

ANALYSIS OF A SIMPLE MODEL FOR ESTIMATING HISTORICAL POPULATION SIZES

T. D. SMITH¹ AND T. POLACHECK²

ABSTRACT

Estimates of historical abundance of animal populations are important in many management decisions. Historical estimates based on a simple model of population growth have been made for several populations of dolphin involved with the yellowfin tuna purse seine fishery. We used the data for the bridled dolphin, *Stenella attenuata*, to investigate the behavior of the model by which these historical estimates were calculated. For populations with low net reproductive rates, the effect of bias in the estimates of the input parameters on the estimated historical abundances was approximately linear and additive. When all the input parameters were independently estimated, the variances of the historical abundance estimates were dominated by the variance of the initial abundance estimate and the coefficient of variation of the historical estimate was less than the largest coefficient of variation of any parameter.

Many decisions about the management of animal populations are based on the estimates of abundance of the population relative to its historical or preexploitation size. These estimates are basic to any application of the theory of maximum sustained yield as incorporated in several international marine mammal management agreements such as the North Pacific Fur Seal Treaty and the International Whaling Convention. Similarly, the concept of "optimum sustainable populations" as specified in the recent Marine Mammal Protection Act of 1972 (MMPA) has been defined in terms of comparing the present size of a population with its original size (Southwest Fisheries Center³). Schools of dolphin of several species (primarily *Stenella attenuata* and *S. longirostris*) have been used by purse seine fishermen in the eastern tropical Pacific to locate yellowfin tuna, *Thunnus albacares*, since 1959, as described by Perrin (1969). Significant numbers of dolphin have been killed by becoming entangled in the purse seines. In order to make management decisions under the MMPA about these dolphin populations, the National Marine Fisheries Service (NMFS) needed

estimates of the preexploitation abundance of the various populations. The NMFS convened a workshop of scientists to obtain the estimates based on a simple model of population change (see footnote 3). This paper evaluates the behavior of estimates of abundance obtained from their approach. This is important in order to be able to evaluate the degree of confidence to be placed in such estimates, and hence in management plans based on them.

METHODS AND MATERIALS

The model used to estimate preexploitation abundance is based on a common discrete model of population growth:

$$N_{\tau+1} = N_{\tau} - K_{\tau} + (N_{\tau} - K_{\tau})(b - d) \quad (1)$$

where N_{τ} = the abundance at time τ

b = the birth rate

d = the natural death rate

K_{τ} = the number of animals killed, assumed to occur at the beginning of time interval τ

$N_{\tau+1}$ = the abundance 1 time unit later.

Reversing the procedure (i.e., solving the above equation for N_{τ}) results in the expression

$$N_{\tau} = \frac{N_{\tau+1}}{1 + R_{\tau}} + K_{\tau} \quad (2)$$

where N_{τ} now is the estimate of abundance 1 yr

¹Department of Zoology, University of Hawaii, Honolulu, Hawaii; present address: Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

²Department of Zoology, University of Hawaii, Honolulu, Hawaii; present address: Department of Biology, University of Oregon, Eugene, OR 97477.

³Southwest Fisheries Center. 1976. Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Pacific Yellowfin Tuna Fishery. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-76-29, 53 p.

earlier and R_t is the net reproductive rate ($b-d$). The above model was modified in the procedure used by NMFS to account for situations when the kills occur throughout the time interval instead of instantaneously at the end of the interval, as:

$$N_t = \frac{N_{t+1} + 0.5K_t}{1+R_t} + 0.5K_t \quad (3)$$

This equation can be repeatedly applied to give estimates any number of years (t) into the past. When rearranged to explicitly display the population size t years earlier, and relabeling so that the initial abundance is N_0 , one obtains

$$N_t = \frac{N_0}{\prod_{j=1}^t (1+R_j)} + \sum_{j=1}^t \frac{K_j(1+R_j/2)}{\prod_{i=j}^t (1+R_i)} \quad (4)$$

Note in this form that the time-index t runs backwards from zero. As is apparent in this form, the estimation of abundance t years earlier involves $2t+1$ parameters. The sequences of annual kills and net reproductive rates can be termed the kill and the net reproductive rate vectors, each composed of t elements.

