

Estimating the Dolphin Population Size Yielding Maximum Net Production

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ABSTRACT

A method is presented for estimating maximum net productivity level by comparing gross reproductive rates in three populations at different proportions of original size.

INTRODUCTION

The population size at which the absolute rate of change of population size is largest (maximum net productivity level or MNPL) is interesting both theoretically and in applied population assessments (Holt and Talbot, 1978; Smith and Fowler, 1981). Some general hypotheses have been developed about the relationship of MNPL and equilibrium population sizes (e.g. Gilpin and Ayala, 1976; Fowler, 1981). Fowler tested the hypotheses that density-dependent changes in vital rates, and hence MNPL, occur at a large fraction of equilibrium population size for long-lived species. He concluded that MNPL occurs at population sizes greater than one half, and likely quite near, equilibrium population size.

Few direct estimates of MNPL are available for long-lived species, and virtually none are available for cetaceans. In this paper I describe a method of estimating MNPL for dolphins in the eastern tropical Pacific Ocean, using data on the history of exploitation and the observed vital rates of different but related populations. An example is given using gross reproductive rates for three populations of spinner dolphin (*Stenella longirostris*).

MATERIALS AND METHODS

Dolphins of several species have been killed incidentally to tuna fishing in the eastern tropical Pacific tuna purse seine fishery since the late 1950s. The status of three populations of the spinner dolphin, *S. longirostris*, is described in Smith (1979; 1983). These three populations have been subjected to this incidental mortality for different lengths of time; one population, the eastern spinner dolphin, has been involved since 1959, while two other populations, the northern and southern whitebelly spinner dolphins, have been involved since approximately 1969 and 1973, respectively.

Estimates of the numbers of spinner dolphins killed in this fishery have been made as the product of the mean number of dolphins killed per net set observed aboard fishing vessels and the numbers of net sets made each year. Estimates from Smith (1979) are shown in Fig. 1 for each population. The numbers killed were very high in the 1960s and decreased markedly in the 1970s.

Estimates of the sizes of the three populations in 1979 (Table 1) were made from aerial and research-vessel dolphin-sighting survey data (Holt and Powers, 1982). Estimates of the gross reproductive rates (Table 1) of these three populations were made from data from samples of dolphins killed in the fishery (Perrin, Holts and Miller, 1977; Smith, 1979). The more heavily exploited eastern and whitebelly spinner dolphin populations have

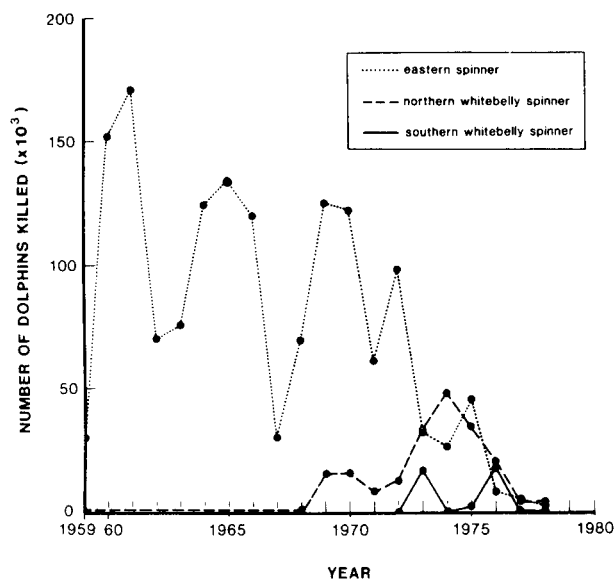


Fig. 1. Estimated numbers of spinner dolphins (*Stenella longirostris*) killed from three populations, from 1959 to 1978, incidental to yellowfin tuna purse seine fishing in the eastern tropical Pacific, from Smith (1979).

Table 1

Estimates of population size in 1979, from Holt and Powers (1982), and average reproductive rate from 1973–1978, from Smith (1979), for three populations of spinner dolphin (*Stenella longirostris*) in the eastern tropical Pacific

Spinner population	Population size ($\times 1,000$)	Gross reproductive rate
Eastern	305	0.098
Northern whitebelly	401	0.088
Southern whitebelly	223	0.067

higher estimated reproductive rates. However, alternate methods of estimating these rates yield different results, and there is considerable uncertainty as to the appropriate estimates (Smith, 1979; Perrin and Reilly, 1984). The values used were selected to illustrate the method of estimating MNPL being described.

