VARIABILITY, TRENDS, AND BIASES IN REPRODUCTIVE RATES OF SPOTTED DOLPHINS, *STENELLA ATTENUATA*

JAY BARLOW[1]

ABSTRACT

Temporal changes were examined in three parameters that affect reproduction of spotted dolphin populations in the eastern Pacific. Of mature females, percent pregnant decreased markedly from the period 1971-73 to the period 1974-83. Within the period 1974-83, percent pregnant remained relatively constant. Of pregnant females, percent lactating increased during the period 1971-83. The percentage of sexually mature females did not change. Potential biases in the measurement of the three parameters were identified by examining the effects of sampling conditions. The percentage of mature females that are pregnant and the percentage of pregnant females that are lactating were found to be robust to sampling conditions. The percentage of mature females in a sample was found to depend significantly on the number of dolphins killed per set, and annual variability was too large to be explained by random sampling error. Comparisons between two populations show that the more exploited population has a lower percent pregnant, although the opposite might be expected from density compensatory effects. Percent lactating and percent immature were higher in the more exploited population.

Changes in the reproductive parameters of cetacean populations can be used to make inferences about the status or general "health" of a population. For instance, increases in pregnancy rates and decreases in the age at attainment of sexual maturity were linked to reductions in Antarctic whale populations (Gambell 1975). Re-analysis of these data, however, revealed unsuspected biases, and Gambell's results are now being questioned (Mizroch 1983). The purpose of this paper is to examine potential biases in measuring reproductive rates of spotted dolphins, *Stenella attenuata*. This species is taken incidentally in the tuna purse seine fishery in the eastern tropical Pacific (Smith 1983). The intent is to determine whether reproductive rates can be measured with sufficient precision to monitor intrapopulation changes or to make interpopulation comparisons.

Previous studies of female reproduction in spotted dolphins of the eastern Pacific have shown an apparent decrease in pregnancy rates from 1973 to 1975 (Perrin et al. 1977), from 1973 to 1978,[2] and from 1971 to 1978 (Hester 1984). Hester (1984) suggested that this decline in pregnancy rates is related to the decline in fishing-related dolphin mortality during the same time period.

Three indices of the reproductive status of female spotted dolphins are examined in the present paper: 1) the fraction of sexually mature individuals that are pregnant, 2) the fraction of pregnant females that are lactating, and 3) the fraction of females that are sexually mature. These measures have been used previously in calculating what has been termed the gross annual reproductive rate (GARR) of spotted dolphins (Perrin et al. 1976). This paper reexamines data from 1971 to 1978 plus additional data from 1979 to 1983 to determine whether the previously noted trends in reproductive rates are real, and if so, whether they are continuing. Also, factors are examined which may be biasing estimates of reproductive rates and which could be causing spurious changes in apparent pregnancy rates and GARR. Finally, differences in these reproductive indices between two geographic stocks of spotted dolphin are discussed in view of their different histories of incidental fishing mortality.

MATERIALS

Reproductive data were collected from a sample of the dolphins killed in tuna purse-seining operations in the eastern tropical Pacific (ETP). Three stocks of spotted dolphins are recognized in this area based on morphological differences (Perrin et al. 1979). Samples considered here include two of these: the northern offshore stock which has been subject to tuna fishing since 1959 and the southern offshore stock which has been subject to exploitation since

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

[2]Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rate of gross annual reproduction in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-78. Admin. Rep. LJ-80-02, 51 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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the early 1970's. In 1971 and 1972, field technicians collected samples predominantly from females with the "adult" or fused color pattern (Perrin 1970). Beginning in 1973, field technicians were instructed to collect samples nonselectively with respect to size and sex. Operationally, this meant working-up specimens in the order in which they appeared on the deck of the tuna vessel. Sampling methods and laboratory procedures are described in detail by Perrin et al. (1976). Sample locations are shown in Figure 1.

Reproductive tracts of mature and nearly mature females were preserved in the field for laboratory examination. In 1971 and 1972, the definition of "mature and nearly mature" was not explicit. In 1973, "mature and nearly mature" was defined as individuals with "mottled" or "fused" developmental color phases (Perrin 1970). Because females in the younger "speckled" color phase occasionally were found to be pregnant, "mature and nearly mature" was redefined operationally (beginning in 1974) as specimens >150 cm total length (TL, measured from tip of rostrum to fluke notch). Laboratory examination of preserved ovaries was used to determine the presence of corpora from past ovulations. Pregnancy was determined by visual examination of the uterus (in later years, fetuses >30 cm TL were removed and measured in the field). Mammary glands were slit and checked in the field for the presence of milk.

In addition to the above life history information, field technicians collected data pertaining to conditions under which the samples were taken. Information used in this report includes the observer's estimate of the size of the school from which the sample was taken, the duration of the chase before the net was set, the number of dolphins known to be killed during fishing operations, and the geographic location at which the sample was taken.

METHODS

Three indices of female reproduction are considered in this paper: the percent pregnant, the percent lactating, and the percent mature. Temporal trends in these three indices were examined by regressing annual means against year (weighting by the inverse of binomial variances).

In calculating the percentages of mature females that were pregnant and that were lactating, specimens were used only if both ovaries were collected and if at least one corpus of ovulation (corpus albicans or corpus luteum) was present. Previously, 1971 and 1972 samples were excluded from calculation of percent pregnant because of undersampling of younger females with a mottled color pattern (Perrin et al. 1977). This was not deemed necessary in this study, because in 1973-83 samples the percent pregnant for mature mottled females (31.1%) was essentially the same as that for mature females with a fused color pattern (31.4%).

