

NOTES

REPRODUCTIVE PARAMETERS OF THE
OFFSHORE SPOTTED DOLPHIN,
A GEOGRAPHICAL FORM OF
STENELLA ATTENUATA, IN THE
EASTERN TROPICAL PACIFIC, 1973-75

Perrin et al. (1976) presented estimates of reproductive parameters of the offshore population of *Stenella attenuata* in the eastern Pacific based on data collected in 1968-73, inclusive. The sample included 3,527 specimens. Only the 1973 sample (2,036) was putatively cross-sectional with respect to age and sex structures of the kill; in earlier years, adult females were selected for examination. The purpose of this paper is to present analyses of samples collected in uniform fashion in 1973, 1974, and 1975, updating the prior report and providing a uniformly developed, albeit short, time series of annual estimates.

Methods and Materials

The data and specimens were collected by NMFS biological technicians aboard commercial tuna vessels. Data collection procedures were the same as described by Perrin et al. (1976). Data on *S. attenuata* were collected on 24 cruises in 1973, 33 in 1974, and 32 in 1975.

The total sample includes 6,243 specimens, 6,168 from precisely known localities (Figure 1). Because of the seasonal nature of the fishery, the sample is heavily biased toward the first half of the calendar year with practically no coverage of the summer months (Table 1).

Laboratory procedures were the same as reported by Perrin et al. (1976), but the analytical methods differed slightly. In calculating gross annual reproductive rate (proportion female \times proportion of total females which are reproductive

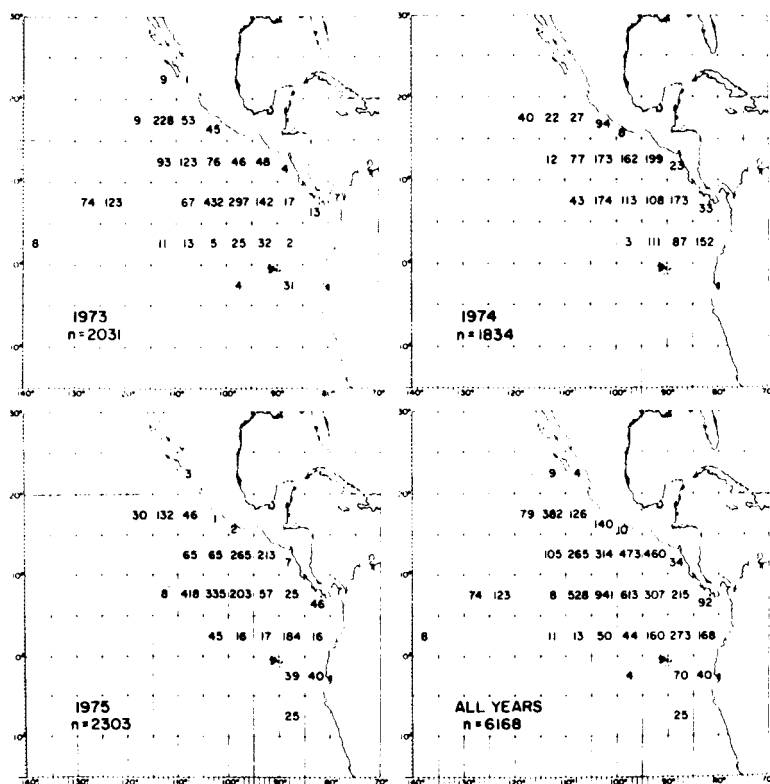


FIGURE 1.—Sample of the offshore spotted dolphin, *Stenella attenuata*, collected in 1973-75, by 5° squares.

TABLE 1.—The sample of the offshore spotted dolphin, *Stenella attenuata*, by sex, year, and month, 1973–75. Date of capture was not available for 18 of the total 6,243 specimens collected.

