

## DYNAMIC RESPONSE ANALYSIS. II. EVALUATION OF DYNAMIC RESPONSE ANALYSIS IN A SIMULATED NO-HARVEST CASE

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### ABSTRACT

A new method of stock assessment, dynamic response analysis, allows a qualitative assessment of stock status relative to its level of maximum net productivity to be carried out with minimal data. This paper evaluates the performance of dynamic response analysis on a simulated population under variable conditions with uncertain data. In the no-harvest case the data consist simply of a temporal sequence of relative population sizes. Dynamic response analysis is most sensitive to the number and precision of the population estimates and least sensitive to environmental variability and the intrinsic population growth rate. Significance levels must be chosen carefully, since some combinations of parameters and error levels result in an unacceptably low proportion of correct assessments. Dynamic response analysis can be a useful stock assessment technique for the management of marine mammals, but attention must be paid to the quantity and quality of the data.

Key words: dynamic response analysis, marine mammal management, Marine Mammal Protection Act.

Dynamic response analysis is a method of stock assessment applicable to a population for which recent records of abundance estimates and harvests are available. The method was developed recently at the Southwest Fisheries Center, National Marine Fisheries Service, in response to monitoring obligations under the Marine Mammal Protection Act. It is, however, a general management technique. Dynamic response analysis determines whether a population is above or below its maximum net productivity level (MNPL). The theory behind the analysis is presented by Goodman (1988). This paper explores the amount and precision of data required for dynamic response analysis to work satisfactorily. The third paper in the series applies the analysis to several northern elephant seal populations (Boveng *et al.* 1988).

One application of dynamic response analysis utilizes an index of population abundance over time, augmented by harvest data, if any, to determine whether

the population growth rate is accelerating or decelerating. A number of potential sources of error could affect the assessment. Environmental conditions may vary, for example, or there may be uncertainty in estimating population size. Before dynamic response analysis is used as a management tool, its robustness to the kinds of data likely to be found in actual practice should be evaluated. The sensitivity of dynamic response analysis to variable and uncertain data is investigated in this paper by analyzing a simulated population with known variability and measurement error.

#### METHODS

The robustness of dynamic response analysis is measured by estimating, under various conditions, the probability that the analysis will give a correct assessment of population size relative to its MNPL. In particular, dynamic response analysis is applied to a depleted population recovering in the absence of harvest. The density-dependent dynamics follow the logistic model. For the no-harvest case, the data consist of estimates of population size (or an index of relative population size) spanning some number of years. The following questions are posed: (1) How many population estimates (censuses) will be required for dynamic response analysis to work reasonably well? (2) How precise must the population estimates be? (3) How sensitive is the method to the growth rate of the population? (4) How sensitive is the method to environmental variation? (5) How powerful is the method when a significance test is applied? While some details of the results will depend on the specific properties of the logistic model, there are general answers to these questions that will apply, regardless of details, for a wide range of forms of density dependence.

To simulate errors in estimating population size, the sequence of population estimates is chosen from Gaussian distributions whose means are the actual population size (following deterministic logistic growth) and whose variances, expressed as the coefficient of variation, are set as an input parameter. To simulate environmental variability, the carrying capacity parameter  $K$  in the logistic model is chosen, at each time step, from a Gaussian distribution whose variance is set as an input parameter. Since, in the logistic model, the population's present growth rate is determined by the difference between present population size and the maximal population size at carrying capacity, this variation in carrying capacity will cause the observed growth rate to fluctuate. The mean carrying capacity is fixed at unity.

Given a sequence of population estimates with some variability, the status of the population relative to the logistic MNPL of 0.5 may be determined by fitting a second-degree polynomial to the population estimates and examining the sign of the second-degree regression coefficient (Goodman 1988). A negative coefficient indicates that the growth rate is decreasing, and hence that the population is above the MNPL, while a positive coefficient indicates the opposite. Whether the assessment is correct or not depends on whether the midpoint of the deterministic growth sequence is above or below the MNPL. Even in a deterministic system without measurement error, ambiguity about the assessment

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of a sequence of population estimates arises when the sequence includes the MNPL. In this paper the midpoint of the sequence has been chosen as a reference point; this ensures that a population trajectory including the MNPL will be assessed in conformity with the majority of the population estimates it contains. Each simulation was repeated 1,000 times, and the proportion of correct assessments was taken as an estimate of the probability that dynamic response analysis would be correct at that population level. In this implementation of dynamic response analysis, therefore, no statistical test is performed, but the proportion of correct assessments is analogous to the power of the technique—that is, its ability to reject a false case.

The decision strategy outlined above, which considers the direction of the population growth curvature only, is the simplest application of dynamic response analysis. Because it is easy to understand and apply, this decision strategy has been employed in the following simulations to assess relative sensitivity. In actual practice, however, dynamic response analysis is unlikely to be used in such a simplistic manner. Other kinds of information will usually be available and, if so, can be used to increase the power of the analysis considerably. For example, rough estimates of past abundance can help interpret current estimates, even though past estimates are not sufficiently quantitative to be used as part of a dynamic response analysis.