In calculating the percentage of females that were sexually mature, two different criteria were used for determining maturity. In the majority of cases both ovaries were examined, and the presence of one (or more) corpus of ovulation was taken as evidence of sexual maturity. If ovaries were not collected or examined (which was true for about 30% of females over 150 cm TL), a length criterion was used for maturity. Samples from 1971 and 1972 were excluded from these analyses because sampling was not random in those years.

"Length at attainment of sexual maturity" was determined by the method used by Perrin et al. (1977). Based on the sample for which ovaries were examined, this length was estimated as the length at which the number of longer immature individuals equals the number of shorter mature individuals. For the northern stock, the length at the onset of sexual maturity was determined independently for each year 1974-83 (176.5, 177.5, 177.0, 177.0, 178.0, 177.5, 179.0, 178.5, 180.0, and 182.0 cm, respectively). In 1973 the decision to collect ovaries was not based on specimen length. The apparent trend in these data yields a significant regression ($P = 0.0008$); hence, regression estimates were substituted for annual estimates for 1974-83, with an extrapolation to 1973. These values were 175.6, 176.1, 176.6, 177.1, 177.6, 178.0, 178.5, 179.0, 179.5, 180.0, and 180.5 cm, respectively, for 1973-83. For the southern stock, insufficient data exist to calculate a length at attainment of sexual maturity for individual years, hence the collective value was used for all years (175.0 cm).

Six factors were examined to determine whether annual changes in the above percentages of pregnant females were caused or affected by changing biases in the sampling methods. These factors include 1) geographical provenance, based on two strata (Fig. 1) which roughly correspond to the historical tuna fishing grounds (inside the Commission Yellowfin Regulatory Area, CYRA) and a more recently exploited area (outside the CYRA); 2) the quarter of the year; 3) the length of chase, or the time between sighting the dolphin school and capture (net set); 4) the observer's estimate of the dolphin school size (only available since 1973); 5) the number of dolphins known to have been killed in the set; and 6) the total number of tons of tuna caught in the set.

The selection of these six factors was guided to

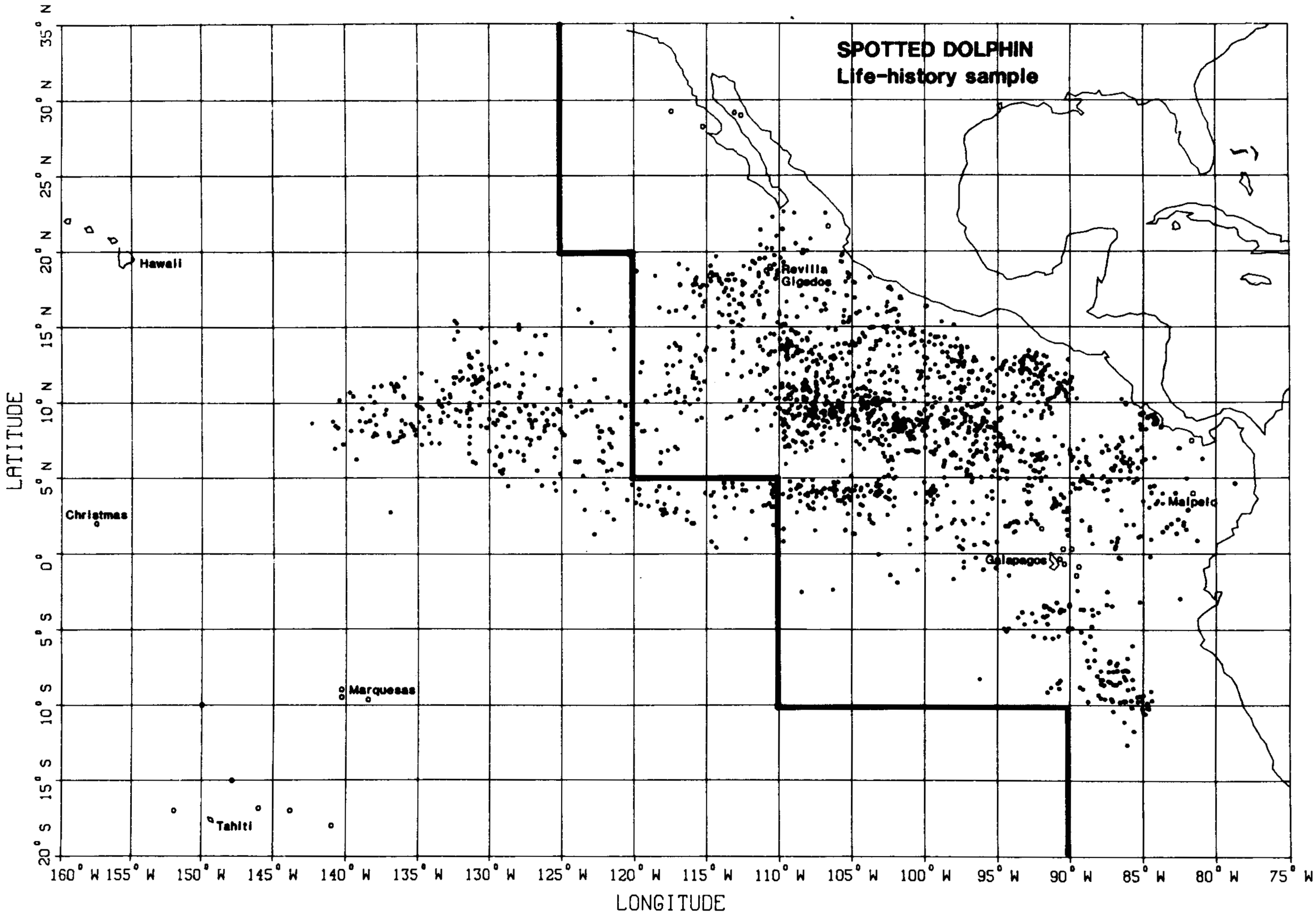

FIGURE 1.—Locations at which male and female spotted dolphins were collected for life history studies, 1968-83. Bold line indicates western border of the Commission Yellowfin Regulatory Area (CYRA). Figure taken from Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass. 1984. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. Admin. Rep. LJ-84-02, available from NOAA, Southwest Fisheries Center, La Jolla, CA 92038.

