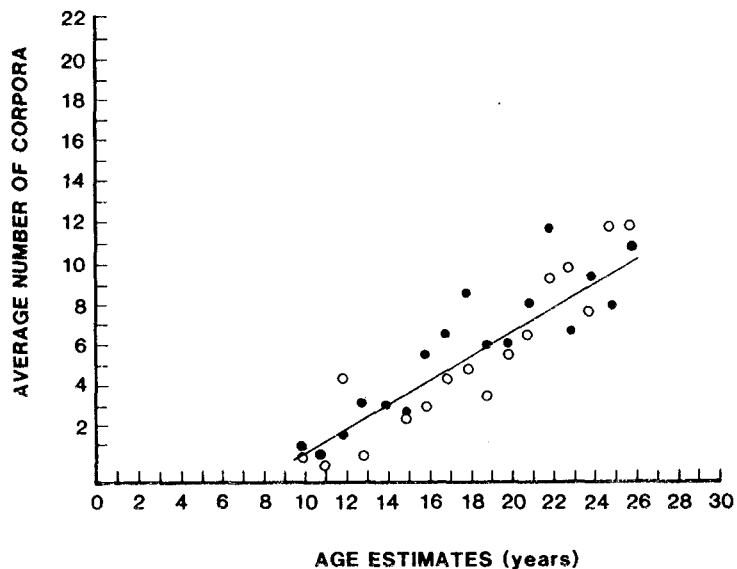


FIGURE 1.—Linear regression of number of corpora on estimated age as gross estimates of ovulation rates in female spotted dolphins. Points represent averages for 1-yr age classes (1973-78 samples = closed circles; 1981 sample = open circles).

