Abstract.–We examined the average age at attainment of sexual maturity (ASM) and several other reproductive parameters for evidence of density compensatory responses in two stocks of the spotted dolphin, *Stenella attenuata*. The northern offshore and southern offshore stocks were compared because both have been exploited by the yellowfin tuna purse-seine fishery, but at different rates. We predicted decreasing trends in the ASM and increasing trends in the pregnancy rate for each stock because both have declined in abundance. A lower ASM and a higher pregnancy rate were predicted for the sample from the northern offshore stock because it has been exploited to a greater extent than the southern offshore stock. No statistically significant trends were found in the ASM, but the increase in the proportion of sexually mature females simultaneously pregnant and lactating for the northern offshore stock and the decrease in the proportion of mature females in the population for the southern offshore stock over time were statistically significant. The mean estimate of ASM was significantly higher for the northern offshore stock, 11.1 years (SE=0.236), than for the southern offshore stock, 9.8 years (SE=0.264). No significant differences between stocks were found in the mean estimates of reproductive parameters. Our analyses of temporal trends in several biological parameters did not provide conclusive evidence for compensatory responses having occurred, and therefore some possible explanations are considered.

Comparison of age at sexual maturity and other reproductive parameters for two stocks of spotted dolphin, *Stenella attenuata*

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As population abundance declines, compensatory responses, such as increases in survival and pregnancy rates and a decrease in the average age at attainment of sexual maturity (ASM), are thought to occur (Eberhardt, 1977; Eberhardt and Siniff, 1977). Each situation must be carefully evaluated to determine whether compensatory responses will be detected because the magnitude of the parameter response and the range of population densities over which measurements are made are likely to be species specific, environmentally variable, and subject to parameter measurement error (Goodman, 1981; Fowler, 1981, 1988; DeMaster, 1984a; York, 1987). For species that are difficult to observe, unbiased estimates of survival rates are difficult to obtain, precluding their use as potential biological indices (Barlow and Boveng, 1991). Reproductive rates, however, are generally more easily measured and, if their relationship to population density is determined, may provide indices of compensatory responses for populations (Perrin and Donovan, 1984). For instance, Barlow (1985) reported that in the spotted dolphin (*Stenella attenuata*), the fraction of mature females pregnant, and the fraction of mature females simultaneously pregnant and lactating, may correlate well with per capita resource availability because these parameters were found to be relatively

free of collection biases. The identification of biological indices (i.e., biological parameters that correlate with population abundance) would provide a useful management tool to distinguish between trends in population abundance resulting from exploitation or changes in environmental conditions (Hanks, 1981; Gerrodette and DeMaster, 1990).

The spotted dolphin is an ideal choice for this analysis because a lengthy time series of biological and population abundance data are available. This species is used as a cue by purse-seine vessel operators to find yellowfin tuna in the eastern tropical Pacific (ETP) (Perrin, 1969). Dolphins are incidentally killed during fishing operations, and the spotted dolphin population has had the largest number of animals killed in almost every year since 1959 (Smith, 1983; DeMaster et al., 1992). Two stocks of spotted dolphin, the northern offshore and southern offshore stocks, are recognized as separate management units in the ETP (Perrin et al., 1985). During the first decade of the purse-seine fishery, the 1960's, the large numbers of dolphins killed caused the abundance of these two stocks to decline. The northern offshore spotted dolphin was estimated to be between 35% and 50% of their pre-exploitation abundance (circa 1959) by 1979 (Smith, 1983), while the southern offshore stock was estimated to be at 92–98% of its

pre-exploitation size (circa 1973) in 1979 (Smith[1]). Since 1976, both stocks of spotted dolphin are believed to have declined significantly in abundance (Anganuzzi et al., 1992).