some extent by previous studies. The sex ratio and the fraction of yearling dolphins in a sample were found to vary with kill size (No. 5 above). The fraction of neonatal animals in tuna-vessel samples was found to vary significantly with area, season, chase time, dolphin kill, and tuna catch (Nos. 1, 2, 3, 5, and 6 above)[3]. Preliminary work by A. A. Hohn[4] and M. D. Scott[5] has indicated that immature spotted dolphins may segregate into schools with different characteristic school sizes (No. 4 above).

The significance of each of the above factors was tested separately using a Pearson chi-square. For each test, the null hypothesis was that either percent pregnant, percent lactating, or percent mature is independent of the factor being tested. If this hypothesis is shown to be false, then it is likely that reproductive parameters may be affected by sampling bias. Unfortunately, the above sampling factors are not independent; a factor may appear significant when, in fact, that factor is merely correlated with a causative factor. Because of this, probablilties should be interpreted with caution.

Multiway comparisons were used to discriminate factors which are truly important from those which are correlated to significant factors. A hierarchical approach was used, based on the log-linear model for discrete multivariate analysis (program BMDP4F, Dixon 1981). The above 2-way tests were used to identify factors that may be significant. The factors that were significant in the 2-way tests were used in 3-way tests. The factors which proved significant in the 3-way tests were then included in 4-way tests (which proved to be a practical upper limit on multiway tests using our data set). In this manner, multiway comparisons of factors could be tested, whereas a 7-way test of all factors would not have been feasible.

Analysis of variance (ANOVA) was tried and rejected as an alternative to the log-linear model for multiway comparisons. The method used in this trial was to calculate percent pregnant for each set and to use sets as replicates in an ANOVA. Although ANOVA is recognized to be robust to violations in assumptions, the sample size for individual sets is very small (mean number of mature females per set is 1.6, mode is 1). As a result, the percent pregnant in 72% of sets was either 0% or 100% of mature females. No transformation was able to normalize these data. Using an arc-sine transformation, 2-way ANOVA was not even able to recognize the four significant factors affecting percent pregnant that were identified using a simple Pearson chi-square. Because of these problems, the ANOVA model was rejected for use in the multiway comparisons.

[3]Powers, J. E., and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, 7 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[4]A. A. Hohn, NOAA, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, pers. commun. November 1983.

[5]M. D. Scott, Inter-American Tropical Tuna Commission, P.O. Box 271, La Jolla, CA 92038, pers. commun. November 1983.

RESULTS

Percent Pregnant

The fractions of sexually mature females that were pregnant are given in Table 1 for the samples of the northern and southern offshore stocks collected from 1971 to 1983. Sample sizes decline in the later years for the northern stock, but are typically >100.

TABLE 1.—Fractions a) of females that were sexually mature, b) of sexually mature females that were pregnant, and c) of pregnant females that were lactating. Samples include 1971-83 specimens from the northern and southern offshore stocks of spotted dolphins. Fraction mature was not sampled in 1971 and 1972.

	Year													
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	Overall
Northern stock														
a) Fraction mature			0.56	0.53	0.54	0.50	0.61	0.59	0.59	0.55	0.61	0.56	0.50	0.561
Number in sample			1,149	1,013	1,215	751	995	564	593	509	465	579	137	7,970
b) Fraction pregnant	0.48	0.41	0.42	0.29	0.29	0.34	0.27	0.24	0.30	0.30	0.29	0.32	0.38	0.329
Number mature	79	449	573	487	493	291	375	229	205	148	153	148	37	3,667
c) Fraction lactating	0.26	0.08	0.08	0.17	0.14	0.13	0.35	0.15	0.30	0.23	0.24	0.19	0.28	0.162
Number pregnant	38	180	236	138	130	93	94	52	61	43	42	47	14	1,168
Southern stock														
a) Fraction mature			0.58	—	0.68	0.63	0.61	0.77	0.58	0.73	0.60	0.70	0.69	0.656
Number in sample			24	0	38	254	23	51	166	59	20	199	106	940
b) Fraction pregnant	—	—	0.75	—	0.49	0.48	0.12	0.28	0.22	0.35	0.00	0.32	0.18	0.364
Number mature	0	0	12	0	23	145	8	25	60	17	8	73	22	393
c) Fraction lactating	—	—	0.00	—	0.22	0.04	0.00	0.16	0.08	0.00	—	0.23	0.00	0.087
Number pregnant	0	0	9	0	9	68	1	6	13	6	0	22	4	138

Samples sizes for the southern stock are highly variable between years, and several years have too few specimens to reliably estimate the fraction of the population that would be pregnant. For 1973-83, the overall percentage of pregnant females is, however, significantly higher for the southern stock, 36.4%, than for the northern stock, 31.4% (χ_1^2 = 3.97, P = 0.05). Because of this difference, northern and southern stocks were not pooled in subsequent analyses. Due to the small sample size from the southern stock, examination of trends and biases in female reproductive rates was limited to the northern stock.

