

# Reproductive Estimates as a Source of Information on Survival Rates

TOM POLACHECK

*Department of Biology, University of Oregon, Eugene, Oregon 97403 and National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038*

## ABSTRACT

A method of estimating the survival rates and net rates of population increase is based on estimates of the proportion of animals which are mature, the average age at attainment of sexual maturity, and the adult fecundity rate. The method is most useful for exploring the ranges of survival rates that are consistent with the estimates of these parameters. Several assumptions are necessary to obtain survival-rate estimates, including constancy of survival and fecundity rates and a stable age distribution. The method is applied to data from three dolphin populations in the eastern tropical Pacific. These data are not consistent with a positive net rate of population increase, but several possible sampling biases exist for the data and must be investigated.

## INTRODUCTION

Estimates of survival rates for natural animal populations and especially for marine mammals are difficult to obtain. Analysis of the age structure of a population is perhaps the easiest and most often used approach for obtaining survival estimates (Seber, 1973). However, it may be impossible or impractical to determine the age of a sample of individuals from a population. In contrast, it is often relatively straightforward to classify individuals according to their reproductive state. In many organisms, certain of the reproductive states are of relatively constant duration and may provide a classification of individuals into separate age groupings. Such age groupings have the potential to provide information on survival rates.

In this paper, a method is developed for estimating survival rates using the classification of animals into mature and immature classes. This method is applied to available reproductive data for dolphin populations in the eastern tropical Pacific. The method is not meant to produce precise estimates of survival but is meant to explore the range of survival rates that can be considered both biologically reasonable and consistent with the data.

## METHODS

The method requires prior estimates of three parameters and is based on four specific assumptions. The three parameters are:

- (1) the proportion of females which are mature,
- (2) the average adult female fecundity rate, and
- (3) the age at attainment of sexual maturity.

The first two parameters should be directly estimable from random samples collected for reproductive information. While estimating the age of maturation requires some aging information, it may often be a much easier quantity to estimate than the entire age structure of the population and may even be available from independent sources such as from tagged or captive animals.

The problem then becomes one of finding the sets of survival rates that are consistent with the observed values for these reproductive parameters. To answer this

problem, some assumptions about the age structure and age-specific vital rates are needed, namely:

- (1) the survival rate from birth to the age at attainment of maturity is constant,
- (2) the survival rate past the age at attainment of maturity is constant (but not necessarily equal to the juvenile rate),
- (3) the fecundity rate (i.e. the number of females born to a mature female) of mature animals is constant, and
- (4) the population is in a stable age distribution.

The fourth assumption, that of a stable age distribution, underlies any method of estimating survival rates from the age structure of a population (Seber, 1973). Some alternatives to the other three assumptions are discussed below.

The model used in this paper is based on a Leslie projection matrix modified to include a survival value in the lower right-hand corner:

$$\vec{N}(t+1) = \vec{M}\vec{N}(t) \quad (1)$$

where

$$\vec{M} = \begin{matrix} 0 & 0 & \dots & \dots & \dots & 0 & F_A \\ S_1 & 0 & & & & 0 & 0 \\ 0 & S_2 & & & & \cdot & \cdot \\ \cdot & 0 & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & \cdot & & & \cdot & \cdot \\ 0 & \cdot & \cdot & \cdot & \cdot & 0 & 0 \\ & & & & & 0 & S_m & S_A \end{matrix}$$

and where

$\vec{N}(t)$  = a vector of the number of females in each age class 1 to  $m$ , and the  $m+1$  element equals the number of females older than age  $m$  (i.e. the number of mature females),

$m$  = the age at attainment of maturity,

$S_A$  = the adult survival rate,

$S_i = S_j$  = a constant for  $i = 1$  to  $m$  (i.e. the juvenile survival rate), and

$F_A$  = the adult female fecundity rate.

The use of  $S_A$  in the lower right hand corner of the

matrix  $\tilde{M}$  collapses the size of the projection matrix when survival rates past a certain age are assumed constant. It is well known that a population growing according to a matrix of this form will approach a stable age distribution corresponding to the dominant eigenvector of the matrix. Thus, given the input parameters and the above matrix, any combinations of juvenile survival ( $S_j$ ) and adult survival ( $S_A$ ) rates that would yield a stable age distribution in which the proportion mature equals the observed proportion mature could be considered reasonable estimates of the survival rates. The problem of solving for values of  $S_j$  and  $S_A$  can be reduced to the following two equations (see Appendix):

$$1 = (S_j/\lambda)^m + (F_A/\lambda) + S_A/\lambda \quad (2)$$

$$R = \frac{(S_j/\lambda)^m F_A + S_A}{F_A \sum_{i=1}^{m+1} (S_j/\lambda)^{i-1} + S_A} \quad (3)$$

with symbols defined as above, and where

$\lambda$  = the largest eigenvalue of the matrix  $\tilde{M}$ , or the net rate of increase of the population, and

$R$  = the proportion of females which are mature.