As potential biological indices, we estimated ASM and associated reproductive parameters for two stocks of the spotted dolphin. Although for long-lived mammals, like the spotted dolphin, population growth rates are relatively insensitive to changes in ASM and reproductive rates (Eberhardt and Siniff, 1977; Fowler, 1981; Reilly and Barlow, 1986), these parameters have been correlated with changes in population abundance for other marine mammal species (Fowler, 1987). For instance, a decrease in ASM was correlated with a decline in population abundance for baleen whale stocks (Lockyer, 1984). Similarly, a decrease in ASM for crabeater seals was correlated with an increase in the per capita availability of food resources resulting from the exploitation and subsequent reduction in size of baleen whale stocks (Bengtson and Laws, 1985). Likewise, ASM for the striped dolphin of the western Pacific declined in response to exploitation and reduced population abundance (Kasuya, 1985). Based on the predictions of population responses to changes in density (i.e., increases in ASM and decreases in pregnancy rates as population abundance increases) presented by Eberhardt (1977) and Eberhardt and Siniff (1977), we predicted a decline in the ASM for both the northern offshore and southern offshore stocks of spotted dolphin after 1974 as well as a lower ASM for the more heavily exploited northern offshore stock. Similarly, a higher fraction of sexually mature females pregnant and those simultaneously pregnant and lactating should be observed for the northern offshore stock.
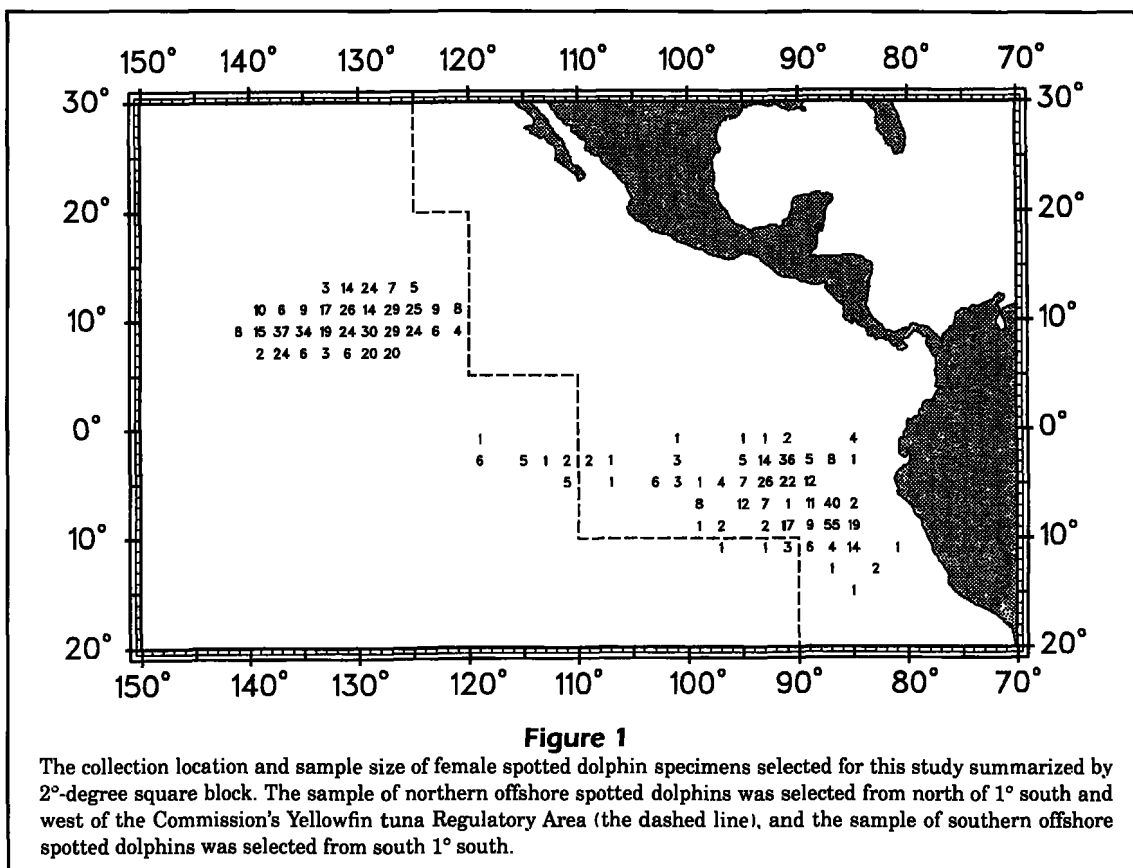
Methods

Since 1968, when the National Marine Fisheries Service (NMFS) first placed observers aboard U.S. vessels to observe fishery activities, life history data has been collected from all cetacean species incidentally killed in the ETP yellowfin tuna purse-seine fishery. Beginning in 1974, life history data collection procedures were standardized, and the original sampling scheme that selectively collected large, female specimens was replaced by a random sampling scheme that selected the first available dead dolphins brought aboard (Perrin and Oliver, 1982). In 1979, the Inter-American Tropical Tuna Commission (IATTC) joined the NMFS in

placing observers aboard U.S. vessels and collecting life history data.