Annual estimates of the percentage of pregnant females are illustrated in Figure 2 for the northern offshore stock. The regression is significant; however, the residuals do not appear randomly distributed. The negative slopes of the regression lines are largely due to high pregnancy rates in 1971-73. Expected values for the percent pregnant in each year were generated in two ways: from the overall percent pregnant and from the "de-trended" regression predictions. Chi-square tests using these expected values show the annual variability in percent pregnant is greater than would be expected from random sampling of a population with a constant ($P < 0.001$) or linearly decreasing ($P < 0.001$) pregnancy rate.

Although natural year-to-year variability in pregnancy rates cannot be ruled out, a changing bias in sampling could also cause larger than expected variability in percent pregnant. To look for such a bias, the sample from the northern stock was stratified by the six sampling factors described above. The percent pregnant in each of these strata is given in Table 2, with the chi-square probabilities that the samples could have been drawn randomly from the pooled sample. Of the factors examined, pregnancy rate was significantly related to sampling season, dolphin kill-per-set, and tuna catch-per-set (henceforth the latter two are referred to as kill and catch).

Because sampling seasons, mean dolphin kills, and mean tuna catches vary significantly between years, these factors cannot be considered independent of year. For instance, the interaction between pregnancy rates and dolphin kill might appear significant due to high kill rates or high catch rates in a year (or years) that coincidentally had high pregnancy rates. Conversely, high pregnancy rates in one year may be due to a sampling bias related to dolphin kill.

Multiway tests were used to identify possible interactions between the three significant factors and year effects. In all cases, 3-way tests indicate that year effects are significant (Table 3). First order effects of kill, catch, and season were not significant; however, higher order effects involving the latter two were important (Table 3). A 4-way test using catch, season, and year also shows significant higher order interactions involving both catch and season (Table 3).

Higher order interactions involving year and another factor indicate that effect of that factor changes with year. Since pregnancy rates appear to have changed markedly from 1971-73 to 1974-83 (Fig. 2), the effect of the significant factors was

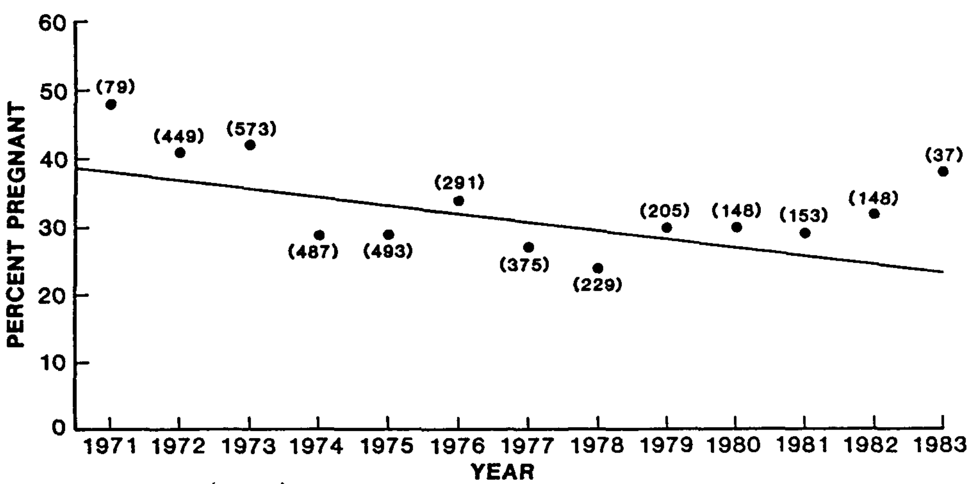

FIGURE 2.—Percentages of mature females that were pregnant for the northern offshore stock of spotted dolphins from 1971 to 1983. Solid line represents weighted regression. Sample sizes are in parentheses.

TABLE 2.—Percentage of sexually mature females that were pregnant (1971-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Pregnant (%)	*N*	Probability
1) Geographic area			
Inside CYRA	33.5	3,032	0.09
Outside CYRA	30.0	633	
2) Season			
1st quarter	34.7	1,799	
2d quarter	33.5	741	0.04
3d quarter	28.9	584	
4th quarter	30.4	542	
3) Chase time (min)			
<20	31.2	1,081	
20-40	34.8	1,440	0.09
>40	31.1	747	
4) School size			
<500	30.2	443	
500-1,500	29.8	741	0.49
>1,500	27.4	693	
5) Number killed			
1-10	29.8	1,104	
11-30	30.1	917	<0.001
>30	37.4	1,301	
6) Tuna caught (tons)			
0-5	29.0	428	
6-15	33.0	848	0.02
16-30	30.4	760	
>30	35.6	1,280	

tested separately for these two time periods. When the years 1971-73 were excluded (Table 4), the interactions between percent pregnant and season, dolphin kill, and tuna catch are no longer significant. When tests are performed on data from 1971 to 1973 alone (Table 4), season and tuna catch are still significantly related to pregnancy rate.

Percent Lactating

Annual trends in percent lactating for the northern stock of spotted dolphins are illustrated in Figure 3. Two cases are considered: 1) the percentage of all mature females that are lactating and 2) the percentage of pregnant females that are lactating. For both cases, a weighted regression shows a significant increase in the fraction of lactating females through time ($P < 0.05$). In the former case, the regression again appears to be driven by anomalous values in 1971-73. Percentages and sample sizes for the latter case are presented in Table

TABLE 3.—Multiway tests of factors affecting percent pregnant. Log-likelihood chi-square was used to calculate the probability that percent pregnant is independent of the stated factor(s) using the log-linear model. Pregnancy state (pregnant/not pregnant) is implicit as the first factor in each comparison.

