RATES OF INCREASE IN DOLPHIN POPULATION SIZE

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ABSTRACT

Annual finite rates of increase in dolphin population size were estimated to vary up to a maximum of 1.09, using simulation, based on ranges in vital rates. Vital rate ranges were defined from values reported in the literature where possible, otherwise by making assumptions about biological or logical limits. Given information on current values, or limits, of one or more vital rate, one can use the figures presented to determine ranges of possible rates of increase in population size. The highest rates estimated here (up to 1.09) are probably unrealistic, because of the unlikely combinations of high fecundity and low mortality needed to achieve them.

Rates of increase in population size are important in determining management strategies for fish and wildlife subject to exploitation. A common management approach for setting incidental mortality or harvest quotas is to use a stock-production model (Schaeffer 1957; Allen 1976) with an assumed maximum rate of increase. For dolphins and other cetaceans, rates of increase have proven extremely difficult to measure directly. Nonetheless, estimates of this parameter are sometimes necessary, e.g., in setting incidental mortality quotas for dolphin populations involved in the eastern tropical Pacific purse seine fishery for yellowfin tuna (Smith 1983). In such situations, even a range, when rigorously defined, can contribute substantially to delineating the management options.

In this paper we define a range of reasonable values of rate of increase (hereafter also referred to as ROI) in dolphin population size, given what is known or can be inferred about their age-specific survival and fecundity distributions, or "vital rates". We estimate rates of increase using population projection matrices for various parameter combinations. We also suggest how the resulting ranges in ROI can be further narrowed, given specific information for an individual population.

There are many slightly different definitions for rate of increase, but all share the commonsense notion of change in population size over time. Caughley (1977) reiterated the distinction between exponential and finite rates: finite rates, here symbolized λ, are related to exponential rates, here symbolized r, by the simple conversion $\lambda = e^r$. (We use the term "finite rates of increase" for λ following Birch 1948.) Further, within exponential rates Caughley distinguished among "intrinsic" (r_m), "survival-fecundity" (r_s) and "observed" ($\bar{r}$), rates.

In this paper we compute a series of r_s values, resulting from ranges of survival-fecundity distributions. The highest value of r_s resulting from the range of vital rates considered is our best estimate of dolphin r_m, or "r-max".

We define the ranges in vital rates based on the literature for dolphins where possible. Otherwise, we rely on information for other large mammals and what appear to be logical or biological limits.

There are two previous studies of a similar nature for delphinids. As part of a general review of life history analysis of large mammals, Goodman (1981) examined the relationships among rate of increase, juvenile and adult survival rates. He looked at single values for calving interval and age at first reproduction across ranges of survival rates. We take a broader look at these relationships, examining ranges for all four parameters.

Polacheck (1984) examined interparameter relationships for eastern tropical Pacific (ETP) dolphins, *Stenella* spp., given specific vital rate estimates available as of 1981, showing the values were not consistent with a positive population growth rate. Since then, revised estimates have become available for some relevant parameters, and this specific case has been reanalyzed, with similar general conclusions.

The only reported dolphin rates of increase are for *Stenella coeruleoalba*. For the year 1974, Kasuya (1976) estimated a rate of 0.024 for the population off Japan. This value was computed in a complex manner, based on an observed fishing mortality, assumed natural mortality, and estimated popula-

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tion size, calving interval and sex ratio. Assuming that calving interval was density dependent, Kasuya (1976) estimated a maximum annual rate of increase of 0.044 for this population of *S. coeruleoalba*.

METHODS

The Model

Population growth rates are estimated here using the familiar Leslie matrix model (Leslie 1945). A simplified parameterization is used for which survival rates and fecundities remain constant over many age classes. Four parameters are required: 1) calving interval for reproductively mature females, 2) average age at first birth for females, 3) annual adult (noncalf) survival rate, and 4) annual calf survival rate. This degree of detail corresponds to the practical limitations in collecting data on wild dolphin stocks.