The offshore stocks of spotted dolphin are distinguished geographically as being north or south of 1° south latitude (Perrin et al., 1985). The specimens used in our study were collected from these areas, but the sample of northern offshore stock animals was additionally restricted to those animals collected west of 120° west latitude (Fig. 1). The northern offshore stock was sub-sampled because exploitation has not been spatially uniform. The yellowfin tuna purse-seine fishery began primarily as a coastal fishery in 1959 and gradually expanded farther offshore. The Commission's Yellowfin tuna Regulatory Area (CYRA) was established in 1968 by the IATTC and provides a useful boundary that separates the inshore fishery area from the westernmost region of the ETP yellowfin tuna fishery (Peterson and Bayliff, 1985). The area west of the CYRA was not fished until the late 1960's, and then only for a few months a year. Exploitation in this region has been significantly less than inside the CYRA but much more than in the southern area which has been fished only sporadically since the early 1970's (Punsly, 1983). Although spotted dolphin move along the 10°N latitude as well as from the south to the west (Perrin et al., 1979a; Au and Perryman, 1985; Reilly, 1990), owing to the large size of the area, interchange between areas is probably limited. A standardized data collection scheme was established at about the same time as the fishery expanded into the western and southern regions of the ETP, and therefore we anticipated that these two distinct geographic regions would provide the best opportunity for testing potential biological indices.

Female spotted dolphins with complete life history data (i.e., geographic position, total body length, teeth collected, and both ovaries examined) collected between 1974 and 1988 were selected for this study. Few specimens have been collected from the southern offshore stock, and therefore all available specimens were prepared. Specimens from the northern offshore stock were selected randomly by year and the sample sizes distributed as evenly as possible between years so that annual estimates of ASM could be calculated. A maximum of 50 specimens per year was the target for selecting specimens from the northern offshore stock sample because Hohn (1989) showed that a sample size of 50 accurately estimated ASM and reduced the variance from an estimate based on a sample size of 25. Thin sections of the teeth were prepared and aged by one of us (ACM) with techniques described in Myrick et al. (1983). Prior to estimating age, all specimens were numerically coded in random order to disguise the specimen number so that no inference could be made about the stock or collection year for any speci-

[1]Smith, T. D. (ed.). 1979. Report of the status of porpoise stocks workshop (August 27–31, 1979, La Jolla, California). U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-79-41, 120 p.

Figure 1

The collection location and sample size of female spotted dolphin specimens selected for this study summarized by 2°-degree square block. The sample of northern offshore spotted dolphins was selected from north of 1° south and west of the Commission's Yellowfin tuna Regulatory Area (the dashed line), and the sample of southern offshore spotted dolphins was selected from south 1° south.

men. The associated life history data were also withheld until each specimen was aged.

ASM and its variance were calculated with the following formula (DeMaster, 1984b; Hohn, 1989).

$$ASM = x + \sum_{i=x}^{j} p_i$$

$$s^2 = \sum_{i=x}^{j} \{[(p_i * (1-p_i)]/(n_i-1)\},$$

where, x = age of the youngest mature animal,
j = age class of the oldest immature animal,
p_i = proportion immature in age class i,
n_i = sample size for age class i.

Because population abundance estimates are not available for the geographic areas from which our samples were collected, we substituted year as a correlate for evaluating potential biological indices. We tested for temporal trends in ASM with a linear regression to determine whether the slope was statistically significantly different from zero. In addition, data for each stock were pooled for all years, and the null hypothesis of no difference between estimates of ASM for the two stocks was tested with a Student's t-test.

Other reproductive parameters examined include the fraction of the females mature, and the fraction of mature females that were either pregnant or lactating, or simultaneously pregnant and lactating. Trends in these parameters between 1974 and 1988 were tested by using a chi-square test for linear trends (Snedecor and Cochran, 1973), and the mean estimates for each parameter, all years combined, were tested for statistically significant differences with a chi-square test.