The data used here to explore this estimation procedure is from the report of NMFS Workshop discussed above (see footnote 3).⁴ From existing unpublished data and reports the Workshop participants used estimates of the population size in

⁴It should be noted that the estimates used here are based on a number of assumptions currently under investigation and that these estimates are subject to significant change in the near future (I. Barret, Director, Southwest Fisheries Center, La Jolla, CA 92038, pers. commun. April 1978).

TABLE 1.—Estimates used for kill and reproductive rate vectors of *Stenella attenuata* in the eastern Pacific.

t	Year	Kill (thousands)	Net reproductive rate
1	1973	120	0.040
2	1972	273	.040
3	1971	185	.040
4	1970	308	.036
5	1969	331	.032
6	1968	164	.028
7	1967	194	.024
8	1966	281	.020
9	1965	297	.016
10	1964	255	.012
11	1963	133	.008
12	1962	106	.004
13	1961	446	.000
14	1960	534	.000
15	1959	129	.000

1974 and the annual incidental kills and reproductive rates from 1959 to 1974. Several sequences of estimated annual kills and reproductive rates were considered, incorporating the uncertainty in the data.

In the present paper the sequences of annual kills and net reproductive rates given in Table 1 are used to illustrate several general aspects of the behavior of Equation (4). These correspond to the "high kill" and "central reproductive rate" sequences for the bridled dolphin, *Stenella attenuata*, in the Workshop report. The estimate of 1974 abundance used by us and the Workshop was 3.5 million.

Estimation of Bias

A sensitivity analysis was done to examine the effects of biased parameter estimates on the backcalculated abundance. A new population size 1 yr earlier, from Equation (3), when each parameter is changed by a specified amount is

$$N'_1(n, k, r) = \frac{N_0(1+n) + 0.5K_1(1+k)}{1+R_1(1+r)} + 0.5K_1(1+k) \quad (5)$$

and in general for t years earlier,

$$N'_t(n, k, r) = \frac{N_0(1+n)}{\prod_{j=1}^t (1+R_j(1+r))} + \sum_{j=1}^t \frac{K_j(1+k) (1+(R_j(1+r)/2))}{\prod_{i=j}^t (1+R_i(1+r))} \quad (6)$$

where N_0 , R_t , and K_t are defined as above, and
 n = the proportion that N_0 deviates from its estimate
 r = the proportion that all elements of the net reproductive vector deviate from their estimates
 k = the proportion that all elements of the kill vector deviate from their estimates.

$N'_t(n, k, r)$ was then compared with N_t from Equation (4) or equivalently $N'_t(0,0,0)$. As a measure of the sensitivity of the basic model, $S_t(n, k, r)$ is defined to equal the percent that $N'_t(n, k, r)$ deviates from N_t .

$$S_t(n, k, r) = \left(\frac{N_t(n, k, r) - N_t}{N_t} \right) \cdot 100. \quad (7)$$

Estimation of Variance

The variance of the backcalculated estimate of N_t from Equation (4) was approximated using the delta method (Seber 1973). This method is based upon a Taylor series expansion for a function in which quadratic and other higher order terms are ignored. If f is a function of the random variables $x_1, x_2, x_3, \dots, x_n$ then the expression for the variance of f by the delta method is

$$V(f(X_1, X_2, X_3, \dots, X_n)) = \sum_{i=1}^n V(X_i) \left(\frac{\partial f}{\partial X_i} \right)^2 + 2 \sum_{i < j} \text{Cov}(X_i, X_j) \left(\frac{\partial f}{\partial X_i} \cdot \frac{\partial f}{\partial X_j} \right). \quad (8)$$

In applying this expression to Equation (4), it is necessary to be able to define which of the parameters should be considered as random variables, and to give reasonable estimates for value of the variances and covariances of these variables. For the purpose of exploring the behavior of Equation (4), we assumed that the estimates of all the parameters in Equation (4) are independent random variables. The covariance terms in Equation (8) are then zero. This approach provides a picture of the variance of the back estimate of abundance if in fact independent estimates of the kills and the net reproductive rates were available for each year. A generalized expression for the variance using this approach is

$$V(N_t) = V(N_0) \left(\frac{\partial N_t}{\partial N_0} \right)^2 + \sum_{j=1}^t V(K_j) \left(\frac{\partial N_t}{\partial K_j} \right)^2 + \sum_{j=1}^t V(R_j) \left(\frac{\partial N_t}{\partial R_j} \right)^2 \quad (9)$$

where all parameters are defined as for the basic model [Equation (4)]. For detailed expressions for each of the right hand terms see Appendix I.