The model is constructed with the assumption that age class 1 corresponds to newly born calves (i.e., censuses occur immediately after the calving season). In fact, the model is not dependent on discrete calving seasons, but this assumption helps in conceptualizing some elements of the model. The fecundities (elements of the first row of the Leslie matrix) represent the number of female calves born in one year per female of a given age class in the previous year. Fecundities for mature age classes are estimated as the annual pregnancy rate (the inverse of calving interval) multiplied by the adult survival rate (the probability that a [pregnant] female will survive to the calving season) multiplied by 0.5 (the fraction of female offspring). The annual pregnancy rate is estimated as the percent of sexually mature females which are pregnant, divided by the gestation period (in years).

The choice of only two different survival rates for all life stages was made because of data limitations for dolphins. Perhaps a more biologically reasonable assumption would be that dolphins have a U-shaped mortality curve which is characteristic of mammals in general (Spinage 1972; Caughley 1977; Siler 1979; Smith and Polacheck 1981). Barlow[2] incorporated this typical mammalian survivorship curve in models of growth for spotted dolphins, *Stenella attenuata*. Our choice of a separate survival rate for calves was based on the common observation of higher mortality in juvenile mammals (Caughley 1977; Siler 1979). For convenience, juvenile mortality factors are compressed into the first year's survival rates. This simplification is justified because population growth rates do not depend on the age at which juvenile mortality actually occurs. We recognize that juvenile mortality factors probably extend past the first year of life, but insufficient data exist to justify including this in our model. Higher mortality in old age was not incorporated in our model, but maximum age was limited to 50 yr. The survival rate at age 50 was thus zero.

We calculate population growth rates for a range of the four vital rate parameters mentioned above. Finite population growth rates, λ, that are associated with these parameter values were calculated by solving Lotka's characteristic equation, using Newton's method. The explicit form of Lotka's equation used is

$$1 = \sum_{x=1}^{50} \lambda^{-x} \, l_x \, m_x$$

where l_x is the survivorship from birth to age class x and m_x is the fecundity of age class x.

Below, we define the ranges used for the four population parameters and describe how they were selected.

Survival Rates

Ranges in Noncalf Survival Rates

Few estimates of adult survival rates for dolphins are available in the literature, primarily because adequate data are difficult to collect. Kasuya (1976) presented annual survival rate estimates of 0.925 and 0.882 for exploited populations of *Stenella attenuata* and *S. coeruleoalba*, respectively; however, his method (log-linear regression) is biased (Barlow 1982), and he did not adjust for the effect of population growth on age structure. A range of 0.85 to 0.97 was chosen for survival rates in this study. Values <0.85 do not allow population growth for the ranges of other parameters appropriate here, hence these values were not considered. Values higher than 0.97 result in more than 22% of the population being over 50 yr old. This is inconsistent with estimates of longevity for delphinids based on tooth layer counts [58 yr in *S. coeruleoalba* (Sacher 1980), 38 yr in *S. attenuata* (Hohn and Myrick[3])], hence values

[2]Barlow, Jay. 1986. Biological limits on current growth rate of a spotted dolphin population (*Stenella attenuata*). Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[3]Hohn, A. A., and A. C. Myrick, Jr. 1986. Age distribution of the kill of spotted dolphins in the eastern tropical Pacific.

>0.97 are untenable as mean per-capita survival rates.

Ranges in Calf Survival Rate

Again little information is available on calf survival for dolphins. Kasuya (1976) estimated a juvenile survival rate that was higher than that of adults, based on a balance equation. His methods assume that populations are neither growing nor declining, and he did not show that this assumption was met. Also his juvenile period included all sexually immature age classes. The overwhelming body of evidence from terrestrial mammals is that very early juvenile mortality is higher than adult mortality (Spinage 1972; Caughley 1977; Siler 1979). Even human populations had a first year survival rate of <0.88 prior to modern antibiotics (Fruehling 1982, data for U.S. circa 1900). An upper limit on calf survival rates was generated by assuming a calf is absolutely dependent on its mother for 1 yr. A calf has the same risk of dying as an adult, plus the additional risk of dying of starvation if its mother dies before completing 1 yr of lactation. The upper limit on calf survival would thus equal the square of the adult survival rate. The lower limit on calf survival rates was chosen as 0.50, a value that seems typical of pinnipeds (Smith and Polacheck 1981) and long-lived terrestrial mammals (Spinage 1972).