Results

Average age at attainment of sexual maturity

ASM was estimated for each year with sufficient data available (Table 1): 1976–1982 and 1984–1988 for the northern offshore stock sample, and 1976, 1979, and 1982 for the southern offshore stock sample. The regression line fit to the data for the northern offshore stock was not statistically significantly different from zero. We did not fit a regression line to the data from the southern offshore stock because only three annual estimates were available. The pooled estimate of ASM for each stock was 11.1 years (SE=0.236; n=520) for

Table 1

Number of samples by year and state of sexual maturity (immature or mature) for the northern offshore and southern offshore stocks of spotted dolphin used to estimate the average age at attainment of sexual maturity.

| | Offshore stock | | | |
| | Northern | | Southern | |
Year	Immature	Mature	Immature	Mature
74	0	0	0	0
75	0	0	0	5
76	13	33	41	101
77	16	28	2	6
78	17	27	1	23
79	18	25	16	49
80	15	28	2	9
81	13	24	6	5
82	12	20	42	68
83	9	9	11	11
84	11	27	1	4
85	17	29	0	0
86	18	28	0	0
87	22	26	0	0
88	14	21	0	0
Total	195	325	122	281

the northern offshore spotted dolphin and 9.8 years (SE=0.264; n=403) for the southern offshore spotted dolphin (Fig. 2). This difference in the ASM was statistically significant (t=14.32, df=13, P< 0.001). The
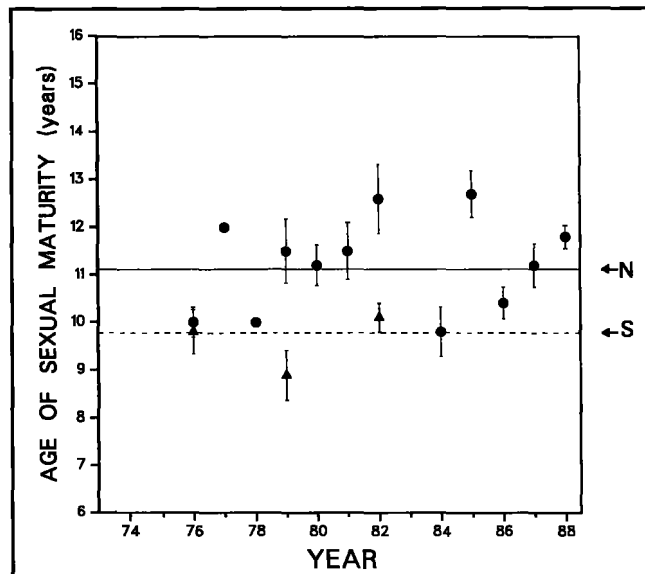

Figure 2

Estimates of the average age at attainment of sexual maturity (ASM) by stock for the offshore spotted dolphin with 1 SE. If no SE bar was plotted, then there were no overlapping indeterminate age classes. Circles represent estimates of ASM for the northern offshore stock and triangles are the estimates for the southern offshore stock. The pooled estimate of ASM for the northern offshore stock (N) is 11.1 years (solid line) and 9.8 years (dashed line) for the southern offshore stock (S).

range in age of animals attaining sexual maturity was largest for the northern offshore stock. The youngest mature animal was 7 years, and the oldest immature was 16 years. The same range for the southern offshore stock was 6 to 11 years (Fig. 3).

Reproductive rates

The statistically significant trends in the reproductive parameters examined were an increase in the proportion of mature females simultaneously pregnant and lactating in the northern offshore stock, the predicted compensatory response, and a decrease in the proportion of mature specimens in the sample from the southern offshore stock. When the data for all years were pooled, no statistically significant differences between the mean parameter estimates for the northern offshore and southern offshore stocks were detected (Table 2).
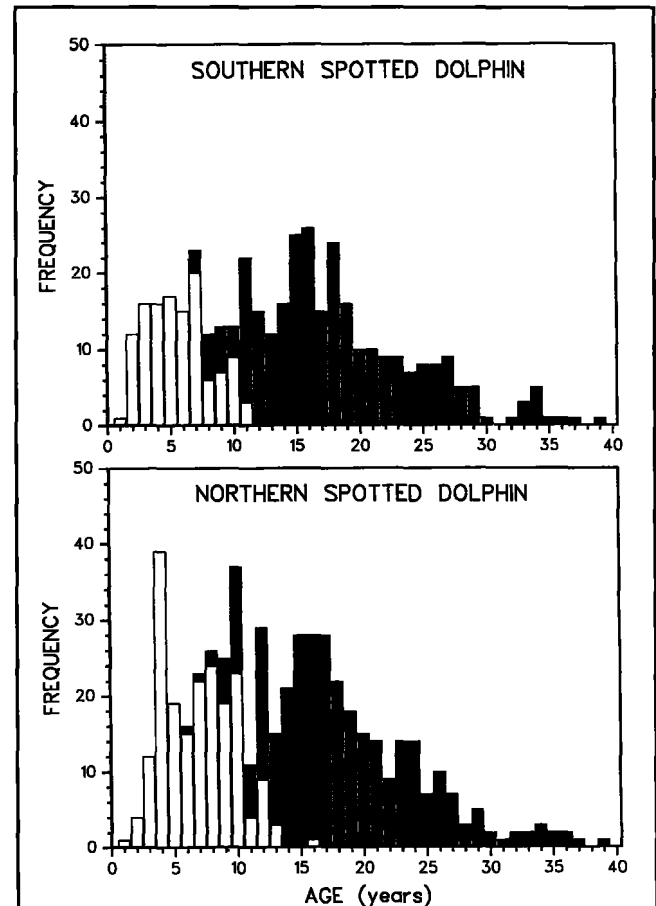