The estimates of dolphins killed (Fig. 1), 1979 population size (Table 1), and gross reproductive rates

(Table 1) can be used to estimate successive population sizes as

$$N_{t+1} = N_t + (\gamma - \mu)N_t - K_t = N_t(1 + \rho) - K_t, \quad (1)$$

where N = population size, in numbers; t = year; γ = gross reproductive rate; μ = natural mortality rate; K = number of dolphins killed by fishery; $\rho = \gamma - \mu$ = net recruitment rate.

In this model recruitment and natural mortality occur simultaneously, with rates applying to the whole population, not just the reproductive portion, at the beginning of the time interval. The catch is assumed to be taken after recruitment and natural mortality have occurred. This model applies only approximately to the incidental killing of dolphins in the eastern tropical Pacific in that recruitment and the incidental mortality occur simultaneously; similarly, the model does not account for age-structure changes which might affect the proportion mature. However, for this example these simplifying assumptions will suffice (Smith and Polacheck, 1979).

Solving equation 1 for the population size in previous years,

$$\hat{N}_t = \frac{N_0}{\prod_{i=1}^t (1 + \rho_i)} + \sum_{j=1}^t \frac{K_j}{\prod_{i=1}^j (1 + \rho_i)}, \quad (2)$$

where N_0 is the population size in 1979, N_t denotes the to-be-estimated population size, t years earlier, and ρ_i denotes the net recruitment rate in the i th year prior to 1979. The properties of this estimate are explored in Smith and Polacheck (1979).

Values of the reproductive rate for each year can be obtained by assuming that the gross reproductive rate is a function of population size,

$$\rho(N) = \gamma(N) - \mu, \quad (3)$$

where $\rho(N)$ = net recruitment rate as a function of population size N , $\gamma(N)$ = gross reproductive rate.

A suitable model for $\gamma(N)$ is given by Allen (1976),

$$\gamma(N) = (\gamma_0 - \gamma_1) \left(1 - \left(\frac{N}{\phi} \right)^\zeta \right) + \gamma_1, \quad (4)$$

where γ_0 = gross reproductive rate for N near zero; γ_1 = gross reproductive rate at equilibrium population size ϕ , ζ = shape parameter for changes in gross reproductive rate.

The shape of this relationship is shown in Fig. 2 for several values of the shape parameter ζ .

An expression for the net recruitment rate as a function of population size is obtained by substituting $\gamma(N)$ from equation 4 into equation 3,

$$\rho(N) = (\gamma_0 - \gamma_1) \left(1 - \left(\frac{N}{\phi} \right)^\zeta \right) + \gamma_1 - \mu \quad (5)$$

The net recruitment rate must be zero when $N = \phi$, implying that $\gamma_1 = \mu$. That is, the gross reproductive rate at the equilibrium population size is the same as the natural mortality rate.

An expression for historical population sizes as a function of several estimated parameters and four unknown parameters is obtained by substituting $\rho(N)$

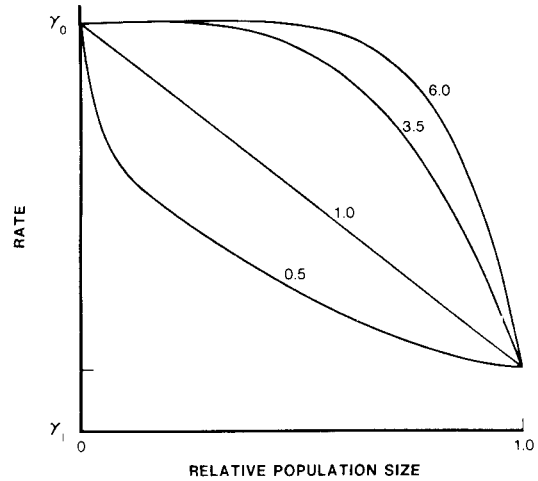


Fig. 2. The gross reproduction rate γ in equation 4 as a function of population size, relative to equilibrium population size (N/ϕ), for values of the shape parameter $\zeta = 0.5, 1.0, 3.5,$ and 6.0 .