As one illustration of a more realistic application of dynamic response analysis, the results of a second series of simulations with a more refined decision process are presented. In these simulations it is assumed that something is known of the precision of the population estimates, and both linear and polynomial regressions are computed for each temporal sequence of estimates. The magnitudes as well as the signs of the linear regression coefficient (the slope) and the second-degree polynomial regression coefficient (the curvature) are considered. If the slope is negative, or if it is not significantly different from zero, this is taken as evidence that the population is above the MNPL. If the slope is significantly positive, the curvature then indicates whether the population is below the MNPL (second-degree polynomial regression coefficient significantly positive), near the MNPL (coefficient not significantly different from zero), or above the MNPL (coefficient significantly negative). The null hypothesis in each case is that the regression coefficient is not significantly different from zero. In each simulation the parameter values are used to generate the true case, and we are evaluating the ability of dynamic response analysis to recognize, after evaluating the significance of the two coefficients, the true case as one of these three levels.

For the simulations reported here, the region "near the MNPL" has been defined as the range of population sizes from 0.4 to 0.6 (as a fraction of  $K$ ). Within this range, if dynamic response analysis determines that the population is either below or near the MNPL, the assessment is tallied as correct. Above a population size of 0.6, only determinations of above MNPL are counted as correct. This classification represents a biologically conservative management approach in which the standards for deciding that the population is above the MNPL (and harvesting, therefore, may be permitted) are more stringent than

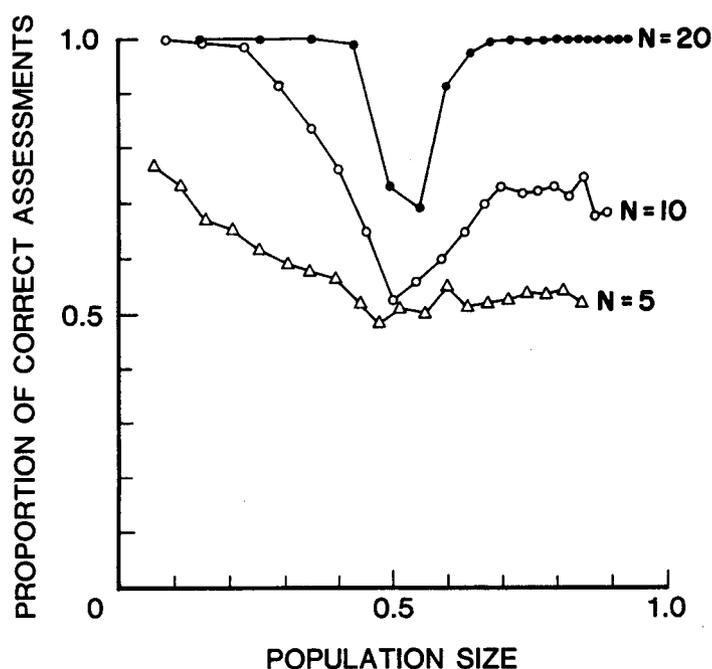


Figure 1. The proportion of correct assessments by dynamic response analysis as a function of population size and  $N$ , the number of population estimates used in each assessment. Values of other parameters are the coefficient of variation of the population estimates ( $CV$ ) = 0.05, the logistic parameter of maximum intrinsic population growth rate ( $r$ ) = 0.15, and the standard deviation of the variation in carrying capacity ( $\sigma_K$  = 0.0).

the standards for deciding that the population is below the MNPL (and protection, therefore, is called for). Other strategies are of course possible.

#### RESULTS

The results of the simulations are presented in Figures 1–7. The probability of a correct assessment by dynamic response analysis is plotted as a function of population size. Each figure typically shows that dynamic response analysis does well at low population levels, but shows a decline near the MNPL (0.5) to about 0.5. This is not surprising. At the MNPL the second derivative of the population growth curve is changing in sign, so a sequence of population estimates centered on this point is about equally likely to show positive as negative curvature. The goal is to confine this decline in assessment accuracy to as narrow a range of population sizes as possible.