Figure 3

Age-frequency distribution of the northern offshore and southern offshore spotted dolphin specimens aged. The open bars represent the sexually immature females in the sample, and the solid bars represent the sexually mature females in the sample.

Table 2

The mean proportion of females by reproductive condition for the northern offshore and southern offshore stocks of spotted dolphin: the proportion of females in the sample that were sexually mature, and the proportion of sexually mature females that were pregnant or lactating, or simultaneously pregnant and lactating.

Reproductive condition	Stock	
	northern	southern
Mature	0.62	0.69
Pregnant	0.33	0.40
Lactating	0.55	0.47
Pregnant and lactating	0.06	0.06

Discussion

Published evidence of density dependence in dolphin species is rare, and results are inconsistent. For example, in Japan, the striped dolphin, *Stenella coeruleoalba*, is heavily exploited, and the length of the lactation period is reported to have declined (Kasuya and Miyazaki[2]). For exploited spotted dolphins in the western Pacific, a decline in the ASM from 10.1 years in the 1961–63 cohorts to 8.6 years in the 1964–66 cohorts was reported, although the regression coefficient was not statistically significant (Kasuya, 1985). The decline in ASM for female striped dolphin from 9.7 years for the 1956–58 cohorts to 7.4 years in the 1968–70 cohorts was statistically significant (Kasuya, 1985). On the otherhand, for the spinner dolphin (*S. longirostris*) in the ETP, the less exploited southern whitebelly stock has a shorter lactation period than the more heavily exploited eastern spinner dolphin, the opposite of what would be expected for a compensatory response. The annual pregnancy rate, however, is lowest for the southern whitebelly stock and highest for the more heavily

[2]Kasuya, T., and N. Miyazaki. 1975. The stock of *Stenella coeruleoalba* off the Pacific Coast of Japan. Pap. ACMRR/MM/SC-25 pres. at FAO Scientific Consultation of Marine Mammals, Bergen, February, 1976, 36 p.

exploited eastern stock, as expected for density compensation (Perrin and Henderson, 1984). Barlow (1985) also reported differences in the proportion of mature female spotted dolphins (*S. attenuata*) that were pregnant between the eastern and western Pacific. The lowest proportion of mature females pregnant was observed in the more heavily exploited population, again, contrary to predictions based on the reported exploitation rates and estimates of population abundance for the ETP spotted dolphin. Also, for ETP spotted dolphins, the proportion of lactating mature females significantly increased from 46% in 1973 to 69% in 1981 ($P<0.05$) presumably in response to exploitation; no other statistically significant trends in reproductive parameters were found (Myrick et al., 1986).

Comparisons with other studies are difficult because in most cases the degree of exploitation relative to K has not been quantified, and techniques to estimate age and ASM vary. In our study, statistically significant temporal trends were not detected for ASM but were detected for some of the reproductive parameters. The increase in the proportion of mature females simultaneously pregnant and lactating for the northern offshore stock and the decrease in the proportion of mature females in the population for the southern stock both suggest that the populations are growing. The fact that we did not observe the predicted compensatory responses in ASM may be due to one or more factors, including 1) too few data, 2) parameter estimation or measurement error, 3) a time lag in the response, or 4) biological differences between the stocks. Too few data and environmental periodicity (e.g., El Niño) may increase the variability in annual estimates of parameters, and both factors would reduce the ability to detect differences in potential compensatory responses (Goodman, 1984). The order in which parameters respond to changes in population density is not known, but time lags in responses may be expected owing to the late age at which these animals reach sexually maturity and the multi-year breeding cycle characteristic of the spotted dolphin (Goodman, 1981).