Tests	Probability
3-way	
a) Year	<0.0001
Season	0.70
Year × season	<0.0001
b) Year	<0.0001
Kill	0.09
Year × kill	0.31
c) Year	<0.0001
Catch	0.14
Year × catch	0.0004
4-way	
Year	<0.0001
Season	0.90
Catch	0.15
Year × season	<0.0001
Year × catch	0.0002
Season × catch	0.003
Year × season × catch	0.07

TABLE 4.—Percentage of sexually mature females that were pregnant, grouped by season, dolphin kill, and tuna catch. The years 1971-73 and 1974-83 are grouped separately. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included.

Year	Pregnant (%)	*N*	Probability
1971-73 overall	41.9	1,101	
Season			
1st quarter	44.0	722	
2d quarter	47.6	210	<0.001
3d quarter	—	0	
4th quarter	25.4	169	
Number killed			
1-10	38.0	171	
11-30	39.5	248	0.23
>30	44.1	651	
Tuna caught (tons)			
0-5	37.6	101	
6-15	44.5	247	0.04
16-30	35.0	226	
>30	45.5	490	
1974-82 overall	29.0	2,566	
Season			
1st quarter	28.4	1,077	
2d quarter	27.9	531	0.39
3d quarter	28.9	584	
4th quarter	32.7	373	
Number killed			
1-10	28.3	933	
11-30	26.6	669	0.27
>30	30.6	650	
Tuna caught (tons)			
0-5	26.3	327	
6-15	28.3	601	0.76
16-30	28.5	534	
>30	29.5	790	

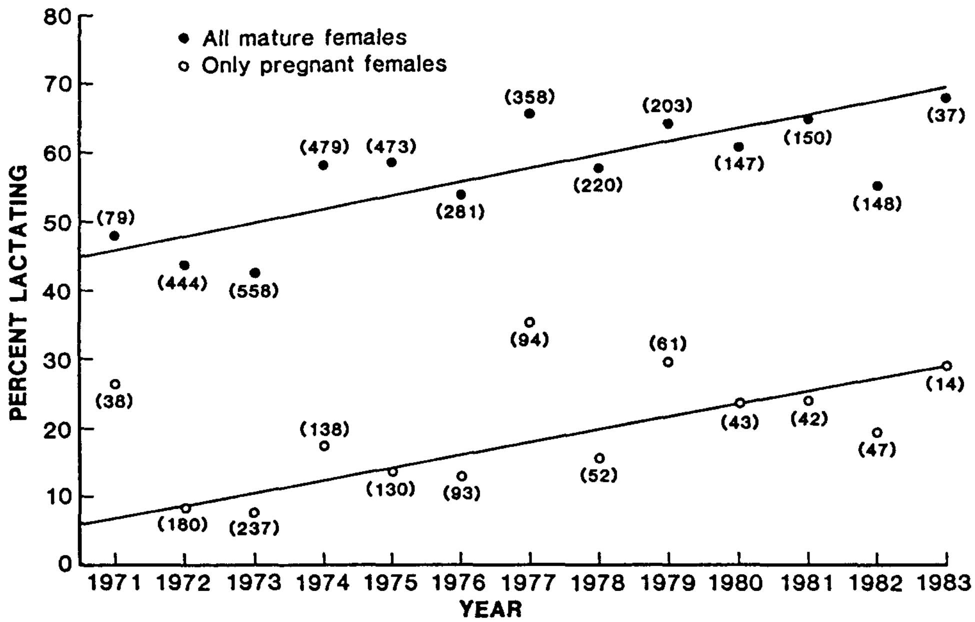

FIGURE 3.—Percentages of mature females that were lactating and percentages of pregnant females that were lactating for the northern offshore stock of spotted dolphins from 1971 to 1983. Solid lines represents weighted regressions. Sample sizes are in parentheses.

1 for both the northern and southern stocks. Again sample size for the southern stock is too small to examine individual years; however, the overall percent of pregnant females that were lactating in 1973-83 samples shows significant differences between stocks (χ_1^2 = 6.50, P = 0.01). Annual variability for the northern stock is greater than expected from random sampling of a population with a constant percent lactating (χ_{12}^2 = 63.5, $P <$ 0.001).

When the sample of pregnant females from the northern stock is stratified by the six sampling factors, lactation state was significantly related to sampling season, dolphin kill, and tuna catch (Table 5). Again, 3-way tests showed that the first order effect of these factors was not significant when year was included as the third factor (Table 6). In each of these cases, the first order effect of year was important. In one case, dolphin kill, a second order interaction between kill and year was also significant.

Percent Mature

The fractions of females that were sexually mature are given in Table 1 by stock and by year (1973-83). Again the sample sizes are sufficient in all years for the northern stock but are inadequate in some years for the southern stock. The southern stock is significantly different from the northern stock in percent mature (χ_1^2 = 31.2, $P <$ 0.001), and (given its small sample size) the southern stock was excluded in subsequent stratifications.

The percentage of all females that are mature from 1973 to 1983 is illustrated in Figure 4 for the northern stock. In this case, the weighted regression is not significant. Using chi-square tests, the level of annual variability in percent mature is larger than would be expected from randomly sampling a population with a constant fraction of mature females ($P <$ 0.001).

For long-lived animals such as dolphins, annual variability in percent mature should be small and changes in this population parameter should be gradual. Since the annual variability observed in the data is larger than would be expected from random sampling error, year-to-year changes in sampling biases are likely. Percent mature was found to be significantly related to three of the six sampling factors examined: sampling season, dolphin kill-per-set, and tuna catch-per-set (Table 7).