Figure 1 presents three curves which show the effect of different numbers of data points. The parameter  $N$  represents the number of population estimates available. The lowest curve, for  $N = 5$ , shows that a sequence of five population estimates is not sufficient, at a value of  $r = 0.15$ , for dynamic response analysis

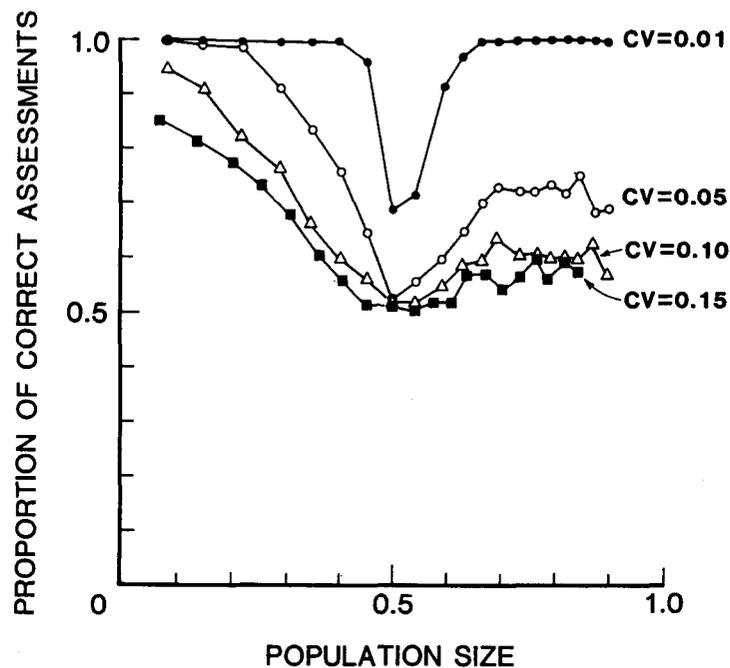


Figure 2. The proportion of correct assessments by dynamic response analysis as a function of population size and CV, the coefficient of variation of the population estimates. Values of other parameters are  $N = 10$ ,  $r = 0.15$ , and  $\sigma_K = 0.0$ .

to work satisfactorily except at very low population levels. There is considerable improvement in the ability to detect a population's status correctly with a sequence of 10 population estimates (middle curve in Fig. 1). With 20 censuses, the technique works very well except in a narrow band near the MNPL. Thus, the analysis is relatively sensitive to the length of the time-series of population estimates.

Figure 2 presents four curves which contrast the effects of the precision of the population estimates. Precision is measured by the coefficient of variation (CV), the ratio of the standard deviation to the mean. When the coefficient of variation is very low (0.01)—that is, with highly precise population estimates—the technique is definitive except in a narrow band near the MNPL. This band rapidly expands as the coefficient of variation increases to 0.05, 0.1 and 0.15 (Fig. 2). As discussed later, even a coefficient of variation of 0.15 is considered fairly precise for many types of population estimation. Therefore, the simulations indicate relatively high sensitivity to the precision of the population estimates.

Figure 3 presents curves which show the effect of different rates of population growth. The logistic parameter  $r$ , which is used here to indicate population growth rate, is the maximum growth rate the species can achieve under uncrowded conditions and abundant resources. The unit of time is the interval between population estimates. In the logistic model the growth rate declines linearly with density, so that at the MNPL of 0.5 the growth rate will be  $r/2$ . Figure 3 shows that populations capable of more rapid growth will be analyzed

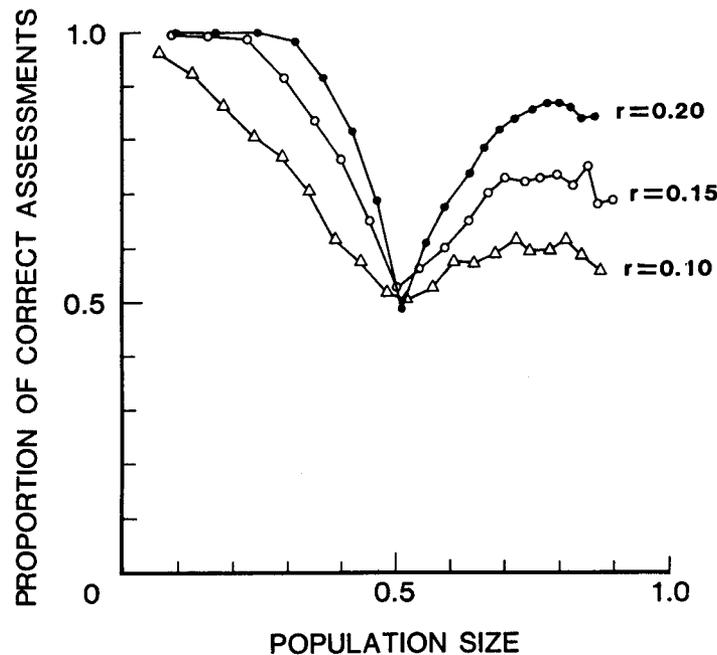


Figure 3. The proportion of correct assessments by dynamic response analysis as a function of population size and  $r$ , the logistic parameter of maximum intrinsic population growth rate. Values of other parameters are  $N = 10$ ,  $CV = 0.05$ , and  $\sigma_K = 0.0$ .

correctly by dynamic response analysis more often than populations with lower growth rates.

Figure 4 shows the effect of environmental variability on dynamic response analysis. The variability is measured by the standard deviation of the carrying capacity  $\sigma_K$ . In these simulations it is assumed that there is no error in the estimation of population size. As the environment becomes more variable, dynamic response analysis is less effective above the MNPL, but even at the highest level of environmental variability shown here ( $\sigma_K = 0.15$ ), the probability of a correct assessment remains high except in the vicinity of the MNPL.

In Figure 5 the stochastic effects of estimation error and environmental variability are combined. Each curve has a specified precision to the population estimates, measured by the coefficient of variation, and a specified variation in the environment, measured by the standard deviation of the carrying capacity. Three cases, ranging from small ( $CV = 0.05$ ,  $\sigma_K = 0.05$ ) to large ( $CV = 0.15$ ,  $\sigma_K = 0.15$ ) variability, are shown. As expected, the proportion of correct assessments decreases with increasing variability in both parameters.

As discussed under Methods, the simulations reported in Figures 1–5 simply use the sign of the second-degree polynomial regression coefficient as the decision statistic. Figures 6 and 7 include the results of a more refined application of dynamic response analysis, using significance tests with both linear and polynomial regressions. These simulations show how a knowledge of the precision of the population estimates can be used to increase the power of the analysis

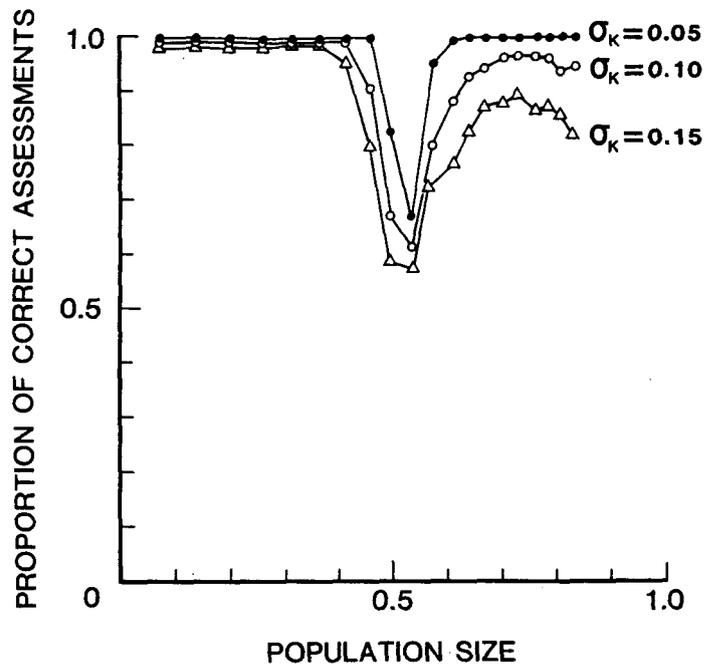


Figure 4. The proportion of correct assessments by dynamic response analysis as a function of population size and  $\sigma_K$ , the standard deviation of the variation in carrying capacity. Values of other parameters are  $N = 10$ ,  $CV = 0.0$ , and  $r = 0.15$ .

greatly. They also provide more realistic estimates of the probability that dynamic response analysis will assess the population correctly.

Figure 6 compares two curves given a sequence of 10 population estimates, an intrinsic population growth rate of 0.15, and a coefficient of variation of 0.3. The lower curve with open triangles is similar to the curves presented in Figures 1–5; that is, it relies on the sign of the second-degree regression coefficient only. Because the coefficient of variation of the population estimates is relatively high ( $CV = 0.3$ ), the curve remains near 0.5 over a wide range of population sizes. Under these conditions, in other words, the assessment is little better than chance. The upper curve shows the improvement possible by using significance tests on both the linear and polynomial regression coefficients. The significance ( $\alpha$ ) levels were set at 5% for the linear regression and at 10% for the polynomial regression. With this procedure, dynamic response analysis is able to assess the status of the population correctly over a wide range of population sizes, even with relatively imprecise population estimates.

Significance levels must be chosen carefully, however, to avoid a drop in the proportion of correct assessments. Figure 7 shows a comparison among three curves, using an example when only five population estimates are available. With such a short time-series ( $N = 5$ ), the sign of the second-degree regression coefficient alone is not very informative, even though the population estimates are precise ( $CV = 0.05$ ). This is shown by the curve with open triangles in