Data for the southern offshore stock of spotted dolphin, in particular, were limited and precluded testing for trends in ASM or the selected reproductive parameters. Although we selected our sample size, a maximum of 50 specimens per year for the northern offshore stock, on the basis of earlier work describing the effect of sample size on the variance for estimates of ASM (Hohn, 1989), our results indicate that larger sample sizes would be required to reduce the variance of the estimates in order to detect small, but biologically significant, changes (e.g., a 1.5-year difference) in ASM. Sample sizes of fewer than 50 per estimate of ASM resulted in too few specimens in the indeterminate age classes (i.e., those age classes with both sexually immature and mature animals) to estimate ASM accurately.

Another concern when analyzing data collected from a kill is whether the age distribution is representative of the population. All immature age classes appear to be underrepresented in both stocks, especially age classes between 10 and 15 years of the northern offshore stock (Fig. 3). This phenomenon was noted in a previous aging study of ETP spotted dolphin but occurred about five age classes earlier than the one we observed (Barlow and Hohn, 1984). This difference may be a result of different readers estimating age,

although a Kolmogorov-Smirnov test to compare the age-frequency distributions of sexually immature and sexually mature animals from the two studies concluded that the samples were likely drawn from the same population. The underrepresentation of the immature age classes may be a result of segregation in the population by age and sex, fairly typical in large mammal populations, and may affect the estimation of ASM. We investigated the effect of this underrepresentation by assuming a stable age distribution and by apportioning the animals in the indeterminate age classes by sexual maturity under different assumptions of sexual maturity for animals in those age classes, and then calculated ASM. On the basis of segregation by age and sex observed in other species of large mammals, we predicted that the most reasonable scenario for reconstructing the age distribution is that the "missing" animals would be sexually immature. If this indeed were the case, we have underestimated ASM. Under this and other scenarios we investigated, estimates of ASM were consistently over- or under-estimated for both stocks. Therefore, possible sampling biases were unlikely to be responsible for the observed differences in ASM between the northern offshore and southern offshore stocks of spotted dolphin.

The hypotheses we tested required that several implicit assumptions be made, including: 1) constant data collection biases, 2) minimal interchange of animals between areas, 3) consistent estimation of specimen age, 4) linear compensatory response with change in population abundance, 5) constant carrying capacity (K), and 6) equivalent initial life history parameters for the two stocks. The first three of the assumptions are believed to hold reasonably well. Barlow (1985) tested several of the same life history parameters we examined and found them to be relatively insensitive to a number of potential data collection biases; no major changes in the collection of life history data were made after 1974, thus supporting constant data collection bias as a reasonable assumption. Furthermore, the fishery operates in the same areas from year-to-year at approximately the same time of year. In fact, 60% of our sample from the northern offshore stock was collected between July and September, and a further 38% was collected between April and June; in the south, 57% of the sample was collected between January and March, and 27% was collected between October and December. This pattern of sample collection was consistent from year-to-year, and therefore would not affect the pooled or annual estimates of ASM or reproductive parameters. Geographic variability has been noted in earlier studies of spotted dolphin life history data (Hohn and Hammond, 1985; Barlow, 1985);

thus selecting specimens from discrete areas as we did reduces the potential for geographic variability to obscure population compensatory responses. Similarly, estimating the age of all specimens at one time and in the blind ensured that age estimates were made as consistently as possible. Information about the validity of assumptions 4) and 5) is not currently available, but violations of the assumptions may provide explanations for our results. There is evidence for differences in the morphological and life history characteristics between the northern offshore and southern offshore stocks of spotted dolphin (see Perrin et al., 1976, 1979b, 1991[3]; Barlow, 1985; Hohn and Hammond, 1985; Myrick et al., 1986; Bright and Chivers[4]) that are likely correlated with the different oceanographic environments of the areas inhabited by these stocks (Au and Perryman, 1985; Reilly, 1990).

We did not find conclusive evidence for compensatory responses in these stocks of spotted dolphin as only one reproductive parameter for each stock showed a statistically significant trend. However, observed trends in both parameters suggest the populations are below K and declining. Our comparison of ASM's suggest further biological differences between the northern offshore and southern offshore stocks or populations. Currently, the order of compensatory responses and their dynamics are not known. In order to be useful as a biological index, a measure of the status of the population must be known and the dynamics of the parameter over a wide range of population densities quantified (Fowler and Siniff, 1992).

Acknowledgments

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[4]Bright, A. M., and S. J. Chivers. 1991. Post-natal growth rates: a comparison of northern and southern stocks of the offshore spotted dolphin. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-30, 24 p.

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