As noted the method used for approximating the variance of a function depends on the higher order terms in the Taylor's series expansion being small. The higher order terms in the delta method expression for the variance of N_t are composed of the

second and higher order derivatives of N_t with respect to N_0 , K_t , and R_t , and the higher order central moments of the probability distributions of the estimates of N_0 , K_t , and R_t (i.e., skewness, kurtosis, etc.). The second and higher derivatives with respect to N_t and K_t are zero. Thus the terms involving R_t are the only higher order terms not equal to zero. The higher order derivatives of N_t with respect to R_t involve R_{t+1} to increasing negative powers. The three higher order moments of R_t are always decreasing since R_t is much less than one. Thus each of the higher order terms in the delta method expression for the variance of N_t are each less than the first order term in R_t (iii of Appendix I). The contribution of this first order term in R_t to the variance of N_t is small, as shown below. Thus the error induced by ignoring the higher order terms in the Taylor's series appears small.

The objective in doing the variance calculations was to understand the behavior of the variance of the population size when estimated by the basic back projection model [Equation (4)]. Thus a range of variances was calculated for a range of reasonable values of the variances of the estimated parameters. However, in our example of bridled dolphin estimates of the variance of many of the parameters were not available. Many of the kill estimates were not independently estimated and hence have large unknown covariances (Smith and Polacheck⁵). Estimates of net reproductive rate were obtained by extrapolation from other populations and from assumptions about density dependence. It is not clear that the uncertainty in these estimates can adequately be described by the notion of variance. Thus, the variances that we used and that we calculated for N_t should not be interpreted as actual estimates of variance for this population.

RESULTS

Bias

The results of the sensitivity analysis of the basic model will be presented by examining the effects of varying each of the variables n , k , and r of Equation (7), separately, and then in combinations.

The sensitivity of the back projected estimates

⁵Smith, T. D., and T. Polacheck. 1977. Uncertainty in estimating historical abundance of porpoise populations. Contract Rep. MM 7A C006, 39 p. Marine Mammal Commission, 1625 Eye Street, Washington, DC 20006.

(S_t) for a fixed number of years t into the past is linear with respect to n or k (Figure 1). This linearity can be seen in Equation (6) since n and k enter only as linear terms in the numerator. Positive

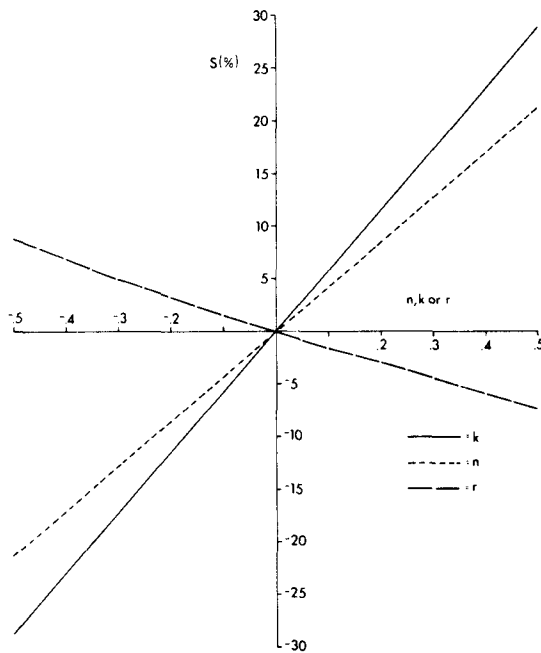


FIGURE 1.—Sensitivity of the model $S_t(n, k, r)$ in 1959 for a range of deviations in the initial number (n), for a range of deviations in the kills (k), or for a range of deviations in the net reproductive rate (r), for *Stenella attenuata* in the eastern tropical Pacific.

values of either n or k yield positive deviations in the back estimates. However, the farther back the population is projected in time, the smaller the contribution of N_0 to the back estimate becomes relative to the contribution of the kills. Thus the effect of bias in the estimate of the initial numbers (n) becomes progressively smaller the farther back in time the population is projected, while the consequence of a consistent bias in the kill estimates (k) becomes larger (Figure 2). Since the annual kills have no simple relationship to time, the effect of a particular value of n or k over time (Figure 2) cannot be described by any simple function. This trade off in the sensitivity of the back projected estimates between n and k is exact in the sense that for any decrease over time in the slope of S with respect to n there is an equivalent increase in the slope of S with respect to k . This can be seen by evaluating the partial derivatives of S with respect to n and with respect to k and noting that they sum to 1.