from equation 5, noting $\gamma_1 = \mu$, into equation 2. The unknown parameters are $\gamma_0, \gamma_1, \zeta$ and ϕ .

$$\hat{N}_t(\gamma_0, \gamma_1, \zeta, \phi) = \frac{N_0}{\prod_{i=1}^t \left(1 + (\gamma_0 - \gamma_1) \left(1 - \left(\frac{N_i}{\phi} \right)^\zeta \right) \right)} + \sum_{j=1}^t \frac{K_j}{\prod_{i=1}^j \left(1 + (\gamma_0 - \gamma_1) \left(1 - \left(\frac{N_i}{\phi} \right)^\zeta \right) \right)} \quad (6)$$

The equilibrium population size ϕ in equation 6 can be estimated from equation 6 itself, by taking t to be the year exploitation began for each population. That is,

$$\hat{\phi} = N_t(\gamma_0, \gamma_1, \zeta, \hat{\phi}), \quad (7)$$

where t is sufficiently large, for given values of $\gamma_0, \gamma_1,$ and ζ . This equation must be solved iteratively.

Values for the remaining three unknown parameters in equation 6, $\gamma_0, \gamma_1,$ and ζ , can be obtained by minimizing the differences between estimates of gross reproductive rates for the three populations (Table 1) and the modeled values of gross reproductive rate from equation 4. For convenience, the sum of squares of differences can be minimized,

$$\sum_{i=1}^3 (\hat{G}_i - (\gamma_0 - \gamma_1) \left(1 - \left(\frac{N_{0i}}{\hat{\phi}_i} \right)^\zeta \right))^2, \quad (8)$$

where $i (= 1, 2, 3)$ denotes the population, \hat{G}_i denotes the observed gross reproductive rate for the i th population, and $\hat{\phi}_i$ is obtained from equation 7 for each of the three populations.

Minimization of equation 8 involves evaluating the sum of squares for all possible values of γ_0, γ_1 and ζ . For each population for each set of values of γ_0, γ_1 and ζ , equation (7) must be solved, iteratively as noted above. Due to the complexity of the equations and the illustrative nature of the calculations, the values of γ_0, γ_1 and ζ yielding a minimum value for equation (8) were

determined by direct examination of the sum of squares surface. Thus the solution obtained is not exact, and no variances have been calculated.

The value of ζ which minimizes equation 8 implies a value of MNPL. This value can be determined by substituting $\rho(N)$ from equation 5 into equation 1, and solving for the population size with maximum rate of change (Allen, 1976), yielding

$$\psi = \phi \left(\frac{1}{\zeta + 1} \right)^{\frac{1}{\zeta}} \tag{9}$$

where ψ denote the maximum net productivity level (MNPL) in numbers of animals.

RESULTS

Using estimates of the number of dolphins killed incidentally (K_j , Fig. 1), the 1979 population sizes (Table 1) and the gross reproduction rates (G_j , Table 1), the estimated values of the gross reproductive rates at population sizes near zero and near equilibrium (γ_0 and γ_1 , respectively) and the estimate of the shape parameter (ζ) are obtained from equations 6, 7 and 8 (Table 2). The

Table 2

Estimates of parameters obtained from minimizing the sum of squares of deviations of observed and predicted rates in equation 8, for spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific

γ_0	γ_1	ζ	ψ/ϕ
0.098	0.048	8.0	0.76

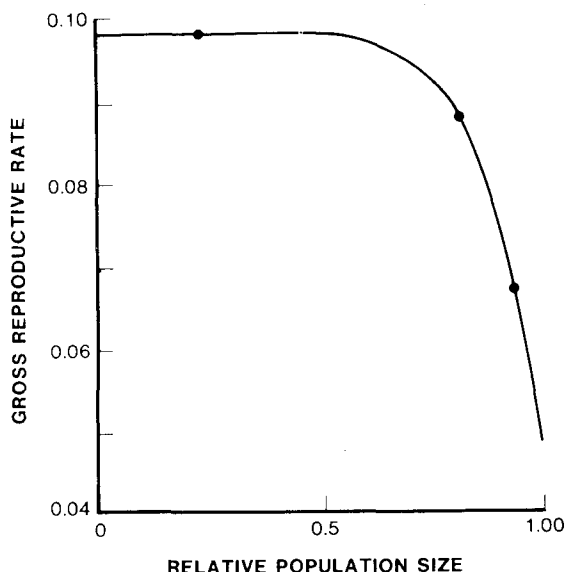


Fig. 3. Observed gross reproductive rates for three spinner dolphin populations versus estimated relative population size, and the estimated gross reproductive rate function from equation 4 obtained by minimizing equation 8.

fit of equation 4 to the observed estimates of gross reproductive rate is shown in Fig. 3. Although the deviations about the line are too small to be apparent in the graph, there is some lack of fit. The maximum net productivity level corresponding to $\zeta = 8.0$, as a fraction of the equilibrium population size, ψ/ϕ , given in Table 2, is obtained from equation 9.

The estimated equilibrium population sizes, ϕ in equation 6, corresponding to the parameter estimates in Table 2, are 1,330, 490, and 240 thousand dolphins, for eastern spinner, northern whitebelly spinner, and southern whitebelly spinner dolphins, respectively (Table 3). The corresponding maximum net production ($MNP = \psi\rho(\psi)$) are 34, 13 and 6 thousand, and are obtained from population sizes of 1,010, 370, and 180 thousand, respectively (Table 3).

Table 3

Estimates of equilibrium population size, ϕ , for three spinner dolphin populations in the eastern tropical Pacific, with estimates of the maximum net productivity (MNP), and the population size producing MNP (MNPL)

Population	ϕ ($\times 1,000$)	MNP ($\times 1,000$)	MNPL ($\times 1,000$)
Eastern	1,330	34	1,010
Northern whitebelly	490	13	370
Southern whitebelly	240	6	180

DISCUSSION

The method of estimating MNPL which I describe has possible application to the dolphin populations in the eastern tropical Pacific. The example calculations given for spinner dolphins suggest that MNPL may occur at a relatively high fraction of equilibrium abundance. However, three uncertainties need further attention.

First, the estimates of gross reproductive rate for eastern tropical Pacific dolphin populations are crude because of possible sample biases and analytical biases owing to the methods employed (Smith, 1983; Perrin and Reilly, 1984). The present results must therefore be considered preliminary pending further investigation of the estimates of gross reproductive rate.

A second uncertainty is that only three data points for gross reproductive rate have been used in equation 8 to estimate three parameters. Additional estimates of gross reproductive rate are needed in equation 8; these could be obtained in two ways. The simplest is to assume that other dolphin species have similar reproductive and natural mortality rates at equilibrium and at near-zero population sizes, and similar MNPL values. For instance, there are two populations of spotted dolphin where data are available. A more complex approach to obtaining additional estimates of gross reproductive rate is to use the estimates for each year, rather than the single average over several years, for each population. This approach would require a more complex form for equation 8, where N_0 would be replaced by the population size in the years corresponding to the available annual reproductive rate estimates. The calculations would become rather sensitive to possible time lags in density-dependent

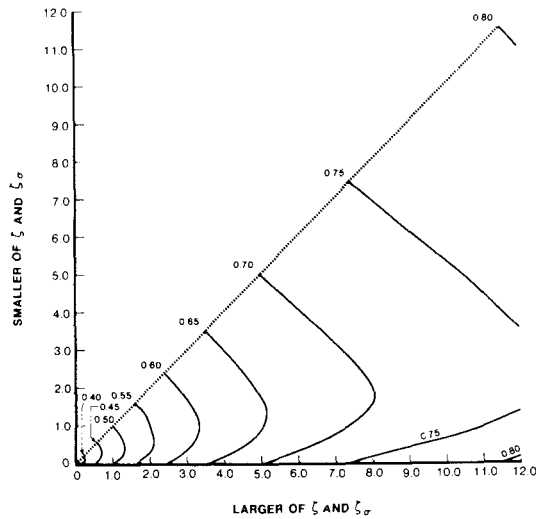


Fig. 4. Population size relative to equilibrium population size (N/ϕ) at which maximum net productivity is obtained (from equation 12) for ranges of values of both shape parameters ζ and ζ_σ .

response, but the problem of overparameterization would be minimized.