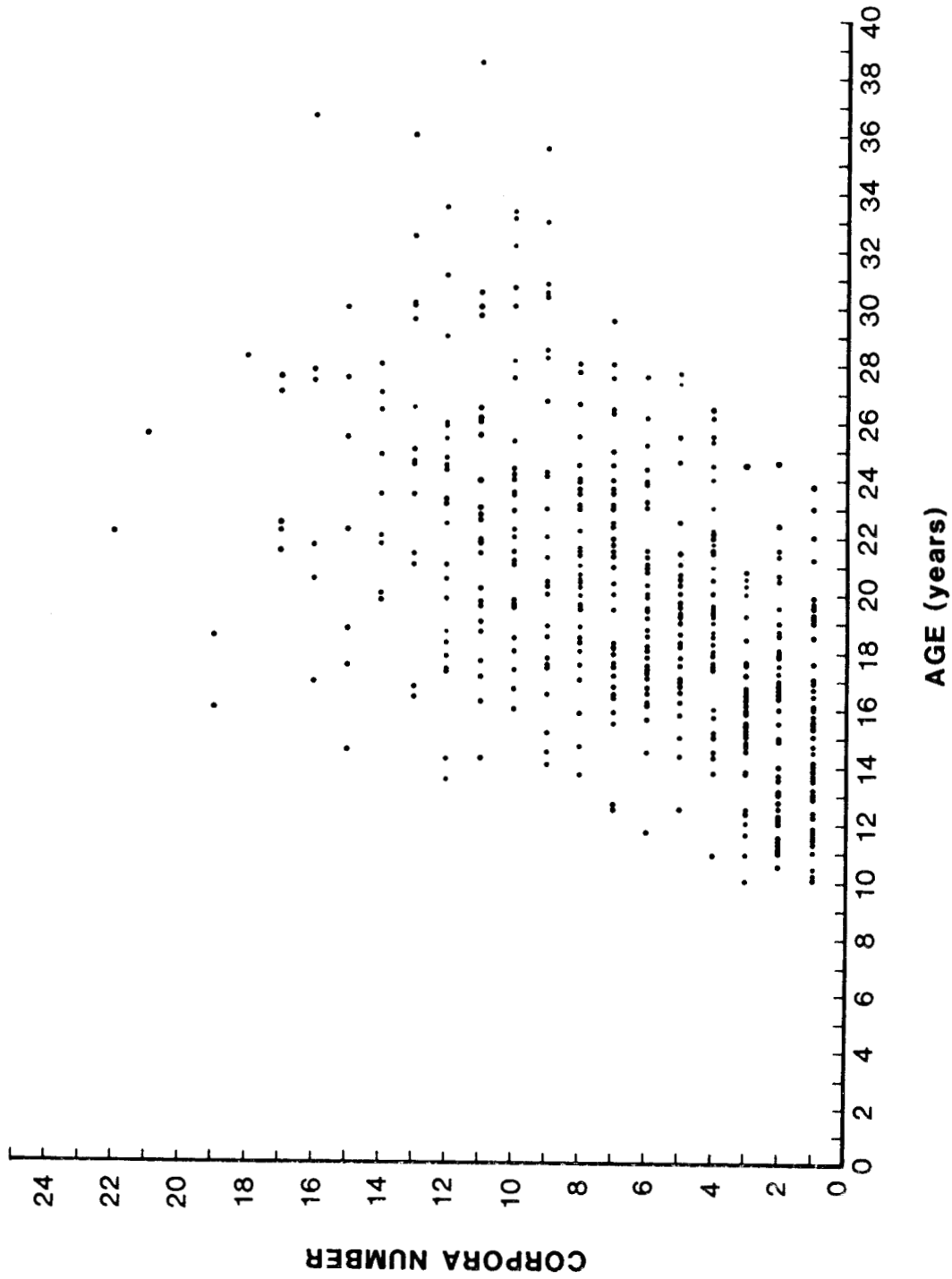


FIGURE 2.—Plot of total corpora (excluding corpora atretica) on estimated age for 542 mature female spotted dolphins collected in 1973-78 and 1981.

of pregnant females from 1974 to 1983 (Barlow 1985) and because no significant changes were found in pregnancy rates with age, estimates of calving interval were not calculated for any of these possible stratifications.

Previous estimates of calving interval for *S. attenuata* include 2.5 yr for the southern offshore ETP stock, 2.7-3.4 yr for the northern offshore ETP stock, and 3.5-3.9 yr for a western North Pacific population (all values taken from Perrin and Reilly 1984, table 6). Our estimate, 3.06 yr, is thus close to previous estimates for the ETP northern stock and falls between the estimates for two other populations.

Lactation Period

The calving cycle in mammals can be thought of as a gestation period, a lactation period, and (in some cases) a resting period. Since gestation and lactation can overlap, the calving interval can be less than the sum of the gestation and lactation periods.

In this study, the duration of the lactation period was estimated as the fraction of mature females that are lactating multiplied by the calving interval in years. Again, the assumption is that all reproductive stages of mature females are sampled without bias. The estimated lactation period for the overall sample is 1.66 yr.

Unlike the percent pregnant, the percentage of lactating females has apparently increased over the years between 1973-74 and 1981 (Table 1). Collaborative evidence is provided by Barlow (1985). Barlow's weighted regression of the percent of lactating females regressed against year predicts values of 46% lactating for 1971 and 69% for 1983. These correspond to a change in mean lactation period from 1.4 to 2.1 yr.

There were no significant differences in proportion of lactating females in different age-classes for all aged samples combined ($\chi^2_3 = 2.58$, $P > 0.25$) (Fig. 6).

Evidence exists for considerable individual variability in calving interval and lactation period. The sum of the estimated gestation time (0.958 yr) plus the mean lactation period (1.66 yr) is about 2.6 yr; the mean calving interval, estimated as the inverse of APR, is roughly 3 yr. We might predict from this that individuals would never be simultaneously pregnant and lactating. In fact, 16% of the sampled pregnant females were lactating. This is implicit evidence of individual variability.

Postreproductive Females

Several criteria have been used to identify postreproductive female odontocetes. Perrin et al. (1976) described postreproductive spotted dolphins and Perrin et al. (1977) described postreproductive spinner dolphins, *S. longirostris*. Both studies were based on the presence of atrophic ("regressed" or "withered") ovaries. In both cases, the incidence of postreproductive females was 1% or less of the sample. In pilot whales, *Globicephala macrorhynchus*, Marsh and Kasuya (1984) found changes in the histology of the ovary, such as a decrease in the volume of the cortex and sclerosis of the arterial walls that are age related and associated with senescence. Senescent females were characterized on the basis of follicle abundance and the incidence of follicular atresia.

Postreproductive females also occurred in our sample. Nine of the mature females collected from 1973 to 1982 had atrophic ovaries and thus are considered to have been reproductively senescent. Their mean ovary weights and maximum follicle diameters were significantly different from the means of the other mature females collected during these years (*t*-test, $P < 0.005$) (Table 3, Fig. 7). None was lactating.