The effects of bias in the estimates of the net reproductive rate vector are more complicated than for the other two factors. Positive deviations in the net reproductive rates (r) yield negative deviations in the back projected estimate (Figure 2). The effect of r tends to increase over time (Figure 2). S approaches being linear with respect to r for any particular year, but unlike the relationship for k and n , this result is not exact (Figure 1). The approximate linearity of the sensitivity of N_t

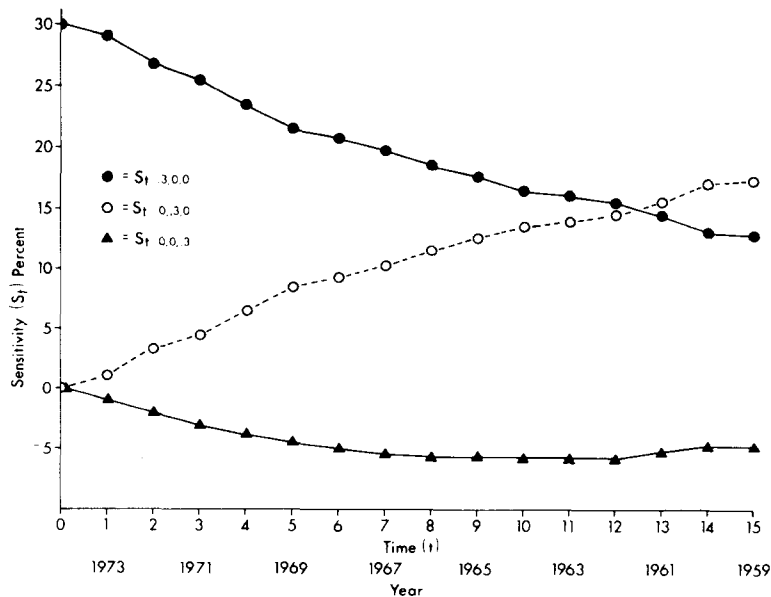


FIGURE 2.—Sensitivity of the model $S_t(n, k, r)$ over time to a 30% deviation in the initial number ($n = 0.3$), in the kill vector ($k = 0.3$), and in the net reproductive rate vector ($r = 0.3$) when all factors are held constant for *Stenella attenuata* in the eastern tropical Pacific.

to r appears to be a general feature of this procedure when r is small. This can be seen by examining S_t expressed as a function of r , which can be obtained explicitly by substituting the definitions of N_t [Equation (4)] and N'_t [Equation (6)] into Equation (7) and simplifying.

The consequences of having two factors varying simultaneously are shown in the series of contours of equal values of S from Equation (7) (Figures 3-5). These contour plots present a visual picture of the sensitivity of the back projection to the different factors. From this set of contour maps, it can be seen that the surface generated by S [Equation (7)] tends to be nearly linear. Since S has no nonlinear terms with respect to n and k , the surface described by S in these two dimensions is simply a plane (Figure 4). There are nonlinear effects between the net reproductive rate and both initial abundance and the sequence of kills. For the example examined here, the nonlinearity between k and r is insignificant. For instance, if r and k both equal 0.50, S deviates from a linear model by <1%. In general the nonlinearity between k and r will be insignificant as long as the kills in any one year do not represent a large proportion of the population and as long as r is relatively small. Also, for the data considered here, the nonlinearity between the net reproductive rates and initial abundance is small but not insignificant. For example, if both n and r equal 0.50, S deviates

from a linear model by as much as 5%. This interaction effect is negative, resulting in a surface's bending downward from a strictly linear model when n and r have the same sign.