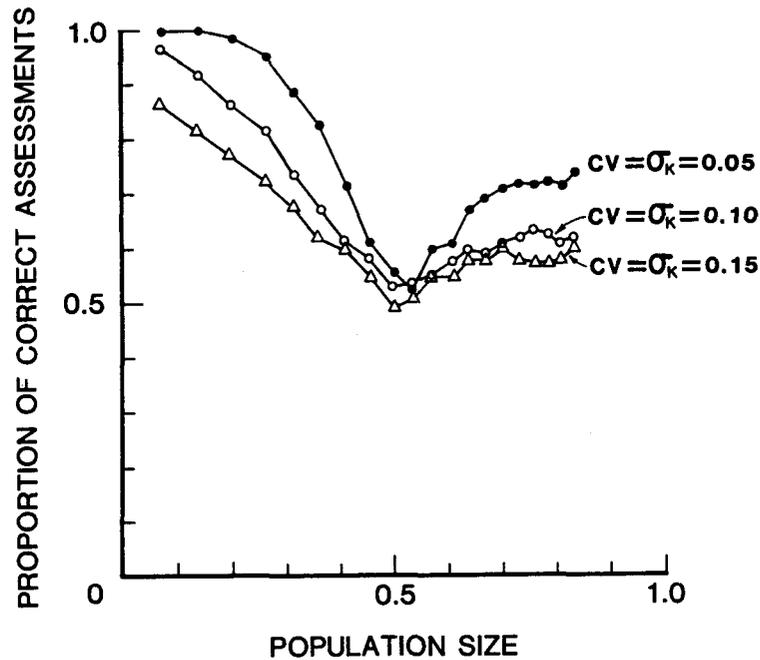


Figure 5. The proportion of correct assessments by dynamic response analysis as a function of population size, precision of population estimates (CV), and environmental variability ( $\sigma_K$ ). Values of other parameters are  $N = 10$  and  $r = 0.15$ .

Figure 7 (a similar curve is shown in Fig. 1) which is again near a proportion of 0.5 correct assessments over a wide range of population sizes. The curve with closed circles shows the performance of the more "advanced" version of dynamic response analysis, using significance levels of 5% and 10% for the linear and polynomial regressions, respectively, as in Figure 6. In this case, however, the analysis does well at low population levels, drops sharply at population sizes above 0.6, and then increases to become high again at population sizes near  $K$ . This effect is due to the relative strengths of the "signals" given by the linear and polynomial regression coefficients. In the range of population sizes from about 0.6 to 0.8, the slope is usually significant but curvature is not, indicating (incorrectly) that the population is near the MNPL.

When the significance test for the detection of slope is made more stringent ( $\alpha = 0.01$ ) and the significance test for the detection of curvature more lenient ( $\alpha = 0.2$ ), the sharp drop in the proportion of correct assessments can be avoided, as shown by the curve with open circles in Figure 7. This latter choice of significance levels leads to satisfactory performance by dynamic response analysis over a wide range of population sizes, as before, and a considerable improvement over relying on the sign of the polynomial regression coefficient alone. Further simulations have shown that the optimal choice of significance levels depends mainly on the number and precision of the population estimates. The nature of the dependence appears to be complicated and no simple rules are offered.

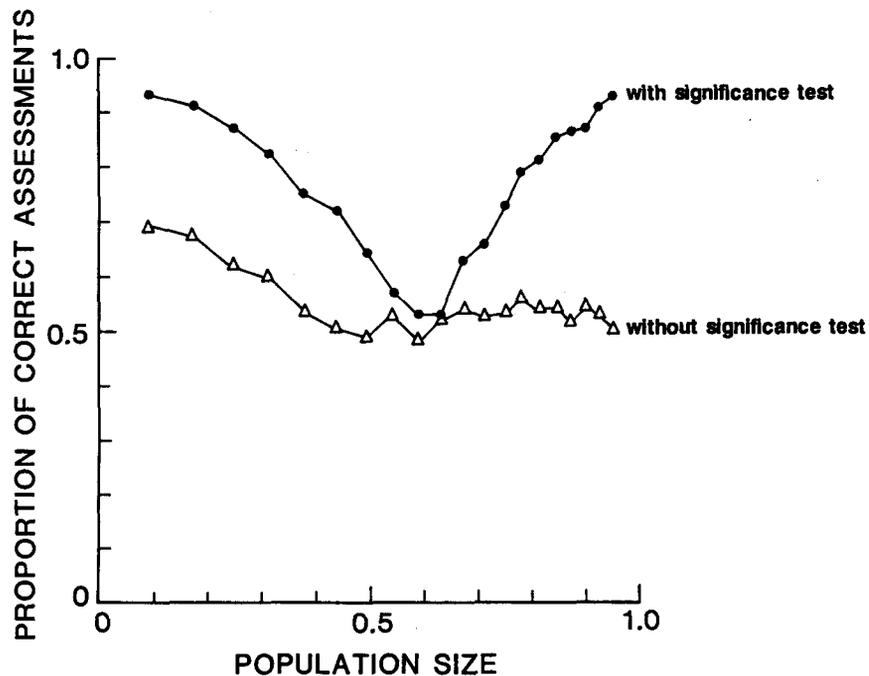


Figure 6. Comparison of the proportion of correct assessments by two different implementations of dynamic response analysis. Values of parameters are  $N = 10$ ,  $CV = 0.3$ ,  $r = 0.15$ , and  $\sigma_K = 0.0$ . Curve with open triangles relies on the curvature of the population growth trajectory only. Curve with closed circles uses a decision procedure which tests the significance of the slope at the 5% level and of the curvature at the 10% level.