Fecundity-Related Rates

Ranges in Calving Interval

Observed calving intervals for dolphins generally range from 2 to 4 yr (Perrin and Reilly 1984); consequently, we have used this range in our computations. Intervals reported for killer whales (which are also delphinids, but not "dolphins") are considerably longer, up to 8 yr (e.g., Jonsgård and Lyshoel 1970).

The literature includes reports of calving intervals <2 yr for dolphins. These reports do not appear to be valid. Reevaluation of data for three of these reports[4] indicates that sampling was biased toward pregnant females (Perrin and Reilly 1984), a result of what may be a general tendency for dolphins to segregate by age/sex groupings[5].

The remaining reports of calving intervals <2 yr are from very small sample sizes.[6] Gestation periods for dolphins are at minimum 10 mo, and intraspecific variation is small. Reported lactation periods range from 1 yr to over 2 yr (Perrin and Reilly 1984). Summing these two periods gives another indication that dolphin calving intervals are not likely to be <2 yr.

An exception to the 2-yr minimum calving interval would possibly be in a population experiencing very high calf mortality, causing premature cessation of lactation, and allowing females the opportunity to begin a new calving cycle (assuming there was no seasonality to breeding which could require a resting period before the next breeding season). To include consideration of this case we would need to devise an arbitrary function relating low calf survival to short calving intervals. The net result would again be low rates of increase. To avoid such complications we have simply used 2 yr as the minimum average calving interval.

Ranges in Age at First Birth

The available data suggest a range in age at attainment of sexual maturity of 6 to 12 yr for dolphins (Perrin and Reilly 1984). Early reports of Black Sea common dolphins, *Delphinus delphis*, attaining sexual maturity at an average of 3 yr (Kleinenberg 1956) are almost certainly due to faulty age determination[7]. Because of the recent findings for *S. attenuata* from the ETP (Myrick et al. 1986), we considered the ages at first birth up to 15 yr. In our formulation of the Leslie model, if females mature and first conceive at an average age of 10 yr, the first nonzero fecundity would be in age class 11 (Table 1).

Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[4]Three reported cases of dolphin calving intervals <2 yr, later found to be biased due to age and sex segregation, are Black Sea *Delphinus delphis* and *Tursiops truncatus* (Kleinenberg 1956) and Western Pacific *Stenella coeruleoalba* (Miyazaki and Nishiwaki 1978).

[5]Hohn, A. A., and M. D. Scott. 1983. Segregation by age in schools of spotted dolphins in the eastern tropical Pacific. Fifth Biennial Conf. Biol. Mar. Mammals, Abstr., p. 47.

[6]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. Southwest Fisheries Center, La Jolla, California, Admin. Rep. LJ-80-02, 51 p.

[7]Myrick, A. C. Jr., Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038, pers. commun. June 1984.

TABLE 1.—Parameters used and values included in the computation of rates of increase in dolphin population size.

Parameter	Values
Calving interval	2 yr 3 yr 4 yr
Age at first birth	7 yr 9 yr 11 yr 13 yr 15 yr
Calf survival rate	0.50 0.52 0.54 ... (Sa)[2]
Noncalf survival rate (Sa)	0.850 0.855 0.860 0.865 ... 0.970

RESULTS

Figures 1 through 5 give finite rates of increase (displayed as $(\lambda - 1) \cdot 100$) for the above ranges of age at first birth, calving interval, and calf and noncalf survival. The lower left corner of each panel is blank because we did not consider cases where calf survival exceeded the square of noncalf survival, for the reason discussed in Methods.

The maximum finite rates of increase which would result from the parameter ranges included here are 1.08 to 1.09. Rates as low as 0.89, i.e., decrease of 11%/yr. also resulted from the parameter ranges used.