If all three factors vary together, the surface

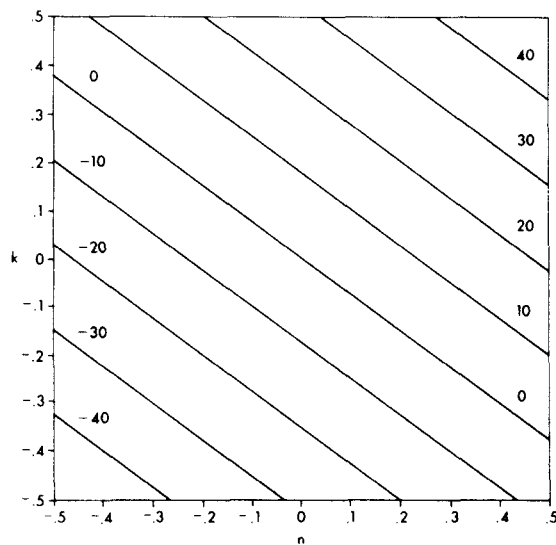


FIGURE 4.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the initial number (n) and in the kill vector (k) when the net reproductive rate vector is held constant for *Stenella attenuata* in the eastern tropical Pacific.

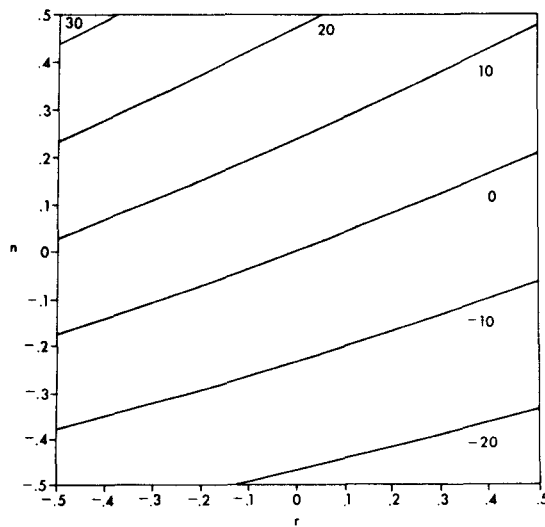


FIGURE 3.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the initial number (n) and in the net reproductive rate (r) when the kill vector is held constant for *Stenella attenuata* in the eastern tropical Pacific.

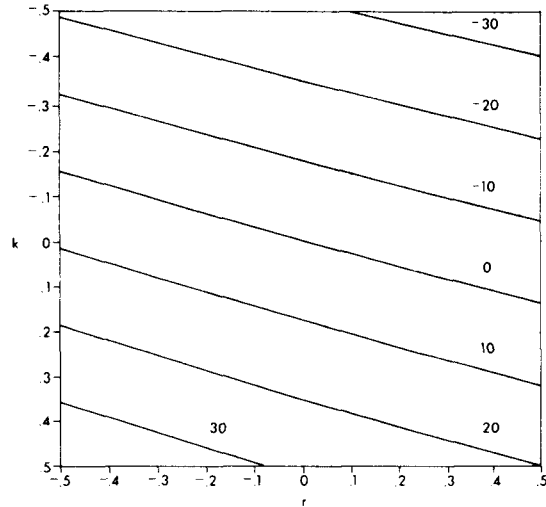


FIGURE 5.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the kill vector (k) and the net reproductive rate vector (r) when the initial number is held constant for *Stenella attenuata* in the eastern tropical Pacific.

generated by S is still relatively linear as there are no terms in S containing n , k , and r and the pairwise nonlinear effects are small as discussed above. Table 2 provides examples of points on this three dimensional surface when n , k , and r are equal in absolute values. It can be seen there, for the example examined, that if the absolute values of n , k , and r are 0.10, the sensitivity of N_{15} ranges from -12 to +12.

An empirical equation can be fitted to the sensitivity surface (S) by fitting a linear function for each factor considered independently and by determining a nonlinear term for n and r . The general form of this fitted equation is

$$\hat{S}_t(n, k, r) = (b_1 K + b_2 n + b_3 r + b_4 nr) \times 100 \quad (10)$$

where the b 's are constant. The exact value of the b 's depends on the number of years the population is projected back in time. For the example considered here, projecting back from 1974 to 1959, the values of the b 's are shown in Equation (11):

$$\hat{S}_{15}(n, k, r) = (0.573k + 0.427n - 0.164r - 0.125nr) \times 100. \quad (11)$$

This empirical approximation [Equation (11)] deviates by <2 from the true values of S_{15} for values of n , k , and r <0.5. This empirical equation is useful as the magnitude of the b 's provides a measure of the relative sensitivity of the different factors. Thus in Equation (11) it can be seen that for the example considered here the 1959 abundance estimate (N_{15}) is most sensitive to bias in the estimates of the kills. This empirical equation also provides an easy way to generate approximate values of S for any combination of values for n , k , and r .