Equations 2 and 3 represent two equations in three unknowns ( $S_j$ ,  $S_A$ , and  $\lambda$ ). If the value of any one of the three unknowns is specified, the other two are uniquely determined. If the assumption is made that the age distribution is stationary (i.e.  $\lambda = 1$ , Seber, 1973), then the method provides a specific set of survival estimates for a set of input parameters. This assumption usually underlies most survival-rate estimates made from age-structured data (Seber, 1973). However, if the net rate of increase is unknown and there are reasons to suspect that the population's age structure may not be stationary, it may be more informative to examine the combinations of survival rates and net rates of increase consistent with the input parameters. For the examples of dolphin populations considered in this paper, there are reasons to suspect that the population's age structure may not be stationary (Smith, 1983). Thus, solutions for the juvenile survival rate and the net rate of increase will be presented as a function of adult survival rate in order to explore biologically meaningful sets of estimates.

To illustrate this method, survival estimates are presented based on estimates of the reproductive parameters for the northern-offshore-spotted population of *Stenella attenuata* and the eastern-spinner and northern-whitebelly-spinner populations of *Stenella longirostris*. One-half the estimated pregnancy rate is used as an estimate of fecundity. The estimated proportion of mature females and the pregnancy rates are based on the pooled data base for 1973 to 1978 for each of the three stocks. (Method 1 of Henderson, Perrin and Miller, 1980). Method 2 of Henderson *et al.* has been shown to be invalid (Perrin and Reilly, 1984). The estimated ages at attainment of maturity are based on the ages estimated in Perrin, Coe and Zweifel (1976), Perrin, Holts and Miller (1977) and Perrin and Henderson (1984). The parameters used are shown in Table 1.

In considering the results, two criteria were used to determine the range of estimated survival rates consistent with the data and biological reality. The first criterion is the biological constraint that survival rates must be less than or equal to one. The second criterion is that juvenile

Table 1  
Parameters values used for estimating survival rates for the three dolphin stocks

	Northern offshore spotted	Eastern spinner	Northern whitebelly spinner
Age at attainment of maturity	8 <sup>1</sup>	5 <sup>2</sup>	6 <sup>2</sup>
Proportion mature <sup>3</sup>	0.561	0.432	0.522
Pregnancy rate <sup>3</sup>	0.376	0.339	0.356

<sup>1</sup> Rounded to the nearest year from the estimate in Perrin *et al.*, 1976.

<sup>2</sup> Rounded to the nearest year from the estimate in Perrin and Henderson, 1984.

<sup>3</sup> From Henderson *et al.*, 1980.

rates must be less than or equal to adult survival rates. While this criterion is not absolute, it is usually considered a characteristic of the survival curve for long-lived organisms (Caughley, 1966).

## RESULTS

Fig. 1 provides an example of estimates  $S_j$  and  $\lambda$  plotted as a function of adult survival rates for the northern-whitebelly-spinner population. The dotted lines corresponding to  $S_j = S_A$  and  $S_j = 1$  represent the upper bound for the survival rates corresponding to the two criteria listed in the methods section. Thus, for example, the highest estimates of juvenile and adult survival meeting both criteria in this figure is 0.81, which corresponds to a net rate of increase of 0.89. Similarly, biological limits are reached when  $S_j = 1.00$  in this figure, with corresponding values of  $S_A = 0.91$  and  $\lambda = 1.05$ . Also indicated in this figure is the line where  $\lambda = 1.00$

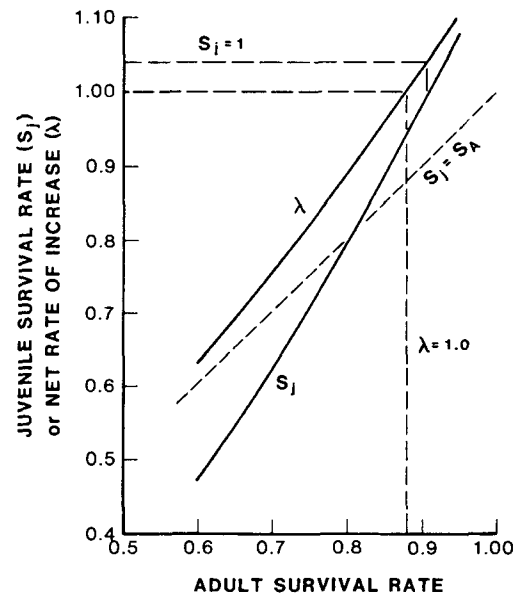


Fig. 1. Estimates of juvenile survival rate ( $S_j$ ) and net rate of increase ( $\lambda$ ) plotted as a function of adult survival rate ( $S_A$ ) for the northern-whitebelly-spinner population of *Stenella longirostris*.