Evidence of decreased fertility was found in some females without atrophic ovaries. Two groups were extracted from the aged sample: 1) those specimens that had 20 or more corpora (all but one was 20 yr old or older), and 2) those specimens that were 20 yr old or older and had only four or fewer total corpora (including atretica). Of the first group ($n = 12$), the mean maximum follicle diameter was larger than that of the atrophic-ovary sample (*t*-test, $P < 0.005$), but the mean weights for both ovaries combined were not significantly different (Table 4). Atretic corpora constituted 24% of the total corpora, less than the frequency of atresia found in the atrophic ovaries (39%). The two specimens in this sample with the highest proportion of corpora atretica also had ovaries with maximum follicle diameter and ovary weights within the range of the atrophic ovaries; in addition, they had no CLs (corpora lutea) or Type 1 corpora. We consider these two females to have been postreproductive. Of the second group ($n = 14$), the mean maximum follicle diameter and ovary weight were not different from those in the sample with more total corpora, but were markedly different from those of the atrophic ovaries (*t*-test, $P < 0.025$). None of these ovaries contained corpora atretica.

Comparison of females in the two groups provides evidence that when the complement of follicles has nearly been expended (through ovulation or atresia), fertility diminishes. Of the first group, 5 of the 12

TABLE 3.—Combined ovary weights, maximum follicle diameter, and corpora counts in "non-atrophic" (normal) ovaries with no corpus luteum ($n = 3,455$) and atrophic ovaries ($n = 9$) of sexually mature female spotted dolphins collected in 1973-82.

Variable	Non-atrophic ovaries		Atrophic ovaries	
	Mean	SE	Mean	SE
Combined ovary weight	4.9	0.05	3.0	0.30
Maximum follicle diameter	2.8	0.06	0.4	0.07
Total corpora excluding atretica	6.8	0.09	12.4	1.36
Total corpora including atretica	7.5	0.11	20.9	1.13
Corpora atretica	0.7	0.04	8.4	1.67
Percent of corpora atretic	6.4	0.30	40.0	7.6

lacked macroscopic follicles. Such specimens have in common: 1) the absence of CLs and Type 1 corpora, 2) a large number of total corpora, 3) a high frequency of atresia (a relatively large proportion of the total corpora), and 4) a maximum follicle diameter of 0.5 mm or less. The incidence of obvious senescence in the sample of spotted dolphins (0.4%) is much less than that in pilot whale samples studied (5% in *Globicephala melana* from the northern Atlantic Ocean [Sergeant 1962] and 25% in *G. macrorhynchus* from the western Pacific [Marsh and Kasuya 1984]). This may be indicative of inherent differences in the social structure or longevity between pilot whales and spotted dolphins.

TABLE 4.—Mean age, maximum follicle diameter, ovary weight, corpora counts, and reproductive states for female spotted dolphins. Type 1 and Type 2 corpora defined by Perrin et al. (1976).

	Age years	Maximum follicle diameter (mm)	Combined ovary weights (g)	Total corpora ¹	Corpora atretica	Percent atretic	Type 1 corpora	Type 2 corpora	Pregnant/lactating (%)
A. Females with 20 or more corpora ($n = 12$)									
Mean	20.2	2.7	4.2	21.3	4.7	21.9	0.5	1.4	40
SE	1.0	0.5	0.5	0.3	0.8	3.6	0.2	0.4	
B. Females 20 yr or older with four or fewer corpora ($n = 14$)									
Mean	22.6	2.5	5.1	2.7	0	0	0.9	0.9	100
SE	0.5	0.3	0.6	0.3	0	0	0.2	0.2	

¹Includes atretica.

specimens were pregnant or lactating. All 14 of the second group were pregnant or lactating. Thus, the first group shows reduced fertility when compared with the second group. Marsh and Kasuya (1984) described an age-related decline in follicle abundance in pilot whales, stating that when follicles are "depleted" the animals become senescent. The reduction in fertility indicated in our sample of spotted dolphins is not strictly age-related; it is more dependent on the number of corpora (including corpora atretica) already present in the ovaries. This has been shown to be true in western Pacific spotted dolphins (Kasuya et al. 1974) and in sperm whales (Best 1967).