However, given the number and precision of the population estimates, optimal significance levels can be found using simulations, as in Figures 6 and 7.

#### DISCUSSION

The simulations described in this paper examine the robustness of two particular implementations of dynamic response analysis under variable conditions with uncertain data. The results presented in Figures 1–4 show that dynamic response analysis is more reliable (1) with a longer sequence of population size estimates, (2) with more precise population estimates, (3) with populations capable of higher intrinsic growth rates, and (4) with lower environmental variability. The qualitative results for these related factors agree with intuition because each either provides a stronger “signal” about population growth rate or allows that signal to be more clearly perceived.

The second set of simulations gives more quantitative estimates of the probability that dynamic response analysis will correctly determine whether a population is above or below its MNPL. Most of the parameter values in the simulations were chosen to approximate values which could be met in the actual

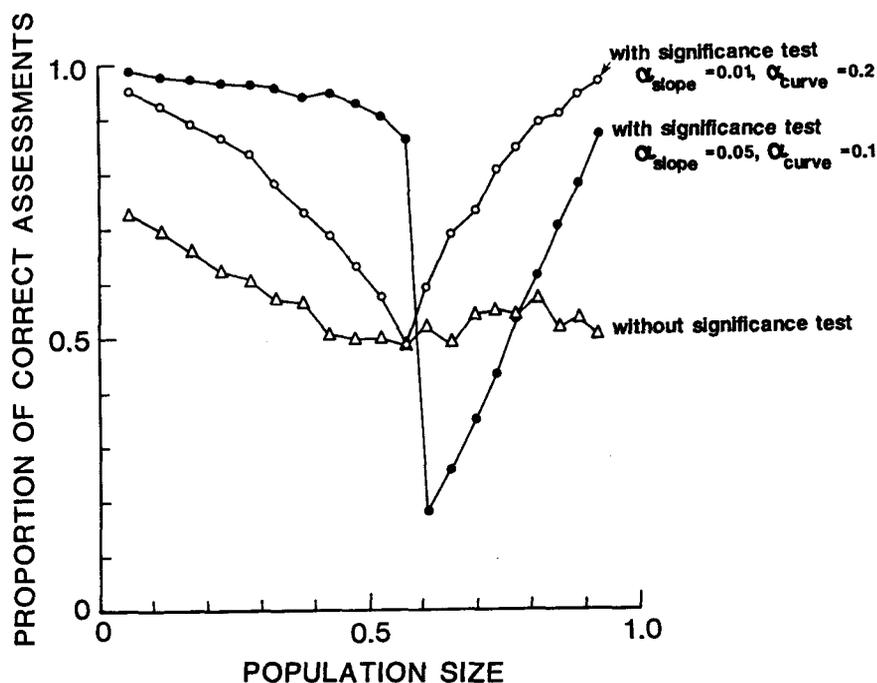


Figure 7. Comparison of the proportion of correct assessments by dynamic response analysis using different significance levels. Values of parameters are  $N = 5$ ,  $CV = 0.05$ ,  $r = 0.15$ , and  $\sigma_K = 0.0$ . Curve with open triangles relies on the curvature of the population growth trajectory only. Curve with closed circles uses a decision procedure which tests the significance of the slope at the 5% level and of the curvature at the 10% level. Curve with open circles uses the same decision procedure but with significance levels set at 1% for the slope and 20% for the curvature.

study of large mammals. It is clear that dynamic response analysis is capable of telling whether an unharvested population is above or below its MNPL merely from an historical sequence of abundance estimates. However, it is also clear that data used in a dynamic response analysis will have to satisfy fairly stringent conditions before much confidence can be placed in the result.

Probably the most stringent data requirement is a precise method of estimating population abundance (or an index of relative population abundance). It is hardly surprising that a method of stock assessment which relies, as dynamic response analysis does, on the differences in estimated abundance in successive time periods should be very sensitive to the precision of those abundance estimates. Figure 7 shows that, with  $r = 0.15$  and as few as 5 estimates, dynamic response analysis can perform satisfactorily if the coefficient of variation is 0.05 or less. This is rather high precision. Most field studies report less precise estimates of abundance (higher coefficients of variation). Table 1 summarizes the precision of some direct counts of abundance which have been reported for large mammals. All the reported coefficients of variation fall above 0.05, although precision in the range 0.05–0.1 is not impossible to achieve under the right conditions.

Table 1. Precision of direct estimates of abundance for some populations of large mammals. Some of the values for the coefficient of variation (CV) are derived while others are estimated empirically.