Within the ranges of parameters examined here, rate of increase is most sensitive to calving interval and noncalf survival rate, followed by age at first birth, and is relatively insensitive to changes in calf survival rate. This is an expected result following the reports by Eberhardt and Siniff (1977) and Goodman (1981). An increase in calving interval of 1 yr results in a decrease in ROI of about 0.02, holding other parameters constant. For example, the maximum ROI for a 9 yr age at first birth is about 1.07 with a 2 yr calving interval. This ROI drops to 1.05 with a 3 yr calving interval. A decrease of 0.01 in noncalf survival rate results in a 0.01 decrease in ROI, while a 0.10 decrease in calf survival rate decreases ROI by <0.01. Age at first birth appears to be nonlinearly related to ROI over the ranges examined here. An increase in this age from 7 to 9 yr results in a 0.02 decrease in ROI, while an increase

FIGURES 1-5.—Contours of percent rate of increase in dolphin population size ($(\lambda - 1) \cdot 100$), as a function

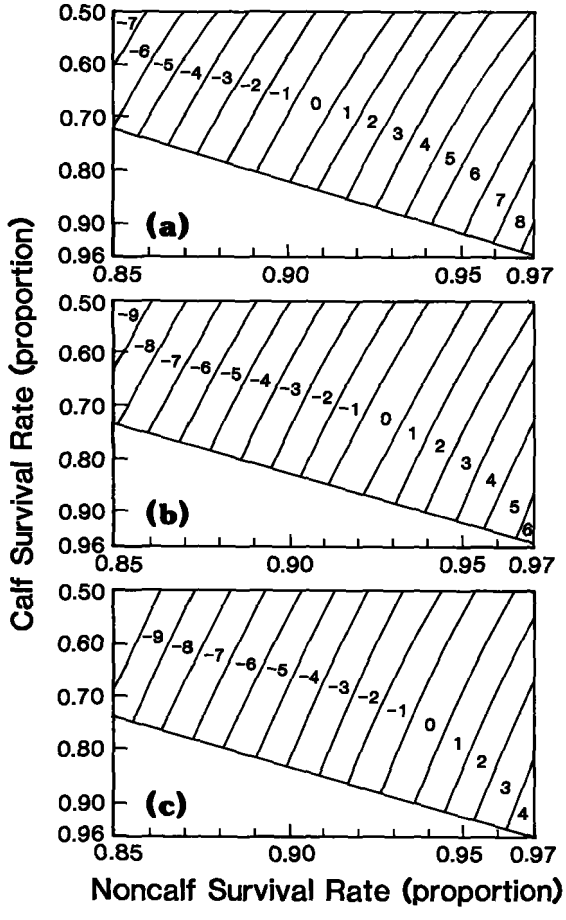

FIGURE 1.—First reproduction of dolphin age class 7 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