Variance

The results of the variance calculations for the

TABLE 2.—Values of $S_{15}(n, k, r)$ when the absolute values of n , k , and r are equal.

Absolute value k = n = r	Sign of k	Sign of n			
		Sign of r		Sign of r	
		+	-	+	-
0.10	+	9	12	0	3
	-	-3	0	-12	-9
0.20	+	16	23	0	5
	-	16	1	-22	-17
0.30	+	24	36	1	8
	-	-10	2	-33	-26

bridled dolphin are summarized in Tables 3 through 6. Calculated values of the variance of N_t from Equation (9), when all of the random variables are assigned a coefficient of variation of 30%, are given in Table 3, over all years from 1974 to 1959. It can be seen that both the variances and the coefficients of variation (CV) generally decrease. The reduction of the CV over time is due to the fact that the major contributions to the back estimates of the population size are the addition of the kills of the previous years, since the reproductive rate is small. The variance of a sum of independent random variables is the sum of their variances. This always results in a CV for the sum which is smaller than the greatest CV of any of the random variables when the expected values of the random variables are positive (Appendix II). As a generalization, it can be stated that when the net reproductive rate is small the CV of the back estimate will not be larger than the largest CV of any of the random variables, and will usually be smaller.

Table 4 shows the breakdown of the variances calculated in Table 3 into their major components. The variance of N_0 is the major factor in the variance of these back estimates. The contribution of

TABLE 3.—Calculated variance and coefficient of variation for the back estimate of dolphin abundance when all random variables have a CV of 30%.

Year	Variance ($\times 10^{11}$)	CV (%)	Year	Variance ($\times 10^{11}$)	CV (%)
1974	11.03	30.0	1966	7.04	19.1
1973	10.22	29.0	1965	6.9	18.0
1972	9.53	27.0	1964	6.8	17.1
1971	8.88	25.7	1963	6.71	16.7
1970	8.35	23.8	1962	6.67	16.3
1969	7.99	22.1	1961	6.71	15.7
1968	7.56	21.2	1960	6.75	15.2
1967	7.25	20.2	1959	6.75	15.1

TABLE 4.—Breakdown of the variance of N_t into the major components that contribute to the calculated variance.

Year	Contribution to the variance of N_t ($\times 10^{10}$) due to the variance in:		
	The initial number	The kills	The net reproductive rate
1974	110.3	0.00	0.000
1973	101.9	.12	.156
1972	94.2	.76	.305
1971	87.1	.10	.452
1970	81.2	1.755	.568
1969	76.2	2.604	.664
1968	72.1	2.70	.735
1967	68.8	2.91	.784
1966	66.1	3.49	.816
1965	64.1	4.16	.835
1964	62.5	4.64	.843
1963	61.5	4.73	.843
1962	61.1	4.99	.840
1961	61.1	5.24	.840
1960	61.1	5.55	.840
1959	61.1	5.56	.840

TABLE 5.—Coefficients of variation (CV) for the back estimates of bridled dolphin in 1959 (N_{15}) for a range of CV for the parameters of the model. The ranges of CV's of the kills, net reproductive rate, and initial abundances were selected to illustrate particular aspects of the behavior of the variances of the back estimates.

CV of the kills	CV of the net reproductive rate	CV of N_0			
		0	10	20	40
0	0	0	4.7	9.5	19.2
	40	2.2	5.3	9.8	19.3
10	0	1.4	5.0	9.6	19.2
	40	2.7	5.5	10.0	19.4
20	0	2.9	5.6	10.0	19.3
	40	3.7	6.0	10.3	19.5
40	0	5.6	7.5	11.2	20.0
	40	6.2	7.8	11.4	20.2
60	60	9.3	10.5	13.4	21.3
100	100	15.5	16.2	18.2	24.7

the variance of N_0 tends to completely dominate the variance of N_t because of the assumed independence of the kill estimates. Table 5 gives the CV for the back estimated population size of dolphin in 1959 for a range of CV for the different parameters involved in the estimate of N_{15} . As can be seen in this table, unless the variance of N_0 is near zero or unless the CV of the kill and reproductive vectors are extremely large ($>60\%$), the CV of the back estimate does not exceed the CV of N_0 .