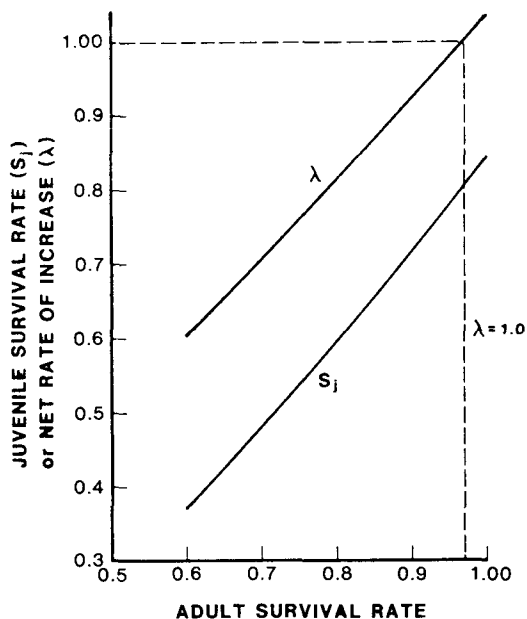


Fig. 2. Estimates of juvenile survival rate ( $S_j$ ) and net rate of increase ( $\lambda$ ) plotted as a function of adult survival rate ( $S_A$ ) for the northern-offshore-spotted population of *Stenella attenuata*.

Table 2

Estimates of juvenile survival rate ( $S_j$ ) and the net rate of increase ( $\lambda$ ) as a function of adult survival rate ( $S_A$ ) for the northern offshore spotted dolphin (*Stenella attenuata*) based on the parameter values in Table 1

$S_A$	$S_j$	$\lambda$
0.60	0.368	0.603
0.70	0.478	0.708
0.80	0.594	0.815
0.90	0.715	0.924
0.95	0.777	0.980

( $S_A = 0.88$  and  $S_j = 0.94$ ), since, from a management perspective, this may be a critical point. In Fig. 2, the results for the northern-offshore-spotted population have been plotted to illustrate a different constraint on the estimates. In this case, the estimates are constrained by biological limits on adult survival rates, with a corresponding maximum possible value for  $S_j$  being 0.84 and for  $\lambda = 1.03$ .

Results for all three populations are presented in Tables 2-4. Note, as is the case for the eastern-spinner population (Table 3), that real-valued solutions may not exist for Equations 2 and 3, since the proportion mature ( $R$ ) considered as a function of  $S_j$  for a fixed value of  $S_A$  has a minimum which can be above the observed value under consideration. While the results in this table suggest that a wide range of adult and juvenile survival rates are consistent with the observed data (except for the eastern-spinner population), none of the tabled values yield non-negative growth rates if the two criteria given in the methods section are applied. Estimated growth rates equal to or greater than one are not possible for the survival rates less than one for the observed data

Table 3

Estimates of the juvenile survival rate ( $S_j$ ) and the net rate of increase ( $\lambda$ ) as a function of adult survival rate ( $S_A$ ) for the eastern spinner dolphin (*Stenella longirostris*) based on parameter values in Table 1

$S_A$	$S_j$	$\lambda$
0.40	0.399	0.473
0.50	0.771	0.727
0.60	•	•
0.70	•	•
0.80	•	•
0.90	•	•
0.95	•	•

• No solution for the juvenile survival rate exists that will balance this version of the matrix for the combination of values for adult survival rates, fecundity rate and age of maturity.

Table 4

Estimates of juvenile survival rate ( $S_j$ ) and the net rate of increase ( $\lambda$ ) as a function of adult survival rate ( $S_A$ ) for the northern whitebelly spinner dolphin (*Stenella longirostris*) based on the parameter values in Table 1

$S_A$	$S_j$	$\lambda$
0.60	0.469	0.630
0.70	0.620	0.755
0.80	0.790	0.888
0.90	0.980	1.031
0.95	1.083	1.107

from the eastern-spinner population. For the northern-whitebelly-spinner population, growth rates greater than one are not possible unless juvenile survival rates exceed adult survival rates. For the northern-offshore-spotted population, net growth rates greater than one require that the survival rate for adults be extremely high (~ 0.97), especially considering that the model makes no provision for senescence. Thus, in a population in which adult survival is constant and equal to 0.97 and the age at attainment of maturity is 8, approximately 28% of the adult population would be over age 50.