Month	1973		1974		1975		Total	
	No.	%	No.	%	No.	%	No.	%
Jan.	267	326	239	300	395	442	901	1,068
Feb.	200	231	428	532	249	312	877	1,075
Mar.	137	210	66	72	133	153	336	435
Apr.	41	46	35	42	135	183	211	271
May	85	156	5	2	34	35	124	193
June	56	69	36	9	30	47	122	125
July	0	0	0	0	6	12	6	12
Aug.	0	0	11	13	2	4	13	17
Sept.	0	0	1	4	0	0	1	4
Oct.	5	16	0	0	31	51	36	67
Nov.	72	103	20	48	32	39	124	190
Dec.	8	9	0	0	0	0	8	9
Totals	871	1,166	841	1,022	1,047	1,278	2,759	3,466
	2,037		1,863		2,325		6,225	

× annual pregnancy rate), Perrin et al. (1976) estimated the proportion of adult females which were reproductive from coloration phase data, based on a subsample of data on percentage mature in the various coloration phases ("mottled" and "fused-adult"). In the present study, a much larger sample of complete reproductive data was available; therefore, the proportion of total females which were reproductive was estimated directly from that sample. Specimens for which ovarian data were lacking or incomplete were allocated to mature or immature categories based on a length criterion. Average length at attainment of sexual maturity was estimated as that length (177 cm) at which the number of shorter but mature specimens in the sample equals the number of longer but immature specimens.

Results and Discussion

Calving Cycle and Pregnancy Rate

The calving cycle, for purposes of analyzing field data, can be divided into three phases: 1) pregnancy, 2) lactation, and 3) "resting" (a catch-

all phase for animals neither pregnant nor lactating, which includes females truly resting, i.e., not ovulating because of being between cycles, those which have just ovulated but have not become pregnant, some with extremely small embryos missed in dissection, those which recently aborted, and those which have prematurely terminated lactation due to death of the suckling calf).

We estimated the length of the cycle (and pregnancy rate) in two ways: 1) based on the reproductive structure of the sample of adult females, i.e., based on the assumption that the samples are not biased with respect to reproductive phase, and that the proportion of a sample of mature females in a particular phase is directly proportional to the relative length of that phase, using the previously estimated (Perrin et al. 1976) length of gestation (11.5 mo) as a time calibration, and 2) based on the estimate of length of gestation and a largely independent estimate of length of lactation.

The first estimate was based on data for 1,876 females classified as pregnant, lactating, pregnant and lactating, "resting," or postreproductive (Table 2). The "resting" females were further subdivided into those with and without a corpus luteum. As discussed above, some proportion of those with a corpus luteum can be assumed to represent females not truly resting (with a corpus luteum of infertile ovulation). In the total sample of 3,443 females, 61 were simultaneously pregnant and lactating (6.1% of the lactating females). Minor differences between the numbers in Table 2 and in table 8 of Perrin et al. (1976) reflect increase of the 1973 sample by eight specimens and reexamination and reevaluation of the materials.

Subtraction of the postreproductive females from the aggregate of mature females of determined reproductive condition and allocation of the females both pregnant and lactating to both

TABLE 2.—Reproductive condition of 3,469 female offshore spotted dolphins, *Stenella attenuata*, collected 1973–75.

Condition	1973		1974		1975		1973–75 pooled	
	No.	%	No.	%	No.	%	No.	%
Sexually immature	522	45.0	465	45.9	580	45.7	1,567	45.5
Sexually mature:								
Condition undetermined	58	5.0	60	5.9	191	15.0	309	9.0
Pregnant only	232	20.0	122	12.1	119	9.4	473	13.7
Pregnant and lactating	16	1.4	23	2.3	22	1.7	61	1.8
Lactating only	226	19.5	256	25.3	264	20.8	746	21.7
"Resting"								
With corpus luteum	34	2.9	32	3.2	28	2.2	94	2.7
Without corpus luteum	66	5.7	48	4.7	64	5.0	178	5.2
Postreproductive	7	0.6	6	0.6	2	0.2	15	0.4
Totals	1,161	100.0	1,012	100.0	1,270	100.0	3,443	100.0

categories provides estimates of the proportions of reproductive females in the three phases of the cycle and, comparing the proportions, of the relative lengths of the phases. Estimated average length of the phases and the total cycle can then be calculated for each 1-yr sample and for the pooled samples, based on the relative lengths of the phases and on the estimated gestation period of 11.5 mo (Method 1 in Table 3). The estimates of average length of cycle thus derived trend from 27.3 mo in 1973 to 42.3 mo in 1975, due to increase in the estimated length of lactation from 11.2 mo to 23.3 mo.

Annual pregnancy rate under Method 1 (also in Table 3) is calculated as proportion of reproductive females pregnant divided by the length of gestation (0.958 yr). The reciprocal of annual pregnancy rate is the estimate of average calving interval.

In the second method of calculating length of calving cycle, we estimated length of lactation by assuming that a suckling calf existed in the samples for each lactating female. Under this assumption, 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 (from which, using the length-age equations published by Perrin et al. (1976), the average age at weaning can be calculated). If the length of lactation increases, the average length

at weaning estimated by this method should increase concomitantly. The calculated length at weaning did not increase sharply between years (Table 4). Under Hypothesis II of Perrin et al. (1976) of the rate of deposition of dentinal growth layers (two in first year and one per year thereafter—the most likely alternative), the estimated length of lactation ranges from 11.2 mo in 1973 to 12.4 mo in 1974. To arrive at estimates of the total length of the calving cycle under Method 2, we used the estimate of time spent in the "resting" phase under Method 1 for 1973 (the year for which the two estimates of length of lactation coincide exactly) or 4.6 mo, for each of the three annual estimates. This estimate is based on the assumptions under Method 1 but must suffice as a first approximation. In estimating pregnancy rate (as reciprocal of calving interval)—Table 3—overlapping cycles were taken into consideration by adjusting the effective length of lactation downward by a factor equal to the percentage of lactating females also pregnant.

The 1973 estimate of length of lactation (and length of cycle, pregnancy rate, and calving interval) is very close to that obtained by Method 1 above (11.2 mo), but the two sets of estimates diverge sharply thereafter. The first method could be invalid and cause diverging estimates if 1) lactating females (and their nursing calves) were overrepresented in the samples for 1974 and 1975 or, conversely, 2) either (or both) pregnant or "resting" females were underrepresented. The first situation could obtain if lactating females and their accompanying calves are more likely to be captured and killed in the net because of limited endurance and ability to escape of the calf, certainly less than those of adults, and the strength of the mother-calf bond. The second method could yield erroneous estimates if 1) nursing calves were overrepresented in the samples or,

TABLE 3.—Estimates of lengths of reproductive phases, pregnancy rate, and calving interval under two methods of estimating length of calving cycle (see text) of the offshore spotted dolphin, *Stenella attenuata*, 1973–75.

Item	1973	1974	1975	1973–75 pooled
Sample size (no.)	574	481	497	1,552
Pregnancy (mo)	11.5	11.5	11.5	11.5
Lactation (mo):				
Method 1	11.2	21.9	23.3	17.4
Method 2 (Hyp. II)	11.2	12.4	12.1	11.9
"Resting" (Method 1)	4.6	6.4	7.5	5.9
Sum of phases:				
Method 1				
Months	27.3	39.8	42.3	34.8
Years	2.28	3.32	3.53	2.90
Method 2				
Months	27.3	28.5	28.2	28.0
Years	2.28	2.38	2.35	2.33
Annual pregnancy rate (APR):				
Method 1	0.452	0.314	0.296	0.359
Method 2	0.472	0.459	0.461	0.463
Calving interval (1/APR):				
Method 1				
Years	2.21	3.18	3.38	2.79
Months	26.5	38.2	40.5	33.4
Method 2				
Years	2.12	2.18	2.17	2.16
Months	25.4	26.2	26.0	25.9

TABLE 4.—Estimates of length of lactation in the offshore spotted dolphin, *Stenella attenuata*, based on the cumulative calf length/lactating females method (see text) 1973–75.

Sample	Lactating females ¹ (no.)	Length ² (cm)	Growth layers	Length of lactation		
				Under hypothesis		
				I (mo)	II (mo)	III (mo)
1973	259	135.8	1.86	11.2	11.2	11.2
1974	301	138.5	2.03	12.2	12.4	12.2
1975	376	138.2	2.01	12.1	12.1	12.1
1973–75 pooled	936	137.8	1.96	11.9	11.9	11.9

¹Includes mature females (>177 cm) without lactation data prorated to lactating and nonlactating based on proportions in sample with lactation data.
²Length at which cumulative number of calves = number of lactating females.

conversely, 2) lactating females were under-represented. Ongoing analyses of data for the spotted dolphin, *S. attenuata* (J. E. Powers pers. commun.), indicate that small calves are probably overrepresented in small single-set samples. In addition, the absence of sharp change in length of calves at weaning as estimated by the cumulative-calves method speaks against the alternative explanation of development between the years of differential bias against calves and lactating females. The balance of evidence favors the first alternative above, that of progressive overrepresentation of both nursing calves and lactating females as the average number of animals encircled has increased and the average number killed per net haul has decreased¹ accentuating the factor of differential stamina.

Gross Annual Reproduction

Estimates of gross annual reproductive rates can be calculated based on the two methods of estimating pregnancy rate (Table 5). It must be noted that if, as discussed above, small calves are overrepresented in small samples (which make up most of the aggregate sample), then pregnancy rate (and, therefore, gross annual reproductive rate) under Method 1 are underestimated to an unknown, but probably small, degree. This factor, of course, would also cause overestimation of the proportion of the total sample female and the pro-

portion of total females which are reproductive, causing a countering overestimation of gross annual reproduction of unknown, but again probably small, size.

Standard errors are attached to the various estimates where sample size ≥ 100 , under the assumption that the binomial distribution tends to normality in large samples (Bailey 1959), allowing calculation of the standard error as:

$$SE = \sqrt{p(1-p)/n}$$

where p = proportion (estimate of parameter)
 n = sample size.

Although gross annual reproductive rate as calculated in Table 5 is a product of three estimates, it can be calculated directly from the total sample (number of females pregnant \div total number of males and females), to yield the same estimate and allowing estimation of the variance by the above method. The total sample size was adjusted downward by a factor equal to the proportion of mature females in unknown reproductive condition. The effect on the variance by the constant used to adjust the pregnancy rate to an annual rate was ignored, because the constant (11.5 mo gestation \div 12 mo, or 0.958) is close to unity.

The estimates of pregnancy rate (and gross annual reproductive rate) for 1973 and 1974 based on structure of the samples (Method 1) are significantly different from each other (using ± 2 SE as an approximation of a 95% confidence interval), and the estimate for 1975, although not statistically different from that for 1974, continues the trend. The estimates based on independent esti-

¹Staff, Porpoise/Tuna Interaction Program, Oceanic Fisheries Resources Division. 1975. Progress of research on porpoise mortality incidental to tuna purse-seine fishing for fiscal year 1975. SWFC Admin. Rep., Natl. Mar. Fish. Serv., La Jolla, Calif., LJ-75-68, 98 p. (Unpubl. rep.)

TABLE 5.—Calculation of estimates of gross annual reproductive rate of offshore spotted dolphin, *Stenella attenuata*, for 1973–75, using two alternative estimates of pregnancy rate (see text). Standard error follows estimate (see text).

Year	A	B	C		A · B · C	
	Proportion female	Proportion of females reproductive	Annual pregnancy rate		Gross annual reproductive rate	
			Method 1	Method 2	Method 1	Method 2
1971			0.546 (86)			
1972			0.465 ± 0.023 (455)			
1973	0.572 ± 0.011 (2,037)	0.544 ± 0.015 (1,161)	0.452 ± 0.021 (574)	0.472 ± 0.021 (574)	0.141 ± 0.008 (2,036)	0.147 ± 0.008 (1,934)
1974	0.548 ± 0.012 (1,863)	0.535 ± 0.016 (1,012)	0.314 ± 0.021 (481)	0.459 ± 0.023 (481)	0.092 ± 0.007 (1,860)	0.135 ± 0.008 (1,750)
1975	0.559 ± 0.010 (2,321)	0.542 ± 0.014 (1,270)	0.296 ± 0.020 (523)	0.461 ± 0.022 (523)	0.087 ± 0.006 (2,321)	0.140 ± 0.007 (2,001)
1973–75	0.560 ± 0.006 (6,221)	0.541 ± 0.008 (3,443)	0.359 ± 0.012 (1,578)	0.463 ± 0.012 (1,578)	0.109 ± 0.004 (6,243)	0.140 ± 0.004 (5,685)

mates of lengths of gestation and lactation also trend downward, but the year-to-year differences are not statistically significant. As discussed above, the balance of evidence favors the (relatively nonvarying) estimates based on Method 2.

Although adequate data for estimating sex ratio and proportion of total females which were reproductive in 1971 and 1972, using the methods employed here, or for estimating pregnancy rate using Method 2, are not available because of selection of adult females for dissection, the estimates of pregnancy rate (using Method 1) for those two years are included in Table 5. The sample for 1971 is too small to allow direct statistical comparison with the estimates for later years, but the 1972 estimate is not significantly different from the estimates for 1973, reinforcing the suggestion that a major shift in population structure or (more likely) in degree of representativeness of the kill or the sample occurred in 1974.

In summary, the balance of evidence indicates that, in management of the dolphin/tuna situation, changes in the structure of the dolphin kill, per se, should not be taken to necessarily mean that parallel changes in reproductive rates have occurred. The changes more likely represent sampling artifacts caused by changes in the fishing and dolphin rescue operations.

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