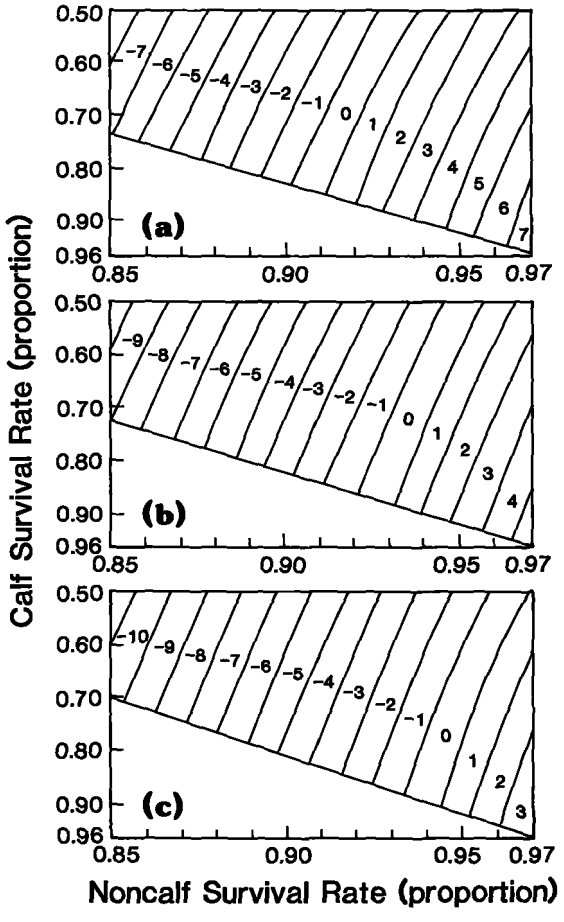

FIGURE 2.—First reproduction of dolphin age class 9 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

from 11 to 13 yr causes only a 0.01 decrease in ROI.

DISCUSSION

The ranges of rate of increase estimated here are potentially useful in bracketing possible ROIs for delphinids in general. For any particular population it should be possible to further narrow the range of likely values of ROI, given available estimates for vital rates. For example, *Tursiops truncatus* from the northeast coast of Florida reportedly attain sexual maturity at 12 yr on the average (Sergeant et al. 1973) and have a 12-mo gestation period (Essapian 1963), giving an estimated age at first birth of 13 yr. Knowledge of this single parameter can narrow consideration to Figure 4. Here the estimated range in ROI is up to a maximum of 1.05, for the extreme case of an average calving interval of 2 yr, and noncalf survival >0.96. Additional knowledge of, say, minimal calving interval for *Tursiops* could further narrow consideration to one of the three panels of Figure 4, and establish minimal survival rates for positive growth rates, or the maximum rate of increase possible, given the above constraints on age at first birth and calving interval.

We assume that the ranges defined here also encompass the limits within which vital rates for any one dolphin species might change in response to changes in population density. This obviously entails making simplistic assumptions about density dependence in vital rates, and therefore in rate of increase.

of calf and noncalf survival rates, for the following combinations of calving interval and age at first reproduction:

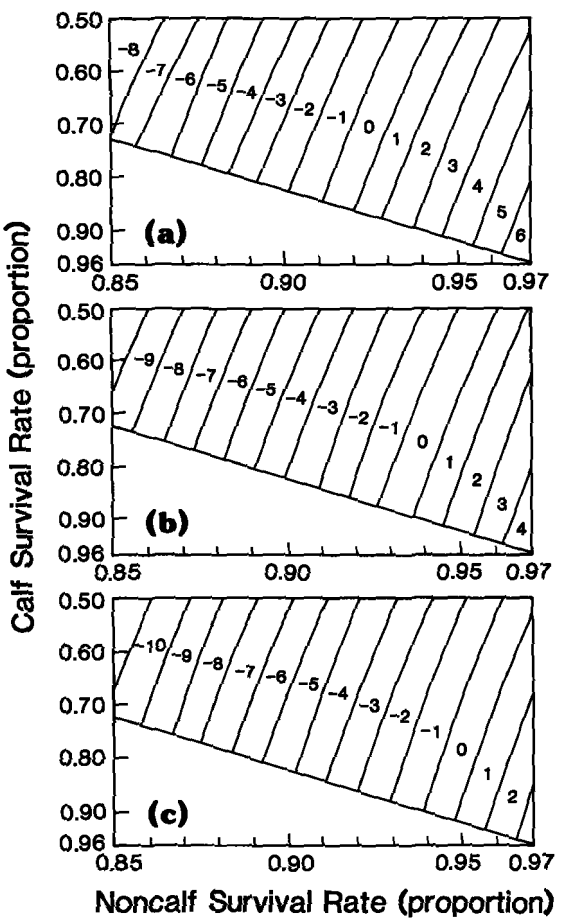

FIGURE 3.—First reproduction of dolphin age class 11 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