### DISCUSSION

The method presented in this paper provides a way to estimate survival rates from minimal data. Although a number of restrictive assumptions about the shape of the age-specific survival and fecundity curves are made, there are a number of ways that the matrix  $\bar{M}$  in equation 1 could be re-parameterized and still be solvable. Such re-parameterizations can be used to explore the sensitivity of a set of estimates to these assumptions. For example, for long-lived mammals, survival rates are usually considered to be increasing from birth to the age at attainment of maturity. To explore the effect of this type of survival curve, the constant juvenile survival rate in the matrix  $\bar{M}$  could be replaced by an increasing function, so that the survival rate at any age between birth and the age of maturity was a function of the estimated survival rate at birth and an animal's present age. In the limit, the effect of this assumption can be examined by assuming that the only difference in juvenile and adult survival rates occurs during the first year of

life. In a similar manner, the effects of assuming constant adult survival and fecundity rates can be explored, as long as the matrix contains only two unknown parameters. Thus, by considering a number of parameterizations for the projection matrix, it would be possible to refine the range of survival rates which are consistent with an observed set of data. In Polacheck (1983), a number of these different parameterizations of the projection matrix for the dolphin example were considered, and the basic results were insensitive to the different matrices.

The effect of the assumption of a stable age distribution is harder to assess. However, the method depends on the assumption of a stable age distribution only in order to compare the observed proportion mature with the proportion mature in a stable age distribution. Since the observed proportion mature is obtained as an average across a number of age classes, this method should be less sensitive to stochastic variations around a stable age distribution and sampling errors than are methods which use the entire age distribution.

The results of the application of this method to the example presented in this paper are rather disturbing, as they suggest that the only estimates of survival rates consistent with the data and with a non-declining net rate of increase are either biologically impossible or unreasonable. The difficulty in obtaining both biologically reasonable estimates of survival rate and estimates of a net rate of growth greater than one are not the same for all three populations. The spinner populations are constrained by biological limits on juvenile survival, while the northern-offshore-spotted population is constrained by limits on adult survival.

As shown in Polacheck (1983), these two different constraints have different implications for the estimates of the input parameters. When the constraints are due to biological limits on juvenile survival rates (i.e. as for the spinner populations), one or more of the input parameters must be underestimated in order to obtain higher estimates of the net rate of growth. In contrast, when the results are constrained by an upper limit on adult survival rates (i.e. as in the northern-offshore-spotted population), one or more of the input parameters must be overestimated. Because the estimates of survival and net rate of increase respond in this manner to the input parameter, increases in the estimated ages at attainment of maturity for the spinner population and decreases in the estimated fecundity rate for the northern-offshore-spotted population would have the non-intuitive effect of increasing the estimated upper bound for the net rate of increase for these populations.

The net rates of increase derived from this method are inconsistent with current evaluations of the status of these stocks (Smith, 1983). Net rates of increase used in those evaluations ranged from 1.00 to 1.06, based in part on comparisons of gross reproductive rates. Moreover, a density-dependent response in the net rate of increase is assumed, so that the most exploited stock should have the highest net rate of increase. In contrast, the estimated net rate of increase in this paper only approaches 1.00 when the survival rates approach biologically unreasonable levels. In addition, the net rates of increase tend to be in an order the reverse of that to be expected under the concept of density-dependent response. Thus, the

eastern-spinner population, which has been the most exploited, has the lowest rates, while the northern-whitebelly-spinner population, which is less exploited, tends to have the highest (Tables 2-4; and see Perrin and Henderson, 1984). If the current evaluations of the status of these stocks are correct, then the results from this method would suggest that the reproductive estimates used here are inconsistent with each other.

Before utilizing the results from this method in any specific application, the sensitivity of the estimates to both the assumptions of the methods and to the value of the input parameters needs to be considered. General conclusions about the sensitivity of this method are not possible, because the method as used here generates a range of estimates consistent with biological constraints on survival rates. The upper limits of this range are a complex, non-linear function of the input parameters. Even if this method is used to generate a single set of survival estimates by specifying the net rate of increase, the estimates will still be a non-linear function of the input parameters. For a specific set of input parameters, the sensitivity of the results can be explored by calculating estimates for a range of values consistent with possible sampling error and biases. Inclusion of such sensitivity analyses for the dolphin examples was beyond the scope of this paper. The sensitivity of the results to the values of input parameters for these dolphin populations is discussed in Polacheck (1983), where it is suggested that potential, but unknown, sampling biases (particularly in the estimates of the proportion mature) are the most likely factor to be affecting the results presented here.