and the basic model [Equation (3)] for the dolphin population examined here is given in Table 6. The simpler model always gives a slightly higher estimate for the size of the back projected population but the increase in the estimate is always $<1\%$. The sensitivities of the two models are nearly equivalent. When the values for the parameters in these models deviate as much as 50% the difference between sensitivities of the two models is $<1\%$. The approximate variances of the back estimates of the two models are also similar.

That the difference between the original and the simpler model is small can be shown by analytically comparing the two models. If the projections are made only 1 yr into the past, the ratio of the estimate from Equation (2) to the estimate from Equation (3) is

$$1 + \frac{0.5R_1K_1}{N_0 + K_1 + 0.5R_1K_1}$$

Only if the value of R_1K_1 is large relative to $N_0 + K_1$ can this ratio deviate significantly from 1. This is only possible if R_1 is relatively large. The general formula for the ratio of the two models is

$$1 + \frac{\sum_{j=1}^t 0.5K_jR_j \left(\prod_{h=1}^j (1+R_{h-1}) \right)}{N_0 + \sum_{j=1}^t 0.5K_j \left(\prod_{h=1}^j (1+R_{h-1}) \right) + \sum_{j=1}^t 0.5K_j \left(\prod_{h=1}^j (1+R_h) \right)}$$

Comparison of Equations (2) and (3).

A comparison of the estimated back abundance as calculated by the simpler model [Equation (2)]

As in the case for projecting back only 1 yr, it can be seen that unless the R_jK_j terms are large relative to N_0 and unless the net reproductive rate is also large, the ratio of the two models will be close to 1.

DISCUSSION AND CONCLUSIONS

The results of this analysis indicate that errors in the input parameters do not compound in this procedure for estimating historical abundance. In fact, a systematic bias in the procedure for the estimation of a single set of parameters (either N_0 or R_i 's or K_i 's) always induces a bias in the back projected estimate which is less than the bias of the estimated parameters. This conclusion follows directly from the linear or near linear relation between S_t and n , k , or r with small rates of change. Moreover, the effects of bias in two or more sets of parameters are nearly additive. The interaction effects of bias in estimates of kills, net reproductive rates, and the initial number tend to

TABLE 6.—Comparison of the back estimate of the abundance of bridled dolphin as calculated by the basic model [Equation (3)] and the simpler model [Equation (2)].

Year	Simple model ($\times 10^6$)	Basic model ($\times 10^6$)	Simple/basic
1974	3.500	3.500	1.000
1973	3.485	3.483	1.001
1972	3.624	3.617	1.002
1971	3.670	3.659	1.003
1970	3.850	3.835	1.004
1969	4.062	4.0416	1.005
1968	4.115	4.093	1.005
1967	4.214	4.190	1.006
1966	4.412	4.386	1.006
1965	4.640	4.612	1.006
1964	4.840	4.811	1.006
1963	4.934	4.905	1.006
1962	5.021	4.991	1.006
1961	5.467	5.437	1.005
1960	6.001	5.971	1.005
1959	6.130	6.100	1.005

be small or nonexistent. This will be globally true for the relationship between k and n , but will be true for the relationship between k , r , and n only when the net reproductive rate is small. The relative importance of bias in K_i 's, R_i 's, or N_0 on N_t depends upon the actual values of the parameter. In the bridled dolphin example, after 15 yr, the back estimates were most sensitive to bias in the kill estimate, slightly less sensitive to bias in N_0 , and considerably less sensitive to bias in the net reproductive rate. However, the importance of bias in N_0 will diminish with the number of years in the back estimate with a proportionate increase in the importance of bias in the kills.

The sensitivity analysis developed in this paper will include the extremes of a complete sensitivity analysis of the model. The values for $S_t(0,k,0)$ are limiting values to a complete sensitivity analysis of the individual elements of the kill vector on N_t . Similarly $S_t(0,0,r)$ is a limit to complete sensitivity analysis of the individual elements of the net reproductive rate. Given the additivity of S_t with respect to n , r , and k , the surface $S_t(n,k,r)$ contains the extremes of a sensitivity analysis in all $2t+1$ dimensions. If in fact the elements within the kill vector and within the reproductive vector are highly interdependent (as is the case for the data used here), then the sensitivity analysis used to look at the effects of bias in this paper approaches a total sensitivity analysis of the back projected estimate given these constraints.