Each of these three significant factors was tested with maturity state and year using 3-way tests (Table 8). For each of these factors, year was a significant factor and all other first order effects were not significant. Only dolphin kill showed a significant second order interaction with year.

TABLE 5.—Percentage of pregnant dolphins that were lactating (1971-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Lactating (%)	*N*	Probability
1) Geographic area			
Inside CYRA	15.7	988	0.30
Outside CYRA	18.8	181	
2) Season			
1st quarter	11.9	611	
2d quarter	17.2	239	<0.001
3d quarter	26.7	161	
4th quarter	20.3	158	
3) Chase time (min)			
<20	14.8	331	
20-40	14.0	479	0.27
>40	18.6	226	
4) School size			
<500	20.0	130	
500-1,000	18.0	211	0.87
>1,500	19.7	183	
5) Number killed			
1-10	19.1	319	
11-30	16.5	267	0.03
>30	12.3	471	
6) Tuna caught (tons)			
0-5	20.5	117	
6-15	16.4	275	0.17
16-30	16.7	221	
>30	12.8	444	

TABLE 6.—Multiway tests of factors affecting the percentage of pregnant females that are lactating. Log-likelihood chi-square was used to calculate the probability that percent lactating is independent of the stated factor(s) using the log-linear model. Lactation state (lactating/not lactating) is implicit as the first factor in each comparison.

3-way tests	Probability
a) Year	<0.0001
Season	0.29
Year × season	0.007
b) Year	<0.0001
Kill	0.79
Year × kill	0.51

TABLE 7.—Percentage of female dolphins that were sexually mature (1973-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Mature (%)	*N*	Probability
1) Geographic area			
Inside CYRA	55.7	6,329	0.19
Outside CYRA	57.5	1,625	
2) Season			
1st quarter	54.2	3,495	
2d quarter	57.2	1,738	0.02
3d quarter	58.2	1,580	
4th quarter	57.6	1,155	
3) Chase time (min)			
<20	54.4	2,067	
20-40	56.1	3,084	0.36
>40	56.5	1,689	
4) School size			
<500	53.5	1,183	
500-1,500	56.8	1,970	0.19
>1,500	56.0	1,753	
5) Number killed			
1-10	57.9	2,465	
11-30	54.9	2,068	0.02
>30	54.0	2,321	
6) Tuna caught (tons)			
0-5	53.3	920	
6-15	55.1	1,779	0.05
16-30	54.5	1,668	
>30	57.7	2,482	

DISCUSSION

Changes in the reproductive status of the female segment of a population can be monitored using a variety of reproductive indices: 1) mean age at sexual maturation, 2) mean length (or weight) at sexual maturation, 3) annual pregnancy rates, 4) calving interval, 5) percentage of mature females that are pregnant, 6) percentage of females that are lactating, and 7) percentage of females that are sexually mature. Changes in each of these are examined below.

Changes in Maturation Parameters

Myrick et al. (1984) have found no significant difference in the age at sexual maturation (ASM) between a sample from 1973 to 1978 and another sample from 1981. In the present study, length at attainment of sexual maturity is estimated to have increased 4.4 cm from 1974 to 1983. If these results hold, dolphins must be growing faster in recent years. Given small sample sizes of aged individuals, significant changes in ASM may be difficult to detect. Previous studies have shown that the age at sexual maturation is quite responsive to population changes in marine mammals (Fowler 1984), while length at maturation tends to show little change. For fin whales, *Balaenoptera physalus*, Lockyer (1972)

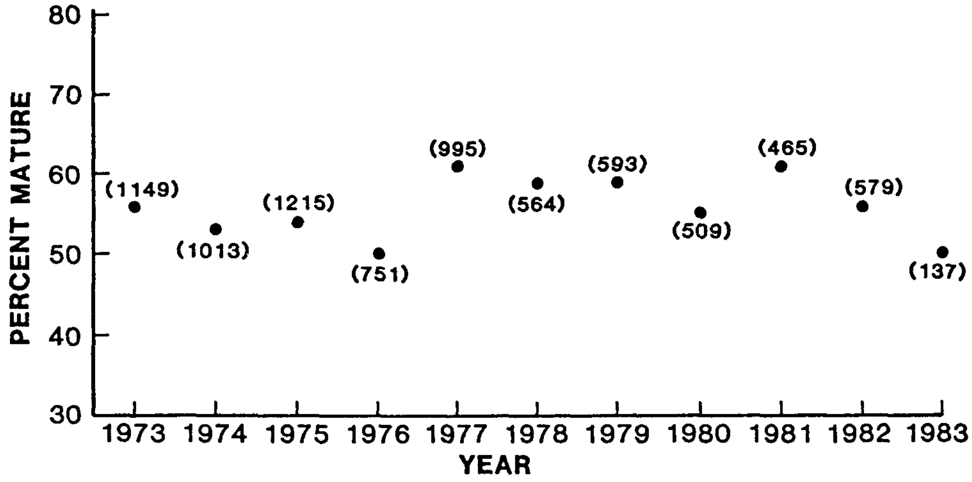

FIGURE 4.—Percentages of all females that were mature for the northern offshore stock of spotted dolphins from 1971 to 1983. Sample sizes are in parentheses.

TABLE 8.—Multiway tests of factors affecting percent mature. Log-likelihood chi-square was used to calculate the probability that percent mature is independent of the stated factor(s) using the log-linear model. Maturation state (mature/not mature) is implicit as the first factor in each comparison.