In conclusion, as shown in this paper, reproductive data can be used to provide estimates for the range of survival rates and net rates of increases that are biologically reasonable and consistent. The method is not only useful for the estimates that it generates but also as a test of the consistency of a set of reproductive estimates and as a check of any independent set of estimates of survival rates and net rates of increase.

#### REFERENCES

- Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47: 906-18.
- Henderson, J., Perrin, W. F. and Miller, R. B. 1980. Gross annual production in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-1978. *Southwest Fisheries Center Admin. Rep.* LJ-80-02, 51 pp.
- Perrin, W. F., Coe, J. M. and Zweifel, J. R. 1976. Growth and reproduction of the eastern spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fish. Bull.*, U.S. 74: 229-69.
- Perrin, W. F. and Henderson, J. R. 1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. (Published in this volume.)
- Perrin, W. F., Hoits, D. B. and Miller, R. B. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. *Fish. Bull.*, U.S. 75: 725-50.
- Perrin, W. F. and Reilly, S. B. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. (Published in this volume.)
- Polacheck, T. 1983. Estimating current rates of increase and survival rates from reproductive data for dolphin populations in the eastern tropical Pacific. *Southwest Fisheries Center, La Jolla CA, Admin. Rep.* LJ-83-11, 25 pp.
- Seber, G. A. F. 1973. *The Estimation of Animal Abundance*. Hafner Publ. Co. Inc., New York, NY. 506 pp.
- Smith, T. D. 1983. Changes in size of three dolphin populations (*Stenella* spp) in the eastern tropical Pacific. *Fish. Bull.*, U.S. 81: 1-13.

## DERIVATION OF EQUATIONS 2 AND 3

For a stable age distribution:

$$N_i(t+1) = \lambda N_i(t) \quad (4)$$

where  $N_i(t)$  = the number of individuals of age class  $i$  alive at time  $t$  and  $\lambda$  = the net rate of increase. Also from the projection matrix  $\tilde{M}$

$$N_1(t+1) = N_{m+1}(t) \cdot F_A \quad (5)$$

$$N_i(t+1) = N_{i-1}(t) \cdot S_{i-1} \quad \text{for } 1 < i \leq m \quad (6)$$

$$N_{m+1}(t+1) = N_{m+1}(t) \cdot S_A + N_m(t) S_m. \quad (7)$$

Note that  $N_{m+1}(t)$  equals the number of adults alive at time  $t$ . Equating Equations 4 and 6 yields.

$$N_i(t) = (S_{i-1}/\lambda) N_{i-1}(t). \quad (8)$$

Beginning with age class 1, repeated applications of Equation 8 yield

$$N_i(t) = (S_j/\lambda)^{i-1} N_1(t) \quad \text{for } 1 \leq i \leq m \quad (9)$$

since  $S_i = S_j$  for  $i = 1$  to  $\bar{m}$  and  $\lambda$  is a constant. Equating the right hand sides of Equations 4 (for  $i = 1$ ) and 5 yields

$$N_1(t) = N_{m+1}(t) F_A/\lambda. \quad (10)$$

Substituting Equation 10 in Equation 9 yields

$$N_i(t) = (S_j/\lambda)^{i-1} (F_A/\lambda) N_{m+1}(t) \quad \text{for } 1 \leq i \leq m. \quad (11)$$

Substituting the right hand side of Equation 11 in Equation 7 when  $i = m$  and then equating the right hand sides of Equations 4 and 7 yields:

$$N_{m+1}(t+1) = \lambda N_{m+1}(t) = N_{m+1}(t) \cdot S_A + (S_j/\lambda)^{m-1} (F_A/\lambda) S_j N_{m+1}(t). \quad (12)$$

Division of  $\lambda N_{m+1}(t)$  and rearranging yields Equation 2. Equation 3 is derived by noting that from Equations 11 and 12, the total population size at time  $t+1$  can be expressed as

$$\sum_{k=1}^{m+1} N_k(t+1) = \sum_{i=1}^{m+1} (S_j/\lambda)^{i-1} F_A N_{m+1}(t) + S_A N_{m+1}(t) \quad (13)$$

Division of the right hand side of Equation 12 by the right hand side of Equation 13 yields Equation 3.