The variance approximations also indicate that variability in the parameter estimates does not result in compounding uncertainty in the back projected estimates. When estimates of the parameters are independent and the net reproductive rate is low, the CV of the back estimate will be smaller than the CV of the input parameters. In our example if all the CV's were equal, the variance of N_0 would make the largest contribution to the estimated variance of N_t . In general this will be true as long as the kills in any one year do not approach the initial abundance. This is a direct consequence of the basic additivity of the model when the net reproductive rate is small.

In Smith and Polacheck (see footnote 4), an alternative probability structure was considered in which the elements within the kill vector and within the net reproductive rate vector were highly interdependent. In this situation, the vari-

ance of N_t is not completely dominated by the variance of N_0 . The variances of N_t calculated using this interdependent probability structure are larger than the variances presented here in which all the parameters are assumed independent. However, the CV of N_t for the dolphin data within this interdependent probability structure is still less than the CV of the parameters if all parameters have equal CV. It appears that even in the situation in which a high degree of interdependence exists within the kill estimate or the net reproductive estimates, the variability in the parameter estimates does not induce compounding uncertainty in the back projected estimate.

The comparison of the results from the basic model [Equation (3)] with the simpler model [Equation (2)] indicate that there are no significant differences between the two models as long as the net reproductive rate is small. Thus it appears that there is no reason to favor the more complex model over the simpler.

In conclusion, it appears that this back projection procedure (either model) has reasonable statistical properties, at least when the net reproductive rates are small. However, Equation (1) is a simplified description of how the abundance of a population changes through time, especially in not accounting for changes in age structure. The authors feel that caution should be used in applying estimates from this procedure to the management of long-lived species since changes in the age structure for long-lived species are likely to be important.

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LITERATURE CITED

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APPENDIX I.—Expressions for the variance components of N_t .

Expression for the right hand terms of Equation (9) are:

$$V(N_0) \left(\frac{\partial N_t}{\partial N_0} \right)^2 = V(N_0) \left(\frac{1}{\prod_{j=1}^t (1+R_j)} \right)^2 \quad (\text{i})$$

$$\sum_{j=1}^t V(K_j) \left(\frac{\partial N_t}{\partial K_j} \right)^2 = \sum_{j=1}^t V(K_j) \left(\frac{1 + 0.5R_j}{\prod_{h=j}^t (1 + R_h)} \right)^2 \quad (\text{ii})$$

$$\sum_{j=1}^t V(R_j) \left(\frac{\partial N_t}{\partial R_j} \right)^2 = \sum_{j=1}^t V(R_j) \left(\frac{N_{j-1} + 0.5K_j}{(1 + R_j)^2 \prod_{k=j+1}^t (1 + R_k)} \right)^2. \quad (\text{iii})$$

APPENDIX II.—Coefficient of variation of a sum of random variables.

The following is a proof that the coefficient of variation of a sum of two independent random variables is smaller than the greatest CV for either of the random variables if the expected value of the random variables is greater than zero.

If A and B are independent random variables such that

$$\begin{aligned} E(A) &= a > 0 \quad E(B) = b > 0 \text{ and} \\ CV(A) &= \frac{\sqrt{V(A)}}{a} \geq \frac{\sqrt{V(B)}}{b} = CV(B) \end{aligned}$$

then

$$\frac{V(A)}{a^2} \geq \frac{V(B)}{b^2},$$

$$V(A)b^2 \geq V(B)a^2,$$

$$V(A)(b^2 + 2ab) > V(B)a^2,$$

$$V(A)(b^2 + 2ab) + V(A)a^2 \geq V(B)a^2 + V(A)a^2$$

$$V(A)(a + b)^2 \geq [V(B) + V(A)]a^2,$$

$$\frac{V(A)}{a^2} > \frac{V(B) + V(A)}{(a + b)^2} = \frac{V(A + B)}{[E(A + B)]^2},$$

$$CV(A) > CV(A + B).$$