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MARINE MAMMAL SCIENCE, 4(3):210–222 (July 1988)

DYNAMIC RESPONSE ANALYSIS. III. A CONSISTENCY FILTER AND APPLICATION TO FOUR NORTHERN ELEPHANT SEAL COLONIES

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ABSTRACT

Dynamic response analysis, a technique for determining stock size relative to the maximum net productivity level (MNPL), was applied to northern elephant seal populations from the South Farallon Islands, Año Nuevo Island, San Nicolas Island and San Miguel Island. Pup counts were used as indices of population size. The application of dynamic response analysis presented here involved some methodological innovations. We present a moving interval method which involves calculating separate dynamic response analyses for intervals of various lengths ranging from four counts to the total number available for the colony. The sign of the second order polynomial regression coefficient computed from a particular interval was used to indicate the colony's apparent status (relative to its MNPL; + = above MNPL, − = below MNPL) on that interval. Consistency in the sign of the second order coefficient, as the interval was moved along the trajectory, was used to determine the minimum reliable interval size. Each colony exhibited growth similar to that of a population below its MNPL. These results are consistent with recent natural history observations at San Nicolas, San Miguel and the South Farallon islands. Natural history observations at Año Nuevo Island suggest that the colony there is now at equilibrium. Thus, if our results from dynamic response analysis of the Año Nuevo colony are correct, it appears that the MNPL may be close to the carrying capacity for these animals.

Key words: dynamic response analysis, *Mirounga angustirostris,* maximum net productivity level, population dynamics, stock assessment.

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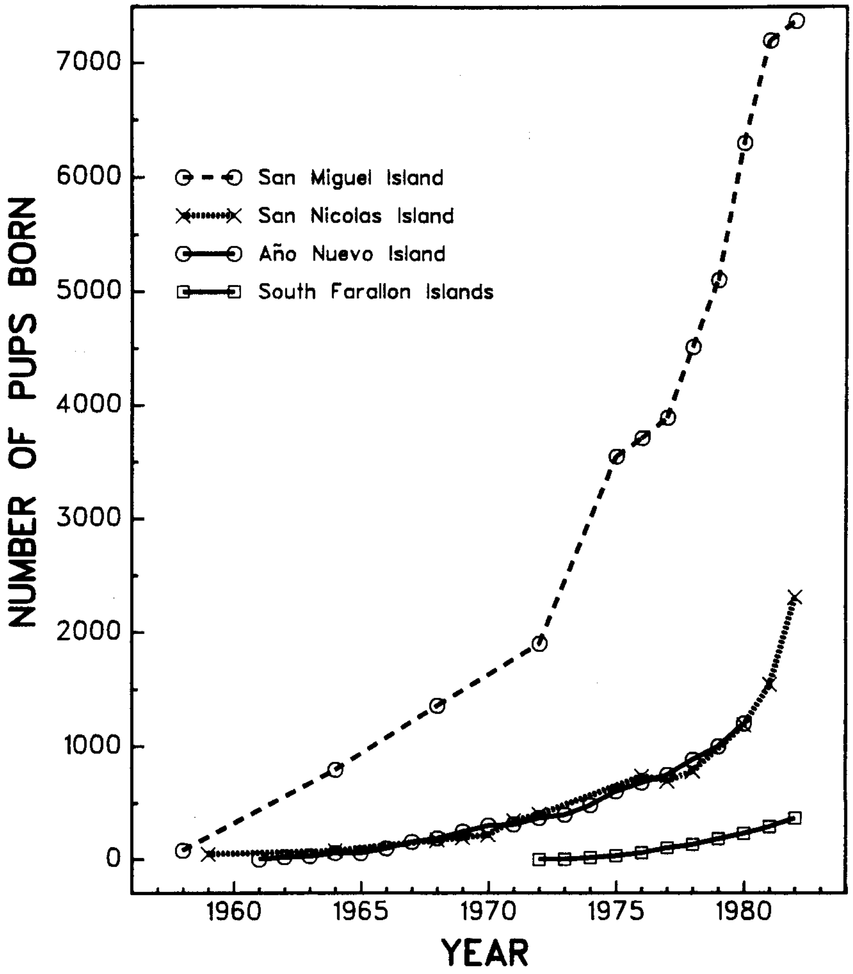

Figure 1. Numbers of northern elephant seal pups born on San Miguel, San Nicolas, Año Nuevo and Southeast Farallon islands. Literature sources of the censuses are cited in the text.