3-way tests	Probability
a) Year	0.003
Season	0.49
Year × season	0.08
b) Year	0.003
Kill	0.16
Year × kill	0.002
c) Year	0.0009
Catch	0.09
Year × catch	0.42

showed a decrease in ASM without any change in the length at which maturity is attained. Laws (1956) predicted an inverse relationship between ASM and early growth rates for marine mammals. Spotted dolphins appear to show an increase in length at maturation with no change in ASM, and thus do not follow predicted patterns.

Trends in Percent Pregnant

Annual pregnancy rates, calving interval, and percent pregnant all measure essentially the same thing. Annual pregnancy rate and calving interval require knowledge of gestation times. Because density compensatory responses have not been shown in cetacean gestation times, it is more straightforward to deal directly with percent pregnant.

What appeared to be a rapid decline in dolphin pregnancy rates from 1973 to 1978 (Henderson et al. fn. 2), now appears as two eras with distinctly different pregnancy rates. The fraction of pregnant females in the 1971-73 samples was quite high. The 10 years since 1973 show a lower and relatively constant fraction of pregnant females. This difference in results is due largely to use of a larger sample size and a longer time series.

There is no evidence of the sort of slow, long-term trends in pregnancy rates that might be associated with changes in population sizes. The reason for the dramatic change in pregnancy rates between 1973 and 1974 is not known. At least three hypotheses could be used to explain this change: 1) it was the result of a naturally high pregnancy rate in 1971-73; 2) it was the result of heavy fishing-related mortality of nursing calves prior to 1974 that resulted in artificially high pregnancy rates; or 3) it was the result of a bias in the sampling by tuna vessels.

The first hypothesis suggests that changing environmental conditions result in annual changes in pregnancy rates. In the ETP the largest environmental perturbations are associated with "El Niño" events which occur on the time scale of from 5 to 10 yr (Rasmusson and Carpenter 1982). El Niño conditions prevailed in 1972 (moderate), 1975-76 (weak), and 1982-83 (very strong). These dates do not help explain the change in pregnancy rates that occurred between 1973 and 1974.

The second hypothesis is that heavy dolphin mortality in the 1960's and early 1970's may have somehow affected dolphin pregnancy rates. Large reductions in dolphin mortality occurred following the passage of the Marine Mammal Protection Act of 1972 (Table 9). If mortality rates were higher for nursing calves, calving interval might have been shortened. This would result in higher pregnancy rates and lower lactation rates, both of which were observed in 1971-73. Analyses have indicated that very young calves are more susceptible to tuna-net mortality (Powers and Barlow fn. 3; Stuntz[6]). Indirectly, high calf mortality may also result from the separation of a calf from its mother during long chases. It is not known if the magnitude of these effects could have resulted in the observed changes in pregnancy or lactation rates.

The third hypothesis is that sampling methods were somehow different between 1971-73 and 1974-83. The only difference in the sampling design was that in 1971-73, scientific technicians were placed only on tuna vessels that agreed to cooperate. Beginning in 1974, the selection of vessels was random. It is difficult, however, to see how this change would affect the percent pregnant in the samples. As was noted above, percent pregnant was significantly correlated with sampling season, dolphin kill-per-set, and tuna catch-per-set during the years 1971-73, but not during the years 1974-83. The reason for this difference is not known, but this would seem to be evidence that sampling was more random in the latter period.

The observed change in percent pregnant from 1971-73 to 1974-83 cannot be explained with certainty. The high pregnancy rates in 1971-73 can be logically explained by direct or indirect effects of the fishery or by sampling biases in those years (Hypotheses 2 and 3). Determining whether either (or both) hypothesis is true may not be possible with existing data.

Trends in Percent Lactating

Changes were also found in the percentage of lactating females. For mature females, the fraction lactating shows low values in 1971-73 and high values in 1974-83, which is opposite the pattern seen for fraction pregnant. This inverse correlation would be expected given that pregnancy state and lactation state are physiologically linked (i.e., cessation of lactation leads to ovulation and pregnancy). Perhaps more meaningful is the increase in the fraction of pregnant females that were lactating. Because being simultaneously pregnant and lactating represent the greatest energy drain on female dolphins, this quantity is likely to be very sensitive to changes in environmental conditions. Because nonpregnant females are excluded, this quantity should also be insensitive to sample biases that are related solely to pregnancy state.

Given that no trends were seen in the percent pregnant from 1974 to 1983, we can infer that the calving interval, or the mean period between births for a mature female, also did not change during that time. If calving interval were constant, the increase in the fraction of pregnant females that were lactating indicates that females may be nursing their calves for a longer period of time, hence a longer lactation period. This increase in the lactation period may have resulted from a decrease in fishery related calf mortality during the 1971-83 period. Because calves may be more susceptible to death or separation from their mothers during the chase, capture, and release of a dolphin school, mean lactation periods may have been abbreviated during the earlier years (Hypothesis 2 above).

TABLE 9.—Estimates of numbers of spotted dolphins killed by all purse seine vessels in the eastern tropical Pacific, 1968-78 (data from Smith 1983).

Year	Spotted dolphins killed
1968	178,000
1969	365,000
1970	355,000
1971	176,000
1972	288,000
1973	131,000
1974	95,000
1975	105,000
1976	47,000
1977	22,000
1978	19,000

Trends in Percent Mature

No significant trends in the percentage of females that were sexually mature during 1971-83 are evident for the northern stock of spotted dolphins. Annual variability was far too great to be explained by random sampling error. This parameter showed a significant correlation with dolphin kill-per-set. Therefore, unless sampling conditions remain constant (which they have not), percent mature is not a useful index for monitoring reproductive capability of the spotted dolphin populations.