Species	Method	CV	Reference
Sea lion	Replicated ground counts of live pups	0.06	Calculated from DeLong <i>et al.</i> <sup>a</sup>
Moose	Aerial counts under excellent conditions	0.1	LeResche and Rausch 1974
Gray whale	Derived from shore counts during migration	0.1	Reilly <i>et al.</i> 1983
Large ungulates (6 species)	Derived from aerial quadrat counts	0.11–0.18	Laws <i>et al.</i> 1975
Sea otter	Replicated aerial strip transects	0.13	Estes <sup>b</sup>
Porpoise	Derived from aerial line transects	0.16	Smith 1981
Sperm and fin whales	Derived from catch statistics	0.16–0.46	Allen and Kirkwood <sup>c</sup>
White-tailed deer	Helicopter censuses	0.2	Beasom 1979
Bottlenose dolphin	Aerial strip transects	0.42–0.67	Leatherwood <i>et al.</i> 1978
Walrus	Aerial strip transects	0.25–0.99	Estes and Gilbert 1978

<sup>a</sup> DeLong, R. L., G. A. Antonelis and E. Jameyson. 1982. California sea lion pup production, premature birth, and neonatal mortality on San Miguel Island, 1969–1981. Unpublished manuscript. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115.

<sup>b</sup> Estes, J. A. 1982. Aerial surveys of the California sea otter population, winter 1981–82. Unpublished manuscript. Center for Marine Studies, University of California, Santa Cruz, CA 95064.

<sup>c</sup> Allen, K. R., and G. P. Kirkwood. 1976. Is experimental management of whale stocks practicable? Paper ACMRR/MM/SC/Cmt. 3, FAO Scientific Consultation on Marine Mammals, Bergen.

Indirect methods of abundance estimation, such as estimates derived from mark-recapture data, will usually be less precise than the direct counts shown in Table 1. Fortunately, low precision can be compensated for by a longer temporal sequence of abundance estimates. Figure 6 shows, for example, that a coefficient of variation of 0.3 can still give quite satisfactory results if there are 10 abundance estimates rather than only 5. A coefficient of variation of 0.3 is within a practical range of precision for many population studies.

It is important to recognize that the variation in abundance estimates simulated here is due, in actual practice, to a combination of many factors, including counting errors, differences among observers, variation in sighting conditions, and variation in availability. It could be estimated by a replicated series of counts under actual conditions. However, this measurement error is a minimum estimate of the variation to be expected in a temporal series of abundance estimates (Harris 1986, Gerrodette 1987). Internal population events, such as changes

in behavior or age structure, as well as external changes in the environment, also contribute variability to a series of estimates. Furthermore, a time-series may have positive autocorrelation. These factors should be recognized if precision is estimated from the residuals of a regression of abundance estimates over time.

The simulations have also shown that a reasonably long temporal sequence of abundance estimates is required. As noted above, there is an inverse relationship between the required number and precision of the estimates, so that dynamic response analysis may work equally well with a short sequence of precise estimates or a long sequence of imprecise estimates. The short sequence of precise estimates is to be preferred, however, since the longer the time, the less certain we are that other factors are remaining constant. If the precision of the population index is known, the length of the time-series needed for dynamic response analysis to work satisfactorily can be computed. Boveng *et al.* (1988) explore ways of choosing the length of the time-series even when precision is not known.

Based on the range of parameters reported in these simulations, dynamic response analysis appears less sensitive to environmental variability and the rate of population growth (Figs. 3 and 4). The most variable environment simulated had a coefficient of variation of 0.15 in the carrying capacity  $K$ . With normally distributed variation, this means that approximately 95% of the time the carrying capacity is between 0.7 and 1.3 times its long-term mean value. Simulated values of the intrinsic population growth rate  $r$ , where time is scaled in units of interval between population estimates, ranged from 0.1 to 0.2. Since observed maximum population growth rates will generally be less than the theoretical maximum logistic parameter  $r$ , this range of values for  $r$  is appropriate on an annual basis for pinnipeds (Eberhardt and Siniff 1977, Payne 1977, Eberhardt 1981, Cooper and Stewart 1983), but perhaps slightly high for most cetaceans (Kasuya 1976, Best 1981, Reilly 1984, Breiwick *et al.* 1984, Reilly and Barlow 1986).

For management purposes, a determination that the population is "near the MNPL" is, although not precise, nevertheless informative and useful. In cases of conservative management, such as mandated by the Marine Mammal Protection Act, a population in the immediate vicinity of its MNPL would be managed as if it were below the MNPL—*i.e.*, measures would be taken to protect and increase the size of the population. This conservative management policy is the reason why population densities near the MNPL have been grouped together with densities below the MNPL in this paper.

To reach an assessment that the population is near the MNPL, the significance of the slope and the curvature of the population growth trajectory were evaluated in the second set of simulations. However, when using dynamic response analysis in this way, the significance levels must be chosen carefully. As shown in Figure 7, the use of inappropriate significance levels could result in a low probability of correct assessment over a certain range of population sizes. Such a loss in power can be avoided by the appropriate choice of significance levels, given the number and precision of the population estimates, as shown by the curve with open circles in Figure 7.

