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REPRODUCTIVE MATURITY AND SEASONALITY OF MALE SPOTTED DOLPHINS, *STENELLA ATTENUATA*, IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

We estimated age at attainment of sexual maturity and examined reproductive seasonality for male spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific Ocean. Maturity was determined by histological examination of testes. Average age at sexual maturation was 14.7 yr (the mean of two readers' age estimates). Testis and epididymis weight and seminiferous tubule diameters were reliable indicators of maturity, whereas age, length and color phase were less reliable. Seasonality was determined by changes in testis and epididymis weight, relative quantity of spermatids and spermatozoa, and lumen diameter, as well as an index of testis development (weight of the right testis and epididymis divided by length of the right testis). Testis and epididymis weights and index values peaked in July and August, midway between two predicted mating seasons for the northern offshore stock, but spermatozoa levels were elevated during the predicted breeding seasons.

Key words: spotted dolphin, *Stenella attenuata*, reproduction, sexual maturity, seasonality, testis histology.

Estimates of age and size of dolphins at sexual maturation are useful for comparative biological studies and can provide information for management of populations that are subject to mortality by man. The determination of sexual maturity in male dolphins must initially be based on histological examination of cross-sections of gonadal tissue, which is more accurate than gross observation. From this examination, states of maturity can be correlated with more readily available life history data such as body length, testis weight and age. For spotted dolphins, maturation has been correlated with an ontogenetic series of color phases (Perrin 1969, Kasuya *et al.* 1974). In addition, seasonal trends in testis development can identify or corroborate probable mating seasons.

In this paper, we describe states of maturity (immature, pubertal and mature) for a sample of male spotted dolphins based on testis histology. After defining maturity histologically, we calculated age and body length at attainment of sexual maturity. We also describe relationships between testis weight, testis length, seminiferous tubule diameter, body length, age and color phase as well as seasonal changes in testis tissue characteristics.

Materials and Methods

The Samples

We used spotted dolphin specimens that had been collected by biological technicians from the National Marine Fisheries Service (NMFS) and Inter-American Tropical Tuna Commission aboard tuna purse-seine vessels in the eastern tropical Pacific (ETP). Collection procedures were described by Perrin *et al.* (1976). Specimens from both the northern and southern offshore stocks were examined (for stock definition, *see* Perrin *et al.* 1985).

We used two subsets of the sample from the northern offshore stock. The first, the life history sample, included all specimens collected from 1973 to 1982 for which testis and epididymis weights were recorded (n = 3,061). Generally, only the right testis and epididymis were collected (all testes analyses in this study refer to the right testis only). The samples were preserved in formalin and weighed in the laboratory. The second subset was divided into two samples (Fig. 1): (1) the aged sample consisted of 800 northern offshore specimens that were randomly selected from the 1973–1978 portion of the life history sample for an age distribution study; (2) the histology sample (n = 269) comprised all fused and mottled specimens for which age, testis and epididymis weight, and preserved testis tissue were available; it included 244 specimens drawn from the aged sample and 25 from the study by Perrin *et al.* (1976). Only the specimens from the random aged sample were used to estimate age and length at maturation. The techniques for tooth preparation and age determination were described by Myrick *et al.* (1983). The age estimates used in these analyses were described by Reilly *et al.* (1983). All age estimates for specimens in the aged sample were made independently by two readers. Although there are reader differences in the age estimates, we have no reason to expect that one set of estimates is more accurate than the other. Therefore, both sets are used to estimate age at maturation.

We also examined reproductive seasonality in testis and epididymis weight for the southern stock using criteria used to define maturity in the northern offshore specimens.

The Analyses

The testis tissue was thin-sectioned (6 μm), stained with haematoxylin and eosin, and examined for the presence and abundance of spermatogonia, spermatocytes, spermatids and spermatozoa, as well as for relative quantity of interstitial tissue, tubule elongation, lumen size and seminiferous tubule elon-

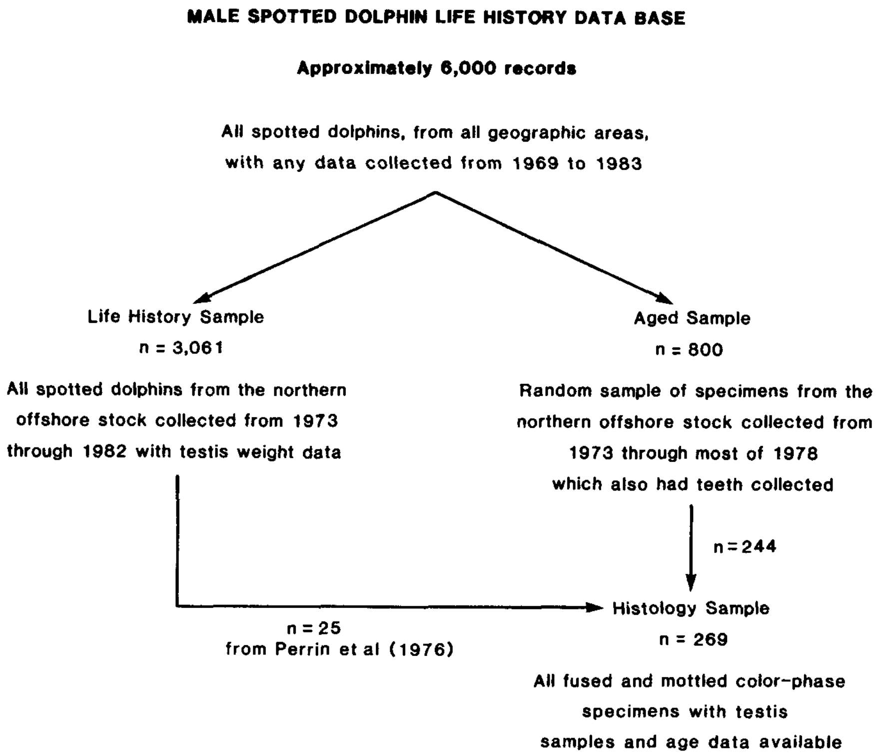

Figure 1. Relationships among the samples described in the text.

gation. We categorized the interstitial tissue according to the amount of tissue present: little, moderate or abundant in quantity. (Some care must be used in interpreting these categories since some interstitial tissue shrinkage occurs during fixation.) We categorized the tubules according to the degree of elongation: none, some or extensive. Lumen size was scored as none, small, medium and large. Tubules with lumen size "none" were those that were densely packed with tissue and spermatogonia. Small lumens were generally filled with tissue although the tissue was less densely packed than in those with no lumen present, partly because the tubules were enlarged. Medium lumen size had less tissue present than in small lumens and the tissue had separated in the center to leave a small, clear open space. Large lumens contained essentially no intra-tubular tissue. Only the products of spermatogenesis, especially spermatids and spermatozoa, were observed in the central lumen, or a large space devoid of tissue occupied nearly the entire tubule. Seminiferous tubule diameter was measured using an ocular micrometer and taken as the mean of at least 5 representative cross-sections of tubules that were circular in appearance.