In addition to the postreproductive females with atrophic ovaries, four mature females with normal-appearing ovaries had no macroscopic follicles (one of the atrophic ovaries contained no macroscopic follicles). This is similar to the condition described by Marsh and Kasuya (1984). The ovaries of these specimens weighed from 2.2 to 5.9 g, had no CLs or Type 1 or Type 2 corpora, and contained 8-22 total corpora, 12% of which were atretic. None were lactating. They are considered to have been postreproductive also.

Spotted dolphin specimens were judged to have been senescent when they had atrophic ovaries or

CONCLUSIONS

Several of our analyses have yielded results similar to those reported previously for spotted dolphins by others, notably Perrin et al. (1976) and Kasuya et al. (1974). We found ovulation rates to have high individual variability with a markedly higher rate of corpus formation in the earlier reproductive years that decreases after a fixed number of ovulations has occurred.

The conclusions reached by Perrin (1969b) and particularly by Kasuya et al. (1974) with regard to the close correlation between color pattern and sexual maturity in spotted dolphins are also supported by our study. Ninety-six percent of the fused, 50% of the mottled, and only 4% of the speckled specimens were sexually mature. Fused specimens had more corpora and appeared to have been sexually mature longer than mottled specimens of the same age or length.

Our estimated length of the calving interval (3.03 yr) is within the range of earlier estimates calculated for this stock by Perrin and Reilly (1984). It is also within the range of estimates for two other spotted dolphin stocks.