[6]Stuntz, W. E. 1980. Variation in age structure of the incidental kill of spotted dolphins, *Stenella attenuata*, in the U.S. tropical purse-seine fishery. Admin. Rep. LJ-80-06, 29 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Variability in percent mature with sampling conditions may result from several interacting factors. Preliminary data have indicated that spotted dolphins in the ETP may segregate on the basis of reproductive maturity (A. A. Hohn fn. 4 and M. D. Scott fn. 5). Schools that consist principally of immature dolphins may have a smaller characteristic school size, may be less likely to have large numbers of tuna associated with them, and may be more vulnerable to high kills-per-set due to the inexperience of younger dolphins. Also, the consistent underrepresentation of immature age classes in the spotted dolphin age distribution (Barlow and Hohn 1984) indicates that a very significant bias may occur in the sampling of immature animals. These are largely speculations, and until a well-supported explanation for sampling variability is presented and until some method of removing this bias is found, percent mature should not be used as an index of changes in spotted dolphin reproduction.

Gross Annual Reproductive Rate

Changes in GARR have been used as a measure of changes in the net rate of growth for a population (Smith 1983). This approach has been faulted on the basis that it does not consider age structure effects (Polacheck 1982), and more critically on the basis that such an approach is theoretically unsound (Goodman[7]). These criticisms do not, however, detract from the usefulness of GARR as an index of gross per capita reproduction for a population.

If GARR were robust to sampling conditions, it could be one of the most useful indices of population reproduction. One advantage is that a GARR index considers percent pregnant and percent mature simultaneously, and hence compensatory changes in these two do not affect the index. Simply stated, GARR is calculated as (the fraction of females in a population) × (the fraction of females that are mature) × (the fraction of mature females that are pregnant)/(gestation time). Unfortunately, percent mature is a major component in these calculations, and this parameter has been found to be dependent on sampling conditions. Until sampling problems associated with estimating percent mature are resolved, GARR is not likely to be a useful index of change in reproductive rates.

[7]Goodman, D. 1984. Uses of the gross annual reproduction rate calculation in the dolphin assessment. Admin. Rep. LJ-84-22C, 17 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Between-Population Comparisons

The northern and southern stocks of spotted dolphins have been subjected to very different levels of fishing-related mortality. Smith[8] has estimated the northern stock to be at 38-55% of its 1959 level and the southern stock to be at 93-98% of its historical level. Density dependent increases in reproductive rates might be predicted for the northern stock relative to the southern stock.

The percentage of mature females that were pregnant differs significantly between the northern and southern stocks. Surprisingly, however, the southern stock was found to have the higher percent pregnant (36% vs. 33%). Another exploited population of spotted dolphins in the western Pacific was found to have an annual pregnancy rate of 0.254 (Kasuya 1976), which (with a gestation time of 11.2 mo) would give an average percent pregnant of about 24%. Considerable variability in percent pregnant can thus exist between spotted dolphin populations, none of which is obviously related to density compensatory effects. Sampling of the southern population has, however, been sporadic, and if annual variability in pregnancy rates is greater for that stock, a few years' data may not be sufficient to accurately estimate a long-term mean. Nonetheless, the tendency for a more exploited stock to have lower reproductive rates is worrisome, and future life history comparisons between the northern and southern stocks would probably be useful.

Evidence for density compensatory changes in pregnancy rates were also lacking when two spinner dolphin, *S. longirostris*, populations were compared (Perrin and Henderson 1984). They found similarly that the more heavily exploited stock (eastern spinners) had a lower percent pregnant than the less heavily exploited stock (whitebelly spinners). The opposite would be predicted based purely on density compensatory effects.

The overall percentage of pregnant females that are lactating is significantly higher for the northern spotted dolphins than for the southern stock. The biological significance of this result is questionable given the year-to-year variability in this parameter. Between-population comparisons of this percentage are not likely to be meaningful until the cause of this large annual variability is identified.

As was noted above, the percentage of females that

[8]Smith, T. D. (editor). 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). Admin. Rep. LJ-79-41, 120 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

are mature also appears to be higher in the southern stock than in the northern stock. Given the dependence of this parameter on sampling conditions, little confidence should be placed on this result. The direction of the difference (more immatures in the northern population) is consistent with a higher population growth rate in the north. Work is in progress to determine whether this difference could be due to differences in the age at sexual maturation (Myrick[9]).

No data exist yet on the mean age at sexual maturation for females in the southern stock. As mentioned in the Methods section, data do exist on the "length at sexual maturation" for both the northern and southern stocks. For the northern stock, this length appears to have increased from 176 cm in 1974 to 181 cm in 1983. For the southern stock this length was estimated as 175 cm from the pooled 1974-83 data. The length at sexual maturation is greater for the northern stock, which is consistent with the greater mean asymptotic length of the northern specimens (Perrin et al. 1979).

CONCLUSION

My intent in writing this paper was to identify indices that may be of value in monitoring the reproductive health of spotted dolphins in the eastern Pacific. Two of the indices that were examined (the percentage of mature females that are pregnant and the percentage of pregnant females that are lactating) are likely to be useful for this purpose. Both are relatively insensitive to sampling biases, and both measure important aspects of the female reproductive cycle. Problems exist in measuring the fraction of females that are mature. This parameter is also an important index of net reproduction in a population. It is possible that a stable index of percent mature could be obtained using some stratification scheme. A first approach might be to examine finer scale geographic differences in percent mature. Additional work is necessary before significance can be ascribed to between-population differences in percent mature.

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[9]A. C. Myrick, NOAA, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1984.

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