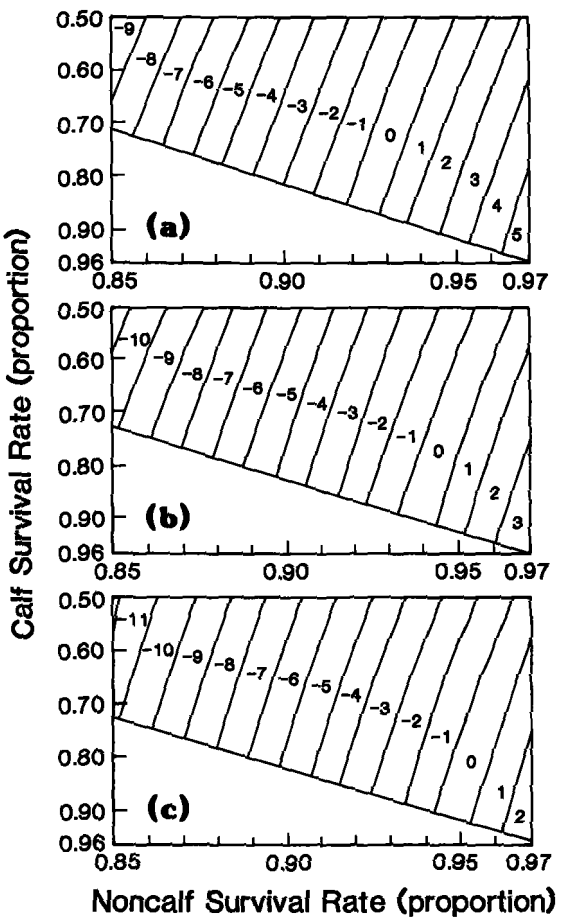

FIGURE 4.—First reproduction of dolphin age class 13 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

These assumptions are implicit in the concept of *r*-max.

There is no evidence that the highest rates of increase calculated here can be achieved by any real dolphin population. Trade offs may exist between survival and reproduction. Because of this, some of the parameter combinations examined here are probably unlikely, especially combinations of the extreme values, i.e., those producing the highest rates of increase.

Although our figures also present minimum values based on parameter combinations we used, we do not believe that these will be useful in setting lower bounds on finite rates of increase. Catastrophic events can always lead to rapid extirpation of a population. In fact, it is clear that dolphins (and other animals with similar life histories) can decrease in number much faster than they can increase.

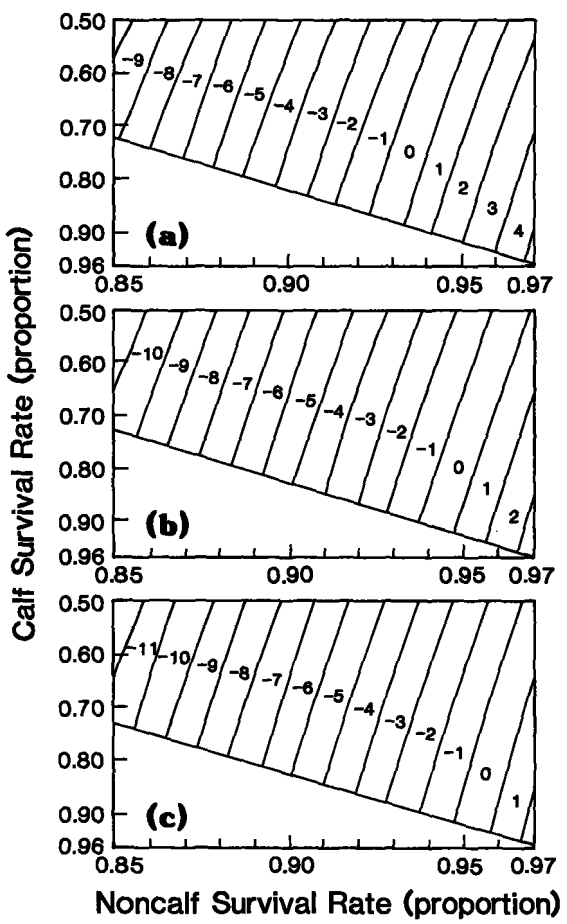

FIGURE 5.—First reproduction of dolphin age class 15 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

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