The third uncertainty in the above estimates of MNPL is that the natural mortality rate is assumed to be constant for all population sizes. This assumption can be explored by replacing μ in equation 3 by one minus the function

$$\sigma(N) = (\sigma_0 - \sigma_1) \left(1 - \left(\frac{N}{\phi}\right)^{\zeta_\sigma}\right) + \sigma_1, \quad (10)$$

where σ_0 , σ_1 and ζ_σ are defined similarly to the corresponding symbols in equation 4. Thus equation 5 is replaced by

$$\rho(N) = (\gamma_0 - \gamma_1) \left(1 - \left(\frac{N}{\phi}\right)^\zeta\right) + (\sigma_0 - \sigma_1) \left(1 - \left(\frac{N}{\phi}\right)^{\zeta_\sigma}\right). \quad (11)$$

Substituting equation 11 for equation 5 in the above development yields expressions parallel to equations 6 and 8. For this model MNPL (ψ) is obtained as the population size N which satisfies

$$\frac{\partial \rho(N)}{\partial N} = 0 = \zeta(\gamma_0 - \gamma_1) \left(\frac{N}{\phi}\right)^{\zeta-1} + \zeta_\sigma(\sigma_0 - \sigma_1) \left(\frac{N}{\phi}\right)^{\zeta_\sigma-1}. \quad (12)$$

This expression is parallel to the calculation used to obtain equation (9), but a similar closed form can not be obtained. The values of MNPL (ψ) from equation 12, assuming $\gamma_0 - \gamma_1 = \sigma_0 - \sigma_1$, are given in Fig. 4, as a contour surface on ζ and ζ_σ . The results are symmetrical in these two parameters and only shown in the first half-quadrant. If $\gamma_0 - \gamma_1 \neq \sigma_0 - \sigma_1$ this surface becomes non-symmetrical.

Values of MNPL for sections through the contour surface in Fig. 4 are shown in Fig. 5, for selected values of ζ_σ . As ζ increases along the abscissa, MNPL first decreases slightly and then increases steadily. MNPL is constrained to a narrowing range for all values of ζ_σ , as ζ increases. For instance, when $\zeta = 8$ in Fig. 5, MNPL ranges from 0.70 to 0.76 when ζ_σ ranges from 0.5 to 8.0.

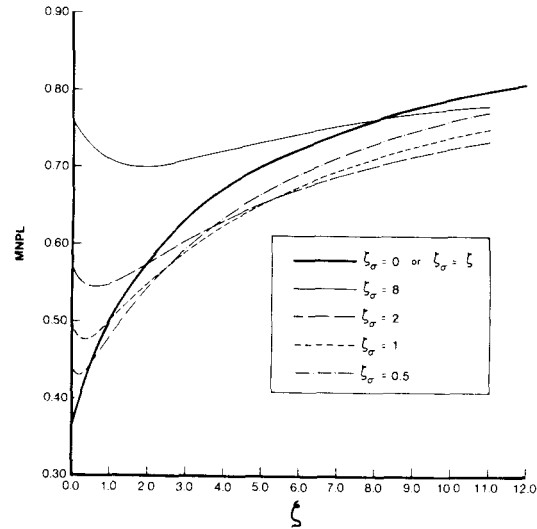


Fig. 5. Maximum net productivity levels (MNPL) versus the value of the shape parameter for changes in gross reproductive rate (ζ), for a series of values of the shape parameter for changes in survival rates (ζ_σ), showing the lack of sensitivity of MNPL to ζ_σ , when ζ is large.

Thus for populations with high MNP levels, the assumption that the natural mortality rate does not change with population size has relatively little effect on the MNPL estimate. Note, however, that estimates of the replacement yield are perhaps greatly affected.

The three uncertainties described suggest several directions which should be followed. Keeping these uncertainties in mind, however, the presently available data for spinner dolphins suggest a rather high value for MNPL, in agreement with Fowler (1981).

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