The general features of the sensitivity of dynamic response analysis reported

in this paper do not depend on the specific nature of the density-dependent response of the population. As emphasized by Goodman (1988), dynamic response analysis makes only a few assumptions about the density-dependent dynamics of a population, and these assumptions are almost certainly satisfied by an actual population. The simulations reported here used the logistic model as a specific example. The results therefore show a decline in power near the logistic MNPL of 0.5, but this decline is expected to occur wherever the MNPL happens to fall for a specific population. Fowler (1981) has argued that for large mammals, the MNPL occurs at a population size which may be near the carrying capacity, whereas for fish, the MNPL will be a smaller fraction of  $K$ . In other words, the yield curve may be skewed to the left or right. One of the strengths of dynamic response analysis is that it does not attempt to estimate the actual MNPL or the shape of the yield curve, but only to answer the qualitative question at hand: whether the population is above or below the MNPL.

Although it does not matter to dynamic response analysis whether the yield curve is symmetric or not, the "peakedness" of the curve will determine how wide the decline in power of the analysis near the MNPL will be. This is because it is the slope of the curve that dynamic response analysis is trying to estimate. If the yield curve has a sharp peak, it will be relatively easy to tell whether the population is on one side or the other. On the other hand, if the yield curve is rather flat-topped, so that the growth rate of the population changes little in response to population size, the effective MNPL is indistinct. This latter situation will reduce the accuracy of dynamic response analysis near the MNPL, but for the same reason it will make the biological consequences of this inaccuracy less important.

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#### LITERATURE CITED

- BEASOM, S. L. 1979. Precision in helicopter censusing of white-tailed deer. *Journal of Wildlife Management* 43:777-780.
- BEST, P. B. 1981. The status of right whales (*Eubalaena glacialis*) off South Africa, 1969-1979. South Africa Sea Fisheries Institute Investigational Report 123:1-44.
- BOVENG, P., D. P. DEMASTER AND B. S. STEWART. 1988. Dynamic response analysis. III. Application to four northern elephant seal colonies. *Marine Mammal Science* 4: 210-222.
- BREIHWICK, J. M., L. L. EBERHARDT AND H. W. BRAHAM. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). *Canadian Journal of Fisheries and Aquatic Sciences* 41:484-496.
- COOPER, C. F., AND B. S. STEWART. 1983. Demography of northern elephant seals, 1911-1982. *Science* 219:969-971.

- EBERHARDT, L. L. 1981. Population dynamics of the Pribilof fur seals. Pages 197-220 in C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. Wiley & Sons, New York.
- EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183-190.
- ESTES, J. A., AND J. R. GILBERT. 1978. Evaluation of an aerial survey of Pacific walrus (*Odobenus rosmarus divergens*). Journal of the Fisheries Research Board of Canada 35:1130-1140.
- FOWLER, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602-610.
- GERRODETTE, T. 1987. A power analysis for detecting trends. Ecology 68:1364-1372.
- GOODMAN, D. 1988. Dynamic response analysis. I. Qualitative estimation of stock status relative to maximum net productivity level from observed dynamics. Marine Mammal Science 4:183-195.
- HARRIS, R. B. 1986. Reliability of trend lines obtained from variable counts. Journal of Wildlife Management 50:165-171.
- KASUYA, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Scientific Reports of the Whales Research Institute 28:73-106.
- LAWS, R. M., I. S. C. PARKER AND R. C. B. JOHNSTONE. 1975. Elephants and their habitats. Clarendon Press, Oxford.
- LEATHERWOOD, S., J. R. GILBERT AND D. G. CHAPMAN. 1978. An evaluation of some techniques for aerial censuses of bottlenosed dolphins. Journal of Wildlife Management 42:239-250.
- LERESCHE, R. E., AND R. A. RAUSCH. 1974. Accuracy and precision of aerial moose censusing. Journal of Wildlife Management 38:175-182.
- PAYNE, M. R. 1977. Growth of a fur seal population. Philosophical Transactions of the Royal Society of London, Series B 279:67-79.
- REILLY, S. B. 1984. Observed and maximum rates of increase in gray whales, *Eschrichtius robustus*. Pages 389-399 in W. F. Perrin, R. L. Brownell, Jr. and D. P. DeMaster, eds. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission, Special Issue 6.
- REILLY, S. B., AND J. BARLOW. 1986. Rates of increase in dolphin population size. Fishery Bulletin (U.S.) 84:527-533.
- REILLY, S. B., D. W. RICE AND A. A. WOLMAN. 1983. Population assessment of the gray whale, *Eschrichtius robustus*, from California shore censuses, 1967-80. Fishery Bulletin (U.S.) 81:267-281.
- SMITH, T. D. 1981. Line-transect techniques for estimating density of porpoise schools. Journal of Wildlife Management 45:650-657.

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