Dynamic response analysis is a technique for assessment of the size of a stock relative to its maximum net productivity level (MNPL). The theory and derivation of the dynamic response method are presented by Goodman (1988). Gerrodette (1988) evaluated the performance of the method when applied to simulated unharvested populations. This study is an application of dynamic response analysis to census data from colonies of northern elephant seals (*Mirounga angustirostris*).

The form of a dynamic response analysis depends on whether the population is harvested and how far the population is from equilibrium (Goodman 1988). Here we use the dynamic response method to analyze four elephant seal colonies (Fig. 1), which have been unharvested, and growing rapidly, since recolonization several decades ago (*e.g.,* Le Boeuf 1977, Antonelis *et al.* 1981, Cooper and Stewart 1983). As it is unlikely that carrying capacity for these populations is expanding in this fashion, the rapid, steady growth suggests that the colonies have not yet reached their equilibrium densities.

Unharvested populations such as these, in a constant environment, will have growth rates which increase over time when the densities are below MNPL, producing trajectories of population size that are concave upward. Growth in the range of densities above MNPL will produce trajectories which are concave downward. These characteristic shapes imply that for an unharvested population growing from low initial density, a dynamic response analysis is equivalent to determining whether the trajectory of population levels is concave upward, concave downward, or not significantly curved. This determination can be accomplished by fitting the trajectory to a nonlinear model (*e.g.,* by polynomial regression) and testing the appropriate fitted parameters.

To make the determination as relevant as possible to the present state of the population (for management purposes), only recent censuses should be used. On the other hand, it is important to base the determination on curvature in the trajectory which is due to density dependent changes in the population growth rate, rather than apparent curvature due to environmental variation or census inaccuracy, so the number of censuses must not be too small. The values for parameters which Gerrodette (1988) used to determine census requirements (model for growth, level of census precision and amount of environmental variation) are unknown for the elephant seal population. Therefore, we present a method which uses the variation in the entire trajectory to estimate the minimum number of the recent censuses which need to be included for a reliable assessment. The recent status of the population relative to its MNPL is then determined from the curvature in the interval spanned by this minimum number of most recent censuses.

METHODS

Statistical approach—We computed multiple linear regressions of pups born versus time and that time squared. The regressions were calculated for intervals ranging from four censuses to the total number of censuses available for that colony. For each interval size, the intervals were moved along the trajectory in steps, at each step adding a more recent census, discarding the oldest census, and computing the regression. Thus, for n total points available, and an interval size of k points, there would be $n - k + 1$ separate regressions.

Each regression is a least squares fit to a second degree polynomial. This model was chosen because the direction of concavity is determined simply by the sign of the second order coefficient. A significantly positive second order term means the census interval is concave upward; a significantly negative second order term means the concavity is downward; and a second order term not significantly different from zero means the interval cannot be distinguished from a linear trajectory. A coefficient was taken to be significantly positive if it was more than two standard errors (Sokal and Rohlf 1981, p. 636) greater than

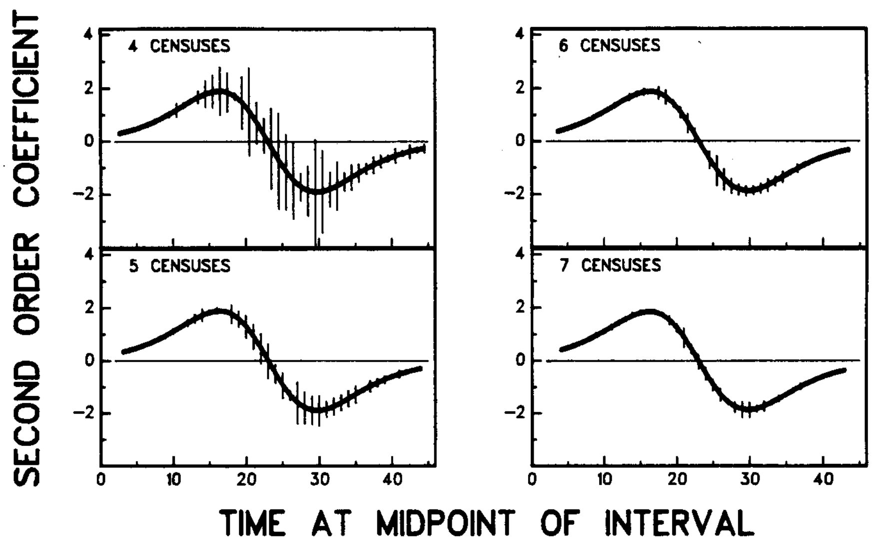

Figure 2. Second order regression coefficients computed from a hypothetical logistic population trajectory using intervals of from 4 to 7 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus two or minus standard errors of the coefficients.