Three states of sexual maturity were defined: immature, pubertal and mature. These were based on criteria of testes maturation used for other mammals (Charny *et al.* 1952, Laws 1956*a*, Hirose and Nishiwaki 1971, Bloom and

Fawcett 1975, Collet and Saint Girons 1984). The primary criterion was the presence or absence of cells in the various stages of spermatogenesis. In specimens classified as immature, seminiferous tubules contained primarily spermatogonia and had no lumen or cells of later stages. The tubules were imbedded in abundant interstitial tissue, densely packed, circular in cross-section and not elongated. The tubules were distinctly smaller than those in pubertal or mature specimens. In specimens classified as pubertal, the seminiferous tubules had slight elongation (although they were still relatively small in diameter), there was little interstitial tissue in the space between tubules, the lumen was small and empty and, most importantly, spermatogonia, spermatocytes and (rarely) spermatids were present. There were no spermatozoa. The primary criterion of sexual maturity was the presence in the tubules of spermatogonia, spermatocytes, spermatids and often spermatozoa. If any spermatozoa were found, the specimen was considered to have been mature. When all stages of spermatogenesis were present, they were in sequential order, by stage of development, from the tubule epithelium to the lumen. Although the presence of spermatozoa explicitly indicates sexual maturity, some specimens with no spermatozoa were also considered mature on the basis of other criteria: distinctly elongated seminiferous tubules with large diameters, a large lumen and little interstitial tissue.

After we had identified maturity states histologically, we estimated the fraction of immature, pubertal and mature specimens within each of the five ontogenetic color phases: neonatal (no spots), two-tone (no spots), speckled (dark spots ventrally), mottled (light spots ventrally and dorsally) and fused (ventral spots convergent) (Perrin 1969).

We calculated an index of testis development (right-testis and epididymis weight in grams divided by right-testis length in millimeters), which defines maturity in terms of unit of testis weight per unit of testis length, to remove variability in testis weights among specimens of different sizes. We calculated the index for specimens from the histology sample for which right-testis lengths were available ($n = 268$) and applied the results to the life history sample to estimate maturity.

On the basis of the histology results, we used a non-parametric method (Cooke[1]) to estimate the age at which males attain sexual maturity. The mean age of attainment of sexual maturity was calculated as

$$\bar{X}_{ASM} = \sum_{i=0}^{k} P_i \quad (1)$$

where

i = age class interval from i to i + 1 yr
P_i = proportion of immature individuals in age class i
k = age class of oldest immature individual.

The formula given by Cooke differs in that he assigns ages to the midpoint of age-class intervals, thus subtracting 0.5 from the above sum. Standard errors

[1] Cooke, J. G. Manuscript. The estimation of mean ages of sexual maturity from age samples. Paper SC/36/022 presented to the International Whaling Commission Scientific Committee, Cambridge, U.K., June 1984.

Table 1. Estimated age, length and gonadal characteristics by state of maturity in *S. attenuata*. Sample sizes were 61 immature, 27 pubertal and 181 mature.[1]

Characteristic and maturity state	Mean	Standard error	Range
Estimated age (years)			
Immature	11.3	0.4	4.0–19.2
Pubertal	16.7	0.7	10.0–24.0
Mature	22.4	0.3	11.8–37.0
Total body length (cm)			
Immature	175.0	0.9	154.0–188.0
Pubertal	186.0	1.7	174.0–204.0
Mature	200.4	0.6	175.0–231.0
Seminiferous tubule diameter (μm)			
Immature	46.1	0.9	29.9–68.8
Pubertal	77.1	3.8	51.8–135.0
Mature	169.1	2.6	92.5–276.0
Right-testis weight (g)			
Immature	18.7	1.1	6.9–52.0
Pubertal	70.2	6.9	21.0–155.0
Mature	498.4	18.8	127.0–1,448.0
Right-testis length (mm)			
Immature	95.6	2.2	64.0–142.0
Pubertal	146.2	6.0	100.0–208.0
Mature	250.1	3.1	113.0–370.0
Index of testis development			
Immature	0.2	0.0	0.1–0.4
Pubertal	0.5	0.0	0.2–0.9
Mature	1.9	0.1	0.7–4.2

[1] Sample size was 60 (rather than 61) for total length of immatures and 180 (rather than 181) for testis length and index of testis development.

in estimates of ASM were calculated from Cooke's variance formula (Cooke, equation 2). We also fit a three-parameter sigmoid curve to the proportion of mature specimens within each age class (regression weights determined by the inverse of the binomial variances):

$$P(X) = \frac{e^{(P1+P2(X)^{P3})}}{1 + e^{(P1+P2(X)^{P3})}} \tag{2}$$

where P(X) is the proportion mature within each age class, X, and P1, P2 and P3 are parameter values.

The body length at which males attain sexual maturity was determined using Cooke's method applied to the proportion of mature males within 5-cm body-length groups.

We analyzed the data for evidence of seasonal trends. The histology sample

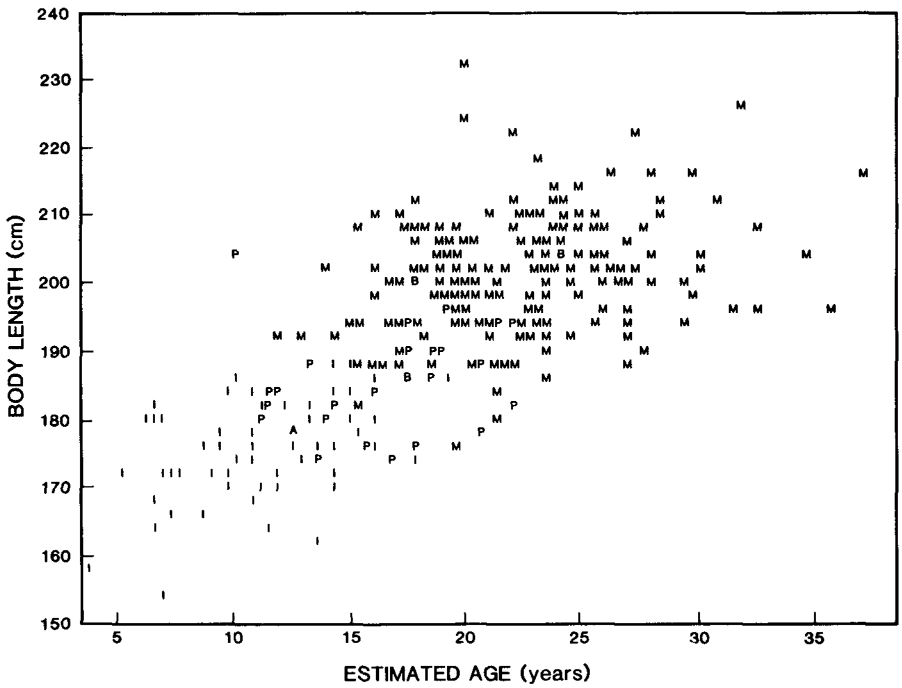

Figure 2. Body length as a function of age. I = immature, P = pubertal, M = sexually mature, A = overlapping immature and pubertal, B = overlapping pubertal and mature.

was examined for seasonal trends in mean tubule diameter, mean lumen diameter and the relative number of spermatids and spermatozoa. Trends in testis and epididymis weights for both the northern and southern stocks in the life history sample were also examined.

We examined the relation between right-testis weights with and without epididymides for the specimens collected in 1982 (the only year for which such data were available).

Results

Of the 269 specimens in the histology sample, 61 were classified as immature, 27 as pubertal and 181 as mature. The mean values for seminiferous tubule diameter, right-testis and epididymis weight, body length, and age were all significantly greater for mature specimens than for immature and pubertal animals (t-tests, $P < 0.001$, Table 1).

Overlap was substantial for age and body length between immature, pubertal and mature specimens (Table 1, Fig. 2). There was less overlap for testis and epididymis weight; testis weight exceeded 140 g in only two non-mature dol-

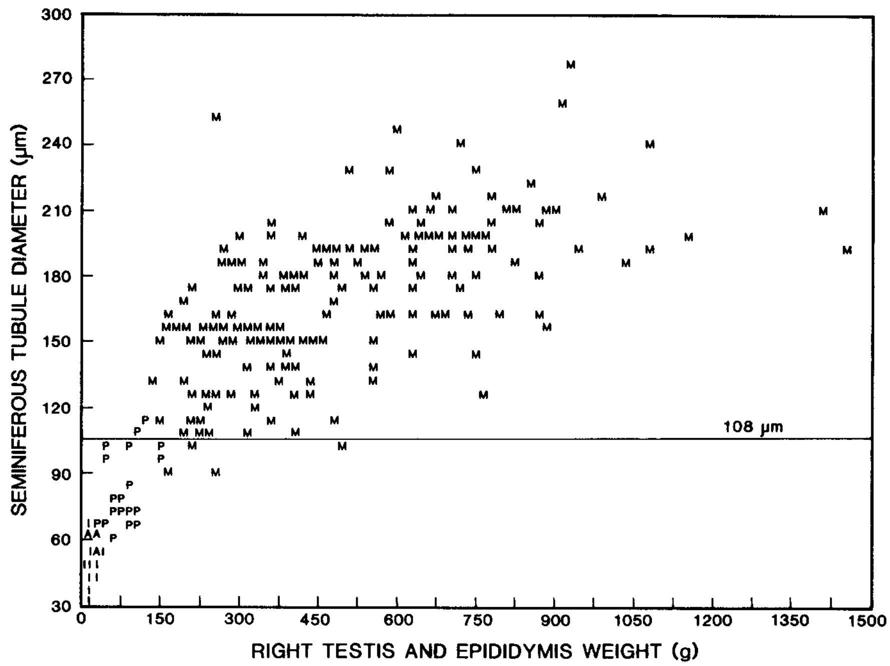

Figure 3. Seminiferous tubule diameter as a function of testis + epididymis weight; 108 µm is the approximate median seminiferous tubule diameter at attainment of sexual maturity. See Figure 2 for data codes.

phins (both pubertal) and only one mature specimen had a testis weight less than 140 g (Fig. 3).

Seminiferous tubule diameter was a good indicator of maturity. Except for two pubertal specimens, all specimens that had a tubule diameter exceeding 108 µm were mature. Only four mature specimens had a smaller tubule diameter (Table 1, Fig. 4).

Color phase was correlated with sexual maturity (Table 2). All but one (0.6 percent, n = 165) of the mature specimens were fused. Similarly, 76 percent of the pubertal specimens (n = 25) were fused. (The exclusion of speckled and younger specimens will not affect estimates of maturation since only 0.8 percent of speckled specimens (n = 520) in the life history sample had testis weights that were equal to or greater than the lowest testis weights for mature (mottled and fused) specimens [Table 2].)

Within each body length group in the life history sample, testes and epididymides were heavier in fused than in mottled specimens (Table 3, Fig. 5). (Neonatal, two-tone and speckled specimens were not plotted because their testis and epididymis weights were much below those of the mottled specimens.) Similarly for the aged sample, when fused and mottled animals within a given body length group were of similar ages, the fused animals had heavier testes and epididymides.

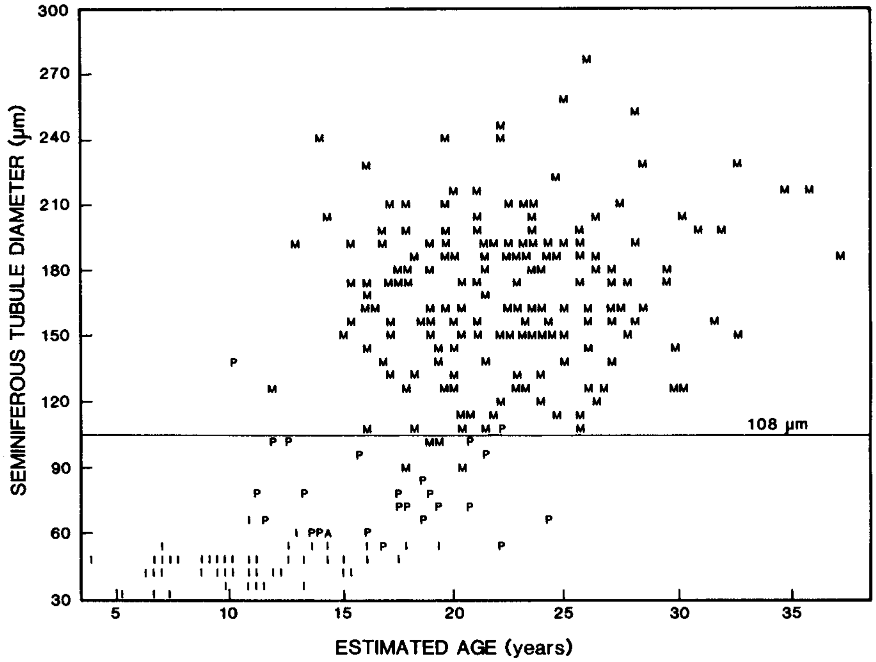

Figure 4. Seminiferous tubule diameter as a function of age; 108 μm is the approximate median seminiferous tubule diameter at attainment of sexual maturity. See Figure 2 for data codes.

Index of Testis Development

The difference between index values for immature, pubertal and mature specimens was significant (ANOVA, $P < 0.0001$, Table 1). The median index value was 0.33 at attainment of puberty and 0.75 at attainment of maturity.

For fused males from the northern offshore stock, the testis index was distributed bimodally (Fig. 6). (This was not the case for testis weight data.) The first peak, from 0.01 to 0.3, corresponds to immature males and the second peak (mode at 1.6) corresponds to mature males. Data for spotted dolphins from the southern stock showed nearly the same pattern.

Mean index values (Table 3) were significantly different among specimens in the five color phases (ANOVA, $P < 0.001$). The mean index value for mottled specimens (0.35) was close to the median index value at attainment of puberty (0.33).

Age at Sexual Maturation

The mean age at attainment of sexual maturity (ASM) for specimens in the histology sample was 13.2 yr (SE = 0.30) based on one reader's estimates and 16.3 yr (SE = 0.44) based on the other reader's estimates ($\bar{x}$ = 14.7). The maturation ogives for these age estimates are shown in Figure 7. The readers'

Table 2. Number of immature, pubertal and mature mottled and fused specimens from the random histology sample.

Color phase	Number immature	Number pubertal	Number mature
Mottled	40	6	1
Fused	14	19	165

differences in estimates are large and partly reflect imprecision in age estimation (Reilly *et al.* 1983). The mean ASM from the average of the two readers' estimates from the aged sample were 16.8 (1973), 15.8 (1974), 14.8 (1976), 16.2 (1977) and 16.2 (1978). (The 1975 sample was too small to allow meaningful analysis.) These estimates show no trend (linear regression, P = 0.70).

The mean body length at attainment of sexual maturity based on the histology sample was 186.4 cm for all years combined. For the larger life history sample from 1974 to 1982, the mean lengths at attainment of sexual maturity (index values ≥0.75) were 185.5, 187.5, 185.8, 188.6, 186.0, 188.8, 186.7, 191.0 and 192.0 cm, respectively. The increase in mean length at sexual maturity during those years was marginally significant (linear regression, P = 0.063).

Seasonality

Mean testis and epididymis weights (Fig. 8) and index values (Fig. 9) for fused specimens (life history sample) showed peaks in July through August and in April. Differences among months were significant (ANOVA, P = 0.001 for testis and epididymis weights and P = 0.0035 for index values). Similar patterns existed for the southern stock for months for which data were available (no specimens were collected in July or August) (Figs. 8 and 9). Since the relationship between weights of the right testis with and without epididymis is nearly linear (Fig. 10), presence or absence of the epididymis made no difference in the trends.

Seasonal changes in testis histology were also evident. Changes in mean tubule diameter of mature specimens followed a seasonal pattern almost iden-

Table 3. Mean testis weight and index of testis development values by color phase in *S. attenuata* (northern offshore stock).

Color phase	Right-testis weight (g)			Index of testis development		
	Mean	SE	*n*	Mean	SE	*n*
Neonatal	2.4	0.2	56	0.06	0.002	55
Two-tone	6.3	0.2	404	0.10	0.003	403
Speckled	15.0	2.2	520	0.16	0.009	524
Mottled	60.1	5.9	501	0.35	0.022	499
Fused	388.8	6.8	1,564	1.55	0.022	1,566

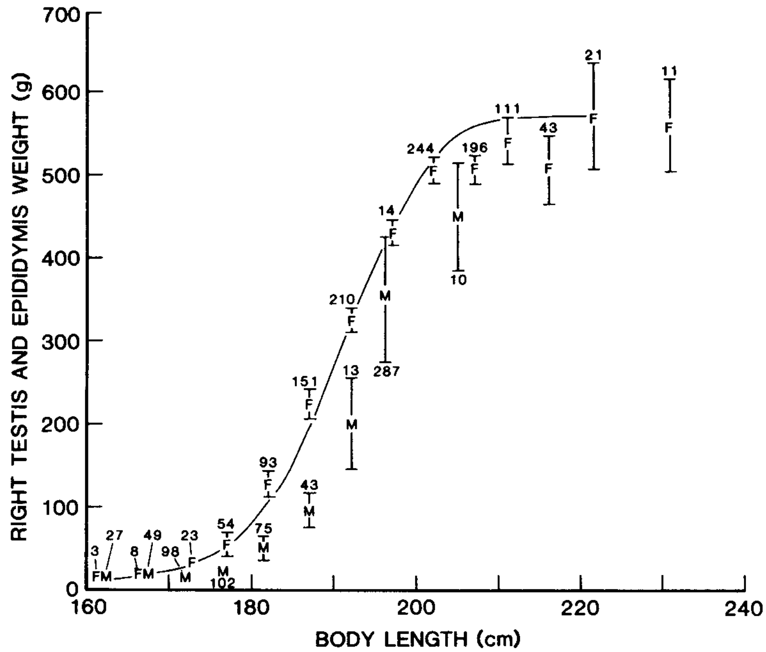

Figure 5. Mean testis + epididymis weight as a function of mean specimen body length in 5-cm length intervals for mottled (n = 431) and fused (n = 1,455) specimens. A three-parameter sigmoid curve is fitted to the data for fused specimens. Error bars represent one standard error from the mean. The sample sizes are given above or below the error bars. M = mottled, F = fused.

tical to that of the testis and epididymis weights and index values (Fig. 11). Monthly differences were significant (ANOVA, P = 0.0325). There was also a seasonal pattern in number of specimens that had relatively large quantities of spermatids and spermatozoa (Fig. 12); the number of specimens with spermatids peaked in April, and the number of specimens with spermatozoa peaked in May. The mean diameter of the lumen was greatest in April. There were also peaks of specimens with spermatids and spermatozoa in January and, although spermatozoa levels declined rapidly from May to August, spermatids were observed in most mature specimens throughout the year. We saw no evidence of full recrudescence.

Discussion

Sexual Maturity

Relatively few estimates of the age at attainment of sexual maturity have been made for dolphins based on histological examination of testes. In most of the studies, specimens were considered to be sexually mature if spermatozoa were found in the testes or epididymides (Sergeant 1962, Sergeant *et al.* 1973, Kasuya *et al.* 1974, Kasuya 1976, Perrin *et al.* 1976, Perrin *et al.* 1977,

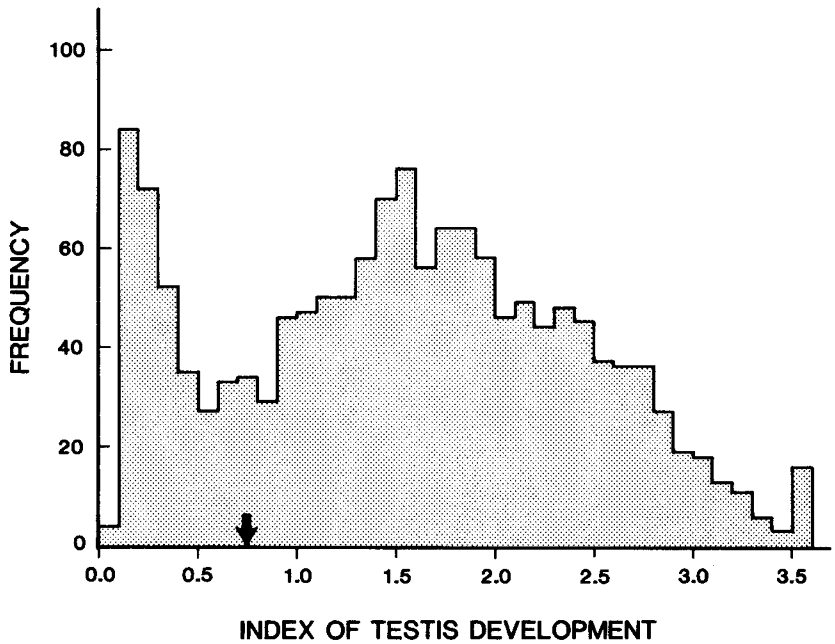

Figure 6. Frequency distribution of the index of testis development (testis + epididymis weight [g] divided by testis length [mm]) for fused specimens (n = 461). The arrow marks the median index value at the attainment of sexual maturity.

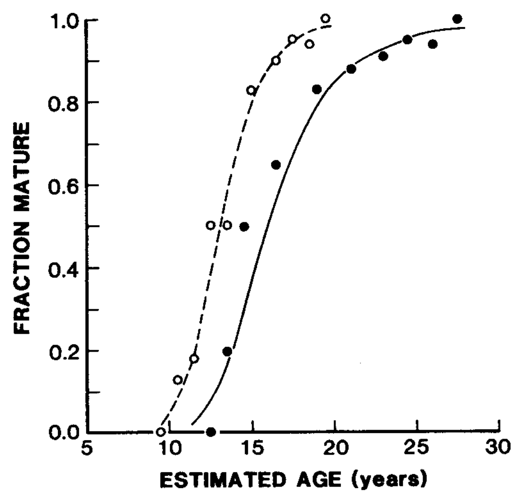

Figure 7. Sigmoid curves fitted to the fraction of sexually mature specimens within each age class based on estimates by each of two readers.

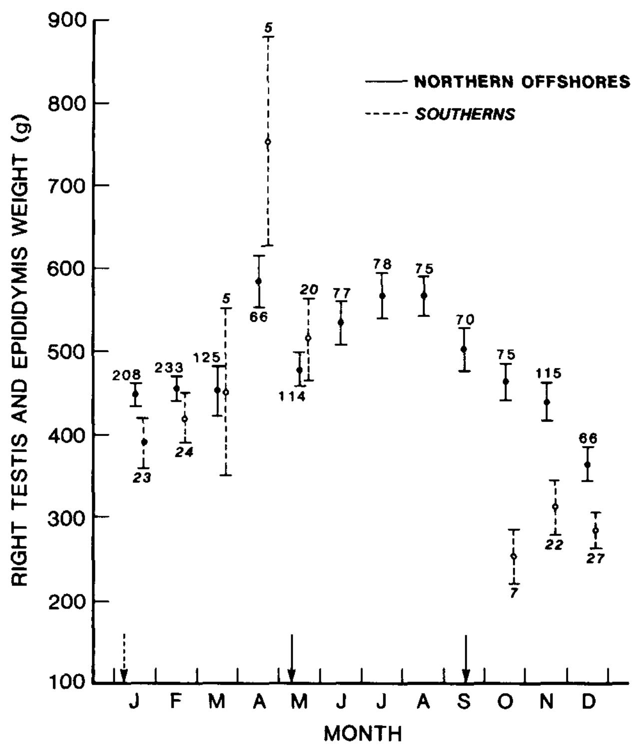

Figure 8. Monthly mean testis + epididymis weight for fused specimens from the northern and southern offshore stocks. Sample sizes are above or below the error bars, which represent one standard error from the mean. The arrows mark the predicted birth dates of the primary calving periods.

Collet and Saint Girons 1984). Sergeant (1962) also considered long-finned pilot whales to be "functionally" mature if the epididymides contained seminal fluid. The state of "pubertal" (also called prepubescent or maturing) has been distinguished from "mature" and "immature" by the presence of spermatogonia and spermatocytes but the absence of spermatozoa (Hirose and Nishiwaki 1971) and relatively narrow seminiferous tubules (Collet and Saint Girons 1984).

Information gained from examination of testes has been used to estimate age, body length and testis weight at maturation in several delphinids (*see* Perrin and Reilly 1984). Estimates of age at maturation for these studies are: *Delphinus delphis,* 6 yr (Collet and Saint Girons 1984); *S. coeruleoalba,* 9 and 8.7 yr (Kasuya 1976, Miyazaki 1977); *S. attenuata,* 11.8 yr (Kasuya 1976) and 12 "layers" (most likely estimate of 11 yr) (Perrin *et al.* 1976); *S. longirostris,* 8.5 to 11.5 yr (Perrin *et al.* 1977); *Tursiops truncatus,* 12 yr (Sergeant *et al.* 1973); and *Globicephala melaena,* 12 yr (Sergeant 1962). It appears that sexual maturity in males is attained at a greater age in spotted dolphins than in many other pelagic dolphins.

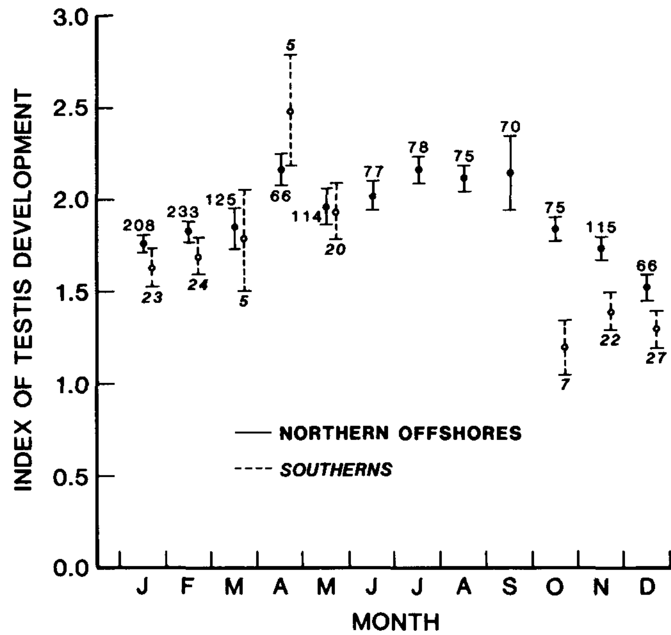

Figure 9. Monthly mean index of testis development for fused specimens from the northern and southern offshore stocks. Sample sizes are above or below the error bars, which represent one standard error from the mean.

Our estimate is higher than that determined for spotted dolphins in the western Pacific. This may reflect real population differences or differences in age determination techniques (*see* Kimura 1980). The methods used to calculate age at attainment of sexual maturity varied greatly, however, for all the species. For example, Kasuya *et al.* (1974), Kasuya (1976) and Miyazaki (1977) estimated median age (and length) at attainment of sexual maturation as that age (and length) at which 50 percent of the specimens were predicted to be mature based on a least-squares linear regression of the proportion of mature specimens within each age (and length) class. Perrin *et al.* (1976) determined that sexual maturation, as indicated by a rapid increase in the diameter of the seminiferous tubules and increase in testis and epididymis weight, is attained at about 10–14 dentinal growth layers (GLGs) and, therefore, the "average" age at sexual maturation is approximately the midpoint of this range. The "average" length of maturation was estimated as the average length of males with 12 GLGs. A similar method was used by Perrin *et al.* (1977) for the spinner dolphin; they determined that spermatogenesis is histologically evident in 50 percent of testes and epididymides that together weighed 94 g. This weight was reached, on "average," at about 9 GLGs, and the average length of specimens with 9 GLGs was 170 cm. Sergeant (1962) first estimated the "mean" body length (16 ft) of functional maturity in the pilot whale as the midpoint between the smallest functionally mature and largest immature spec-

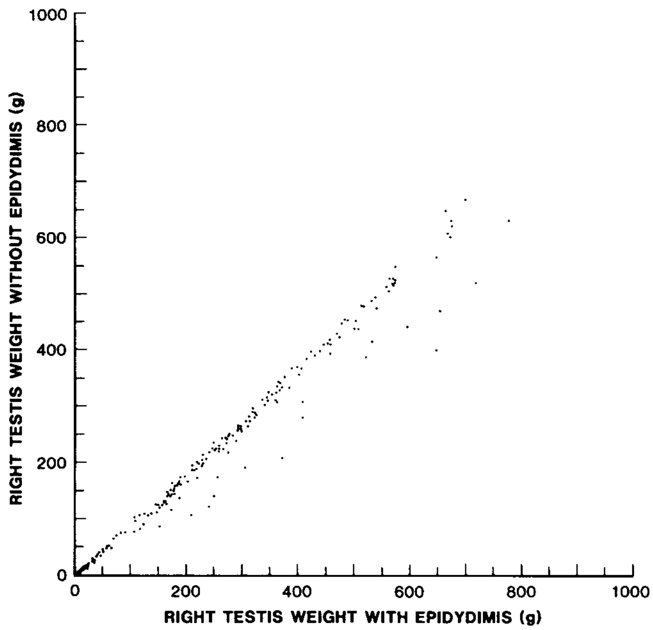

Figure 10. Relation between testis weights with and without epididymis. Each point represents one specimen.

imens. The age at maturation was then estimated to be the estimated age of the mature 16-ft male in the sample. He specified that this estimate of age at maturation would be minimal because of dentinal occlusion. Collet and Saint Girons (1984) used a method for the common dolphin similar to that of Sergeant (1962). Sergeant *et al.* (1973) gave age and length of maturation in bottlenose dolphins, but did not specify how they were obtained. These disparities in the methods used to estimate age at sexual maturation are considerable and indicate that caution must be used in comparing the estimates (*see* also DeMaster 1984).

Laws (1956*b*) found that for 12 species of pinnipeds, 5 species of odontocetes and 5 species of mysticetes, females reach sexual maturity at about 85 percent of asymptotic length (81 percent for (mostly) large odontocetes, 88 percent for mysticetes and 87 percent for pinnipeds). Bryden (1972) added 5 species of pinnipeds, 2 species of odontocetes, and 2 species of mysticetes to this list. Laws (1962) suggested that the mean age of maturation in fin whales in the Antarctic had declined during 1945 to 1956, but that mean length at sexual maturation had not changed. Lockyer (1972) also found a decrease in average age at maturation even though the average length had not changed. Cooke and de la Mare (1983) suggested, however, that these changes were due to sampling bias and not to actual changes in age at attainment of sexual maturity. In contrast, the results of the present study show an increasing length at maturation with time, with no change in the age at maturation. Barlow (1985) also found that

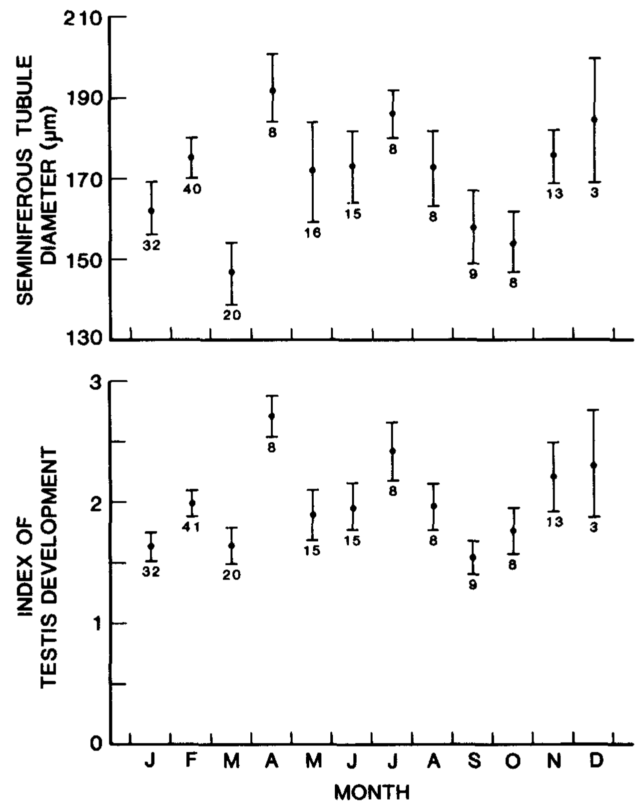

Figure 11. Monthly mean seminiferous tubule diameter and index of testis development values for mature specimens. Sample sizes are below the error bars, which represent one standard error from the mean.

the median length at sexual maturation in female spotted dolphins in the same population had increased between 1974 and 1983. There was no concomitant change in age at maturation for the females (Myrick *et al.*, in press).

It is necessary to have comparable estimates of age and length at maturation in dolphins to make inter- or intra-specific comparisons. We suggest use of the mean age and length estimates (as defined by Cooke) because it is a minimum variance estimator, is easy to compute, does not require a large sample size and provides a variance estimate.

The age at attainment of sexual maturity is higher in males ($\bar{x}$ = 14.7 yr) than in females ($\bar{x}$ = 11.9 yr, Myrick *et al.*, in press) in this population. This difference has also been observed for other dolphins (Sergeant 1962, Kasuya 1976, Perrin *et al.* 1977).

The estimated age (or length) at sexual maturation in our study may be biased by several factors. Age estimates are imprecise, and this imprecision tends to increase with the age of animals (Reilly *et al.* 1983). The age distribution of our sample was not representative of the population; juvenile age classes were

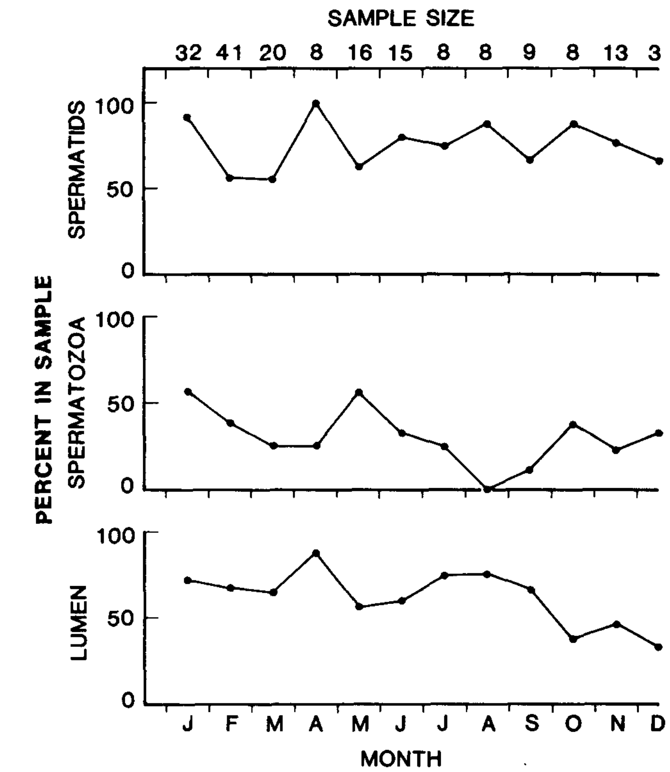

Figure 12. Monthly trends in relative quantities of spermatids, spermatozoa and lumen diameter. The points represent the percentage of mature specimens with most or all of the seminiferous tubules containing spermatids or spermatozoa, and the percentage of specimens with large lumens each month.

underrepresented (Hohn and Scott 1983). If mature animals are more likely to be sampled, the age at sexual maturation would be underestimated. However, the estimates could be overestimates due to a sampling bias caused by segregation of sexually mature, but not yet socially mature, specimens from the main schools (Hohn and Scott 1983).

The results showing correlation of color phase to maturity are comparable to those described by Perrin (1969) and Kasuya *et al.* (1974)—nearly all fused specimens were mature or pubertal and relatively few specimens of other color phases were mature. The development of the fused color phase may be influenced by reproductive hormones, a possibility suggested by Kasuya *et al.* (1974). Color phase may be used to estimate the proportion of sexually mature animals in a sample of spotted dolphins when testis data are not available.

The proportion of mature specimens in the mottled and fused color phases differs for males and females. In females, 96 percent of the fused and 50 percent of the mottled animals are mature (Myrick *et al.,* in press), whereas male mottled specimens are only rarely sexually mature. In addition, the median age of fused females (12.7 yr) and mottled females (9.5 yr) was less than that of males (fused = 14.8 yr, mottled = 10.5 yr).

A nonhistological method for determining sexual maturity in males would be useful. Collet and Saint Girons (1984) used a relation between weight (in g) and length (in cm) of testes (excluding epididymides) to distinguish between states of sexual maturity. They found, from histological analyses of a small sample ($n = 26$), that the ratio of summed right and left testes lengths to summed testes weights (the inverse of the relationship we described) was correlated with state of maturity, where a ratio of about 1.0 identified immature animals. The ratio for mature specimens was 0.2 or less. Index values from Collet and Saint Girons (1984) cannot be compared directly with those from the present study because the testis weights in our sample include the epididymis. But using the mean right-testis length (cm) divided by the mean right-testis and epididymis weight (g) in our study (data from Table 1) gives values of 0.51 for immature, 0.48 for pubertal and 0.05 for mature specimens. Since this sample includes only mottled and fused specimens, the value for immature is lower than for the overall sample of immature specimens (*e.g.*, the mean value for two-tone specimens is 1.0 [Table 2], the same value as immature common dolphins).

Weight of the testis and epididymis can be used as an indicator of sexual maturity within a population. This weight varies greatly, however, between species and stocks, even after considering seasonal differences (*e.g.*, Perrin and Henderson 1984), and thus precludes the use of the weight of testis and epididymis of adults derived from one population to determine maturity in other populations or species. Normalizing testes weight by testes length may provide a more reliable tool for determining sexual state and making interspecific (or stock) comparisons because it accounts for some of the difference in specimen size, thus allowing for direct comparisons of maturity between species. For example, the spotted dolphins in our study and the common dolphins in the Collet and Saint Girons (1984) study had similar index values for immature and mature even though common dolphins have relatively much heavier testes (Perrin and Reilly 1984). We recommend that future studies investigate the general application of this method to describe maturity and allow for direct inter-stock or inter-specific comparisons of sexual maturity in male dolphins.

Seasonality

Seasonal gonadal changes occur in male dolphins from many populations. Ridgway and Green (1967) suggested a mid- to late-summer breeding season for *Lagenorhynchus obliquidens* and *Delphinus delphis* off central and southern California based on increased testes weights and seminiferous tubule diameters and the occurrence of spermatogenesis. Seasonal changes in testis weights or histological characteristics have also been observed in *S. coeruleoalba* (Hirose and Nishiwaki 1971, Miyazaki 1977), *D. delphis* (Fraser 1953, Gurevich and Stewart 1978, Collet and Saint Girons 1984), *S. attenuata* (Perrin *et al.* 1976) and *S. longirostris* (Perrin and Henderson 1984). Seasonal changes in plasma testosterone were noted in bottlenose dolphins, *Tursiops truncatus,* in the western Atlantic (Harrison and Ridgway 1971) and spinner dolphins, *S. longirostris,* in Hawaii (Wells 1984).

The primary calving seasons for spotted dolphins from the northern offshore stock are May and September (Barlow 1984, Hohn and Hammond 1985). Based on a gestation period of 11.5 months (Perrin *et al.* 1976), mating would have to occur in late May and late September to synchronize with the calving seasons. These mating seasons are within the period of elevated testis weight identified in our study.

For spotted dolphins from the northern offshore stock, however, the seasonal peak for testes weight is midway between the two primary calving seasons (Barlow 1984, Hohn and Hammond 1985). Miyazaki (1977) also found the peak time for male seasonality to be inconsistent with the main breeding season in *S. coeruleoalba* off the coast of Japan. He believed that stock migration and the short sampling season biased his results. Such biases would not be important to our study because of the large sample size and year-round sampling. Best (1969) examined histological sections of sperm whale testes and also found that testicular activity did not increase during the primary female breeding season.

Maximum testis (and epididymis) weight is not a good single indicator of reproductive seasonality for these dolphins. Although peaks in lumen diameter and relative numbers of spermatids coincided with a peak in testes weight in April, the level of spermatozoa was highest in May. The mean testes weight and index of testes development values peaked in July and August, months when spermatid levels and lumen diameters were relatively high but spermatozoa levels were low. For the northern offshore stock, one calving season occurred at about the time when spermatozoa levels were high but testes weights and index values were relatively low (September). In the southern stock, the seasonal distribution of testes weights and index values were similar to those in the northern stock, yet only one calving season (in January) has been identified (Barlow 1984, Hohn and Hammond 1985). On the basis of a limited sample, however, Hohn and Hammond (1985) indicated that a second calving season may occur about six months later. We currently have no explanation of why the testis weight seasonality profile is similar and the calving seasons are different between northern and southern offshore stocks. More data from the southern stock are needed to answer this question. Some calving occurs throughout the year in the northern offshore stock, indicating that at least some males do not maintain the same breeding season or they are reproductive throughout the year.

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Literature Cited

Barlow, J. 1984. Reproductive seasonality in pelagic dolphins of the eastern tropical Pacific. Pages 191–198 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

Barlow, J. 1985. Variability, trends, and biases in reproductive rates of spotted dolphins (*Stenella attenuata*). Fishery Bulletin (U.S.) 83(4).

Best, P. B. 1969. The sperm whale (*Physeter catodon*) off the west coast of South Africa. 3. Reproduction in the male. Division of Sea Fisheries Investigational Report No. 72. 20 pp.

Bloom, W., and D. W. Fawcett. 1975. A textbook of histology. 10th Edition, W. B. Saunders Co., Philadelphia, Pa. 1,033 pp.

Bryden, M. M. 1972. Growth and development of marine mammals. Pages 1–80 *in* R. J. Harrison, ed. Functional anatomy of marine mammals. Volume 1. Academic Press, New York, NY.

Charny, C. W., A. S. Conston and D. R. Meranze. 1952. Testicular developmental histology. Pages 597–608 *in* R. W. Miner, ed. Biology of the testes. Annals of the New York Academy of Sciences 55(4):543–742.

Collet, A., and H. Saint Girons. 1984. Preliminary study of the male reproductive cycle in *Delphinus delphis* in the eastern north Atlantic. Pages 355–360 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

Cooke, J. G., and W. K. de la Mare. 1983. The effects of variability in age data on the estimation of biological parameters of minke whales (*Balaenoptera acutorostrata*). Reports of the International Whaling Commission 34:333–338.

DeMaster, D. P. 1984. Review of techniques used to estimate the average age of sexual maturity in marine mammals. Pages 175–180 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

Fraser, F. C. 1953. Report on Cetacea stranded on the British coasts from 1948 to 1966. British Museum of Natural History. 48 pp.

Gurevich, V. S., and B. S. Stewart. 1978. Structure of kill of the common dolphin *Delphinus delphis* from eastern tropical Pacific in 1977. Final report for Contract No. 03-78-M02-0101, Southwest Fisheries Center, La Jolla, California, 19 pp. Available from B. S. Stewart, Hubbs-Sea World Research Institute, San Diego, CA 92109.

Harrison, R. J., and S. H. Ridgway. 1971. Gonadal activity in some bottlenose dolphins (*Tursiops truncatus*). Journal of Zoology (London) 165:355–366.

Hirose, K., and M. Nishiwaki. 1971. Biological study on the testis of the blue white dolphin, *Stenella caeruleoalba*. Journal of the Mammal Society of Japan 5:91–98.

Hohn, A. A., and P. S. Hammond. 1985. Early postnatal growth of the spotted dolphin, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fishery Bulletin (U.S.) 83(4).

Hohn, A. A., and M. D. Scott. 1983. Segregation by age in schools of spotted dolphin in the eastern tropical Pacific. Page 47 *in* 5th Biennial Conference on the Biology of Marine Mammals, Boston, MA. (Abstract.)

Kasuya, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Scientific Reports of the Whales Research Institute 28:73–106.

KASUYA, T., N. MIYAZAKI AND W. H. DAWBIN. 1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. Scientific Reports of the Whales Research Institute 26:157–226.

KIMURA, M. 1980. Variability in techniques of counting dentinal growth layer groups in a tooth of a known-age dolphin, *Tursiops truncatus*. Pages 161–169 *in* W. F. Perrin and A. C. Myrick, Jr., eds. Age determination of toothed whales and sirenians. Reports of the International Whaling Commission, Special Issue 3.

LAWS, R. M. 1956*a*. The elephant seal (*Mirounga leonina* Linn.) III. The physiology of reproduction. Falkland Islands Dependencies Survey, Scientific Reports No. 15. 65 pp.

LAWS, R. M. 1956*b*. Growth and sexual maturity in aquatic mammals. Nature 178: 193–194.

LAWS, R. M. 1962. Some effects of whaling on the southern stocks of baleen whales. Pages 137–158 *in* E. D. Le Cren and M. W. Holdgate, eds. The exploitation of natural animal populations. Blackwell Scientific, Oxford, UK.

LOCKYER, C. H. 1972. The age of sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the ear plug. Journal du Conseil International pour l'Exploration de la Mer 34:276–294.

MIYAZAKI, N. 1977. Growth and reproduction of *Stenella coeruleoalba* of the Pacific coast of Japan. Scientific Reports of the Whales Research Institute 29:21–48.

MYRICK, A. C., JR., A. A. HOHN, J. BARLOW AND P. A. SLOAN. In press. Reproduction of female spotted dolphin, *Stenella attenuata,* from the eastern tropical Pacific. Fishery Bulletin (U.S.).

MYRICK, A. C., JR., A. A. HOHN, P. A. SLOAN, M. KIMURA AND D. D. STANLEY. 1983. Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. NOAA-Technical Memorandum-NMFS-SWFC-30. 17 pp.

PERRIN, W. F. 1969. Color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* Lonnberg (Cetacea, Delphinidae). Zoologica (New York) 54:135–149.

PERRIN, W. F., J. M. COE AND J. R. ZWEIFEL. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata,* in the offshore eastern tropical Pacific. Fisheries Bulletin (U.S.) 74(2):229–269.

PERRIN, W. F., AND J. R. HENDERSON. 1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris,* with different histories of exploitation. Pages 417–430 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

PERRIN, W. F., D. B. HOLTS AND R. B. MILLER. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fishery Bulletin (U.S.) 75(4):725–750.

PERRIN, W. F., AND S. B. REILLY. 1984. Reproduction parameters of dolphins and small whales of the Delphinidae. Pages 97–133 *in* W. F. Perrin, *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

PERRIN, W. F., M. D. SCOTT, G. J. WALKER AND V. L. CASS. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. NOAA-Technical Report-NMFS-28.

REILLY, S. B., A. A. HOHN AND A. C. MYRICK, JR. 1983. Precision of age determination of northern offshore spotted dolphins. NOAA-Technical Memorandum-NMFS-SWFC-35. 27 pp.

RIDGWAY, S. H., AND R. F. GREEN. 1967. Evidence for a sexual rhythm in male porpoises, *Lagenorhynchus obliquidens* and *Delphinus delphis bairdi*. Norsk Hvalfangst-Tid. 1:1–18.

SERGEANT, D. E. 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Fisheries Research Board of Canada, Bulletin 132. 84 pp.

SERGEANT, D. E., D. K. CALDWELL AND M. C. CALDWELL. 1973. Age, growth and maturity of bottlenosed dolphin (*Tursiops truncatus*) from northeast Florida. Journal of the Fisheries Research Board of Canada 30:1009–1011.

WELLS, R. S. 1984. Reproductive seasonality and social behavior of Hawaiian spinner dolphins, *Stenella longirostris*. Pages 465–472 *in* W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.

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