Some of our analyses, however, produced results

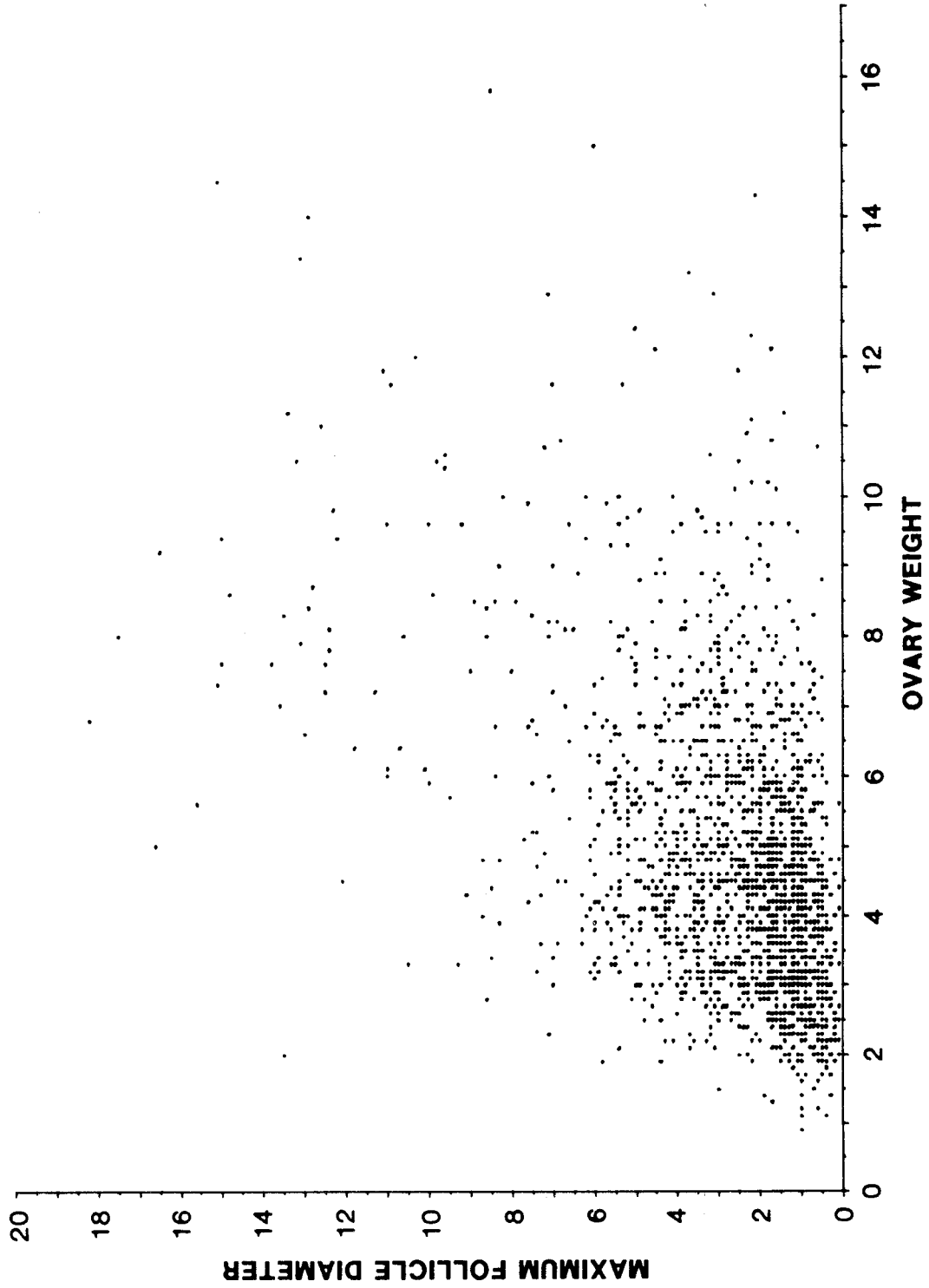


FIGURE 7.—Plot of maximum follicle diameter (mm) on combined ovary weight (g) for 3,464 female spotted dolphins.

that contradict earlier findings. Based on the more reliable method of estimating age in spotted dolphins, we believe that our findings present a clearer picture of the reproductive information than has been reported previously. Our aged samples showed that the youngest sexually mature female was 10 yr old—the same age as the youngest pregnant and the youngest lactating specimens. This suggests that some females must become sexually mature before the age of 10, even though mature specimens younger than 10 were not found in our sample. The average age of a pregnant female in our sample was about 18 yr, and some females of about 35 yr old were pregnant or nursing. These values are substantially higher than estimated previously for this stock (Perrin et al. 1976), but they are similar to, though still somewhat higher than, estimates for the western Pacific stock (Kasuya 1976).

The ASM estimate in this study (about 11.4 yr) is higher than that estimated by Perrin et al. (1976). Our calculations showed no significant difference between the ASM calculated for the 1973-74 sample (taken during years of heavy fishing mortality) and the ASM for the 1981 sample (taken after at least 5 yr of reduced fishing mortality).

An ASM of 11.4 yr means that the youngest average age of first parturition would be 12.3 yr (11 mo later). Since not all females would conceive at first ovulation, the actual average age would be greater than this. The implication of this protracted period before reproduction and a long (3.03 yr) calving interval is that spotted dolphin survival rates must be very high in order to maintain a stable population level.

There is a significant depression in the age structure of the 1973-78 and 1981 aged sample in the 6-12 yr age classes (Hohn and Myrick in prep.²). Similar age-structure patterns, interpreted as reflecting some sort of schooling segregation, have been encountered in studies of other delphinids (see review by Perrin and Reilly 1984). If animals at or near the age of sexual maturity have been regularly under-sampled because their schools were not targets of purse seines (Hohn and Scott 1983), the ASMs calculated for the aged samples could be upwardly biased. However, there is no evidence that the depression in the age structure represents missing animals that were sexually mature.

The annual pregnancy rate averaged 0.33 from

1973 through 1981. There were no sustained upward or downward changes in age-specific pregnancy rates with increased age. A similar result was shown by Kasuya (1976) for the western stock, although his values were somewhat lower than the rates we have estimated for the northern offshore stock. Our estimates are different from those of Perrin et al. (1976) who reported high pregnancy rates among younger specimens and a decreasing rate with increased age.

The implications of an apparent progressive increase in the lactation period are enigmatic. It is probable that the increase in lactation period reflects the decrease in per capita mortality of calves due to the more efficient releasing procedures employed by the purse seine fleet from the mid-1970's onwards. Decreased mortality of nursing calves would be reflected by an apparent increase in the number of lactating females because fewer nursing periods were ended prematurely.

Our study of postreproductive specimens suggests that fertility diminishes as the complement of follicles for a female becomes expended through ovulation or atresia. Female spotted dolphins with atrophic ovaries or with no macroscopic follicles are reproductively senescent. Although the expenditure of follicles progresses with age, reduction in fertility is not strictly age related. The occurrence of reproductive senescence in spotted dolphins in this study was negligible and the number of specimens in this state probably is of limited importance to estimates of reproductive parameters.

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