zero, and negative if more than two standard errors less than zero. All other values were considered not significantly different from zero.

The $(n - k + 1)$ second order coefficients for a given value of k (number of censuses per interval) were plotted against the times of the midpoints of the respective census intervals. We interpreted the results on the basis of the expected qualitative form of a plot of second order regression coefficients from a density dependent growth curve with no environmental variation and no census error. Figure 2 shows plots of the second order regression coefficients obtained by applying our moving interval method to a hypothetical, deterministic population trajectory generated from the well known logistic model. When population size is small, the regression coefficients are positive, reflecting the upward concavity in the growth curve; as population size increases, the regression coefficients decrease and become indistinguishable from zero when the population reaches MNPL; finally, the coefficients take on negative values at population sizes above MNPL.

The details of the shapes of the curves in Figure 2 are dependent on the logistic model used to generate the hypothetical trajectory. For dynamic response analysis, the important (and more general) feature of this expected form is that the curve formed by the coefficients crosses zero only once as the population grows from low density to equilibrium. This feature is not model dependent. Deviations from this form in the plots of regression coefficients computed from real trajectories will indicate that the regressions are revealing local curvature which is due to processes other than density dependent growth from a condition below carrying capacity in a constant environment.

In practice, we need to find the smallest interval size which yields a plot of second order coefficients that does not exhibit the features of responding mainly to environmental noise or census error. In other words, the curve formed by the second order coefficients should cross the zero line a maximum of one time and in a prescribed direction. The minimum interval size which still allows for statistical tests in a second degree polynomial model (three parameters) is four censuses. If the second order coefficients based on intervals of four censuses cross the zero line more than once, the interval size is increased to five counts, and so on until the curve formed by the coefficients crosses the zero line either once, or not at all.

The vertical bars in Figure 2 represent plus or minus two estimated standard errors of the regression coefficients. Because there was no environmental variation or census error in the underlying logistic model, these error bars represent uncertainty in the regression coefficients introduced by using a quadratic polynomial to fit portions of a logistic curve. The uncertainty is substantial with four censuses per interval but diminishes rapidly when five or more censuses are used. By using the quadratic model in "local" analyses of the shapes of portions of the trajectory, we avoid the need to assume a specific model for the entire trajectory which would put constraints on the location of the MNPL (Goodman 1988).

In a sensitivity analysis of the dynamic response method, Gerrodette (1988) showed that a two-step procedure (testing the significance of a linear regression on the census interval and then testing for curvature with a polynomial regression only if the linear slope was significantly positive) gave higher proportions of correct determinations over a broad range of population sizes than simply considering the direction of curvature. This two-step procedure was not used in the stage of our method where we determined the correct number of censuses to use based on plots of second order terms. However, for making the decision about status relative to the MNPL, we tested for a significantly positive slope of a linear regression on those censuses prior to evaluating the direction and significance of the curvature.

Data set—Because dynamic response analysis depends on the shape of the population trajectory, rather than the actual population size, an index which is approximately a scalar multiple of total population size will suffice (Goodman 1988). We used published counts of northern elephant seal pups born at four rookeries (Fig. 1) as indices of population sizes. The 11 pup counts from the South Farallon Islands are from Huber *et al.* (1983). There are 20 published counts from Año Nuevo Island (Orr and Poulter 1965, Radford *et al.* 1965, Rice *et al.* 1965, Le Boeuf and Briggs 1977, Le Boeuf and Bonnell 1980, Reiter *et al.* 1981). The 13 counts from San Nicolas Island are from Bartholomew and Boolootian (1960), Odell (1971, 1974), Antonelis *et al.* (1981), Le Boeuf (1977), Le Boeuf and Bonnell (1980) and Stewart and Yochem (1984). The 12 counts from San Miguel Island are from Bartholomew and Boolootian (1960), Odell (1974), Le Boeuf (1977), Antonelis *et al.* (1981), Mate (1977), Le Boeuf and Bonnell (1980), Bonnell *et al.* (1980) and Cooper and Stewart (1983). Cooper and Stewart (1983) estimated the per capita growth rates to be 0.136 at San Miguel Island, 0.165 at San Nicolas Island, 0.158 at Año Nuevo Island, and 0.533 at the Farallons (the latter rate was attributed mostly to immigration).

We assume that the proportion of pups in the total population is constant. This constancy of age structure is not likely in a population growing under density dependence. In simulations of growth of closed populations, Birkson and DeMaster (1985) evaluated the practical reliability of pup counts as population indices and found slight biases, the directions of which depend on whether the pup census precedes or follows a period of density dependent survival. Elephant seal pup mortality between birth and weaning appears to be density dependent (Reiter *et al.* 1981, Huber *et al.* 1983). According to Birkson and DeMaster (1985), this implies that the population should reach its MNPL before the pup trajectory would indicate that the MNPL had been reached. However, the probability of a pregnant female hauling out to pup on a particular island may be density dependent as well (Reiter *et al.* 1981). Thus, there may be density dependent processes both preceding and following the censuses used in this study and the resulting direction of bias cannot be predicted.

In light of the considerable importance of immigration by breeding age animals contributing to growth of some elephant seal colonies (*e.g.*, Huber *et al.* 1983), there is a further disturbance of age structure. For lack of reliable adult censuses, the degree of deviation from the stable age distribution is unknown. For purposes of exploring the methodology, we have proceeded with this data set as if the proportionality assumption were met, but for the purpose of conducting an actual assessment of the elephant seal populations, the problem of age structure would require further examination.

We have used the terms 'colony' and 'population' interchangeably. We recognize that the breeding colonies are probably not distinct populations, but we assume that the density dependent responses to growth by reproduction and by immigration combine in such a way that the production curve (dN/dt *vs.* N) is smoothly unimodal over the region of interest and that it correctly reflects the implicit concerns of status assessment under the Marine Mammal Protection Act (MMPA).

The method we present can absorb year-to-year variation or "noise" in the environment but not long-term systematic environmental change. Therefore, we assume that the MNPL has maintained a stationary mean (though not that the MNPL was necessarily constant) during the time spanned by the censuses.

RESULTS

Figures 3–6 show series of plots of the second order regression coefficients computed from various sizes of census intervals for each colony. These plots were compared to the expected qualitative form (*e.g.*, that of plots in Fig. 2) to determine the appropriate number of censuses to use for the dynamic response analyses.

Año Nuevo Island—When an interval of four censuses is moved along the Año Nuevo trajectory, the second order regression coefficient computed at each

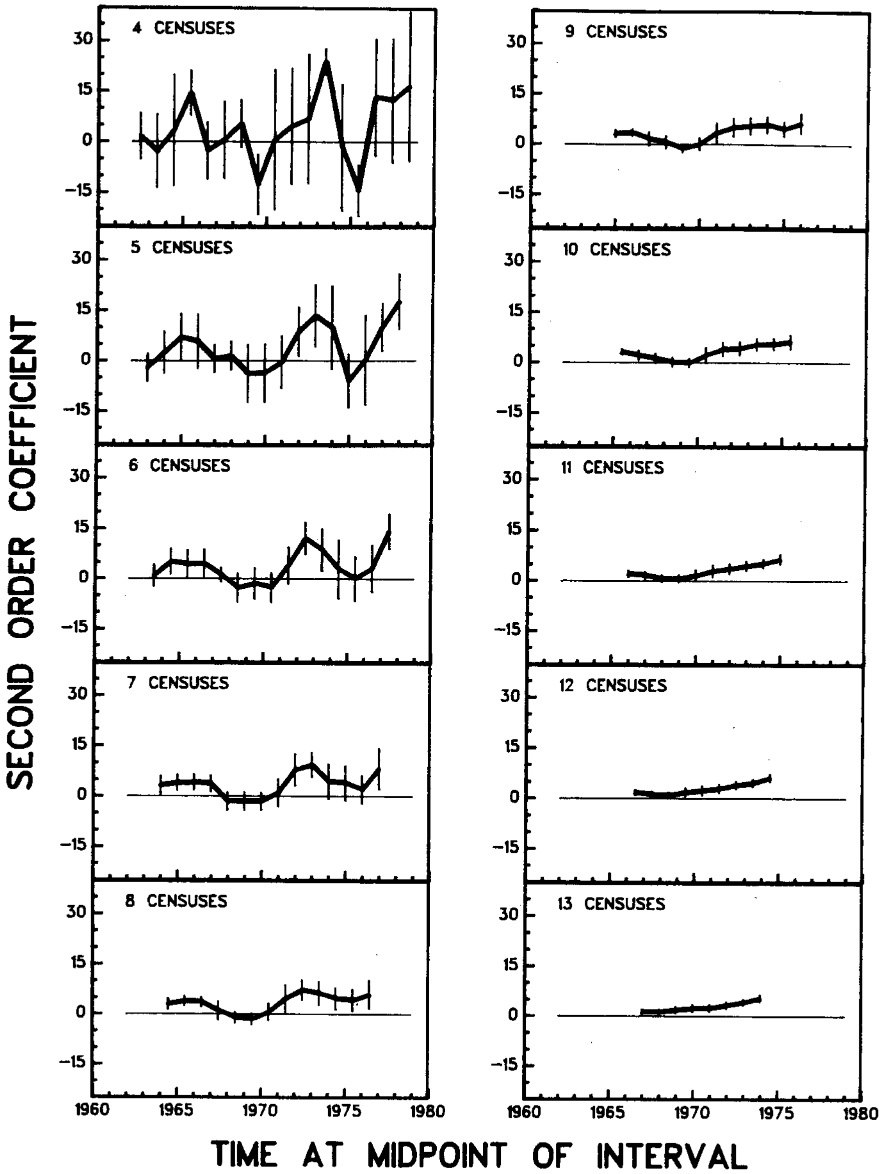

Figure 3. Second order regression coefficients computed from the Año Nuevo Island pup count trajectory using intervals of from 4 to 13 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus or minus two standard errors of the coefficients.

step fluctuates over a broad range of positive and negative values (Fig. 3). This variation in the curvature suggests that intervals of four censuses are insufficient for distinguishing between curvature due to density dependence and that due to environmental variation or census error.

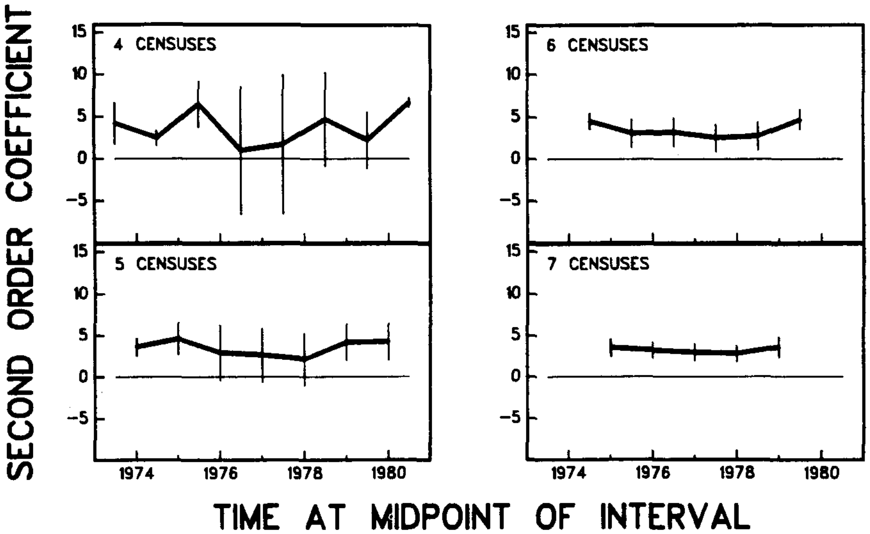

Figure 4. Second order regression coefficients computed from the Farallon Islands pup count trajectory using intervals of from 4 to 7 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus or minus two standard errors of the coefficients.

Using intervals ranging in size from 5 to 11 censuses, at Año Nuevo, reduces the variation in the curvature; but in every case, the second order coefficients drop from positive to zero and then become positive on the most recent intervals (Fig. 3). Only when 12 or more points are included are the coefficients consistent with our requirement that the plot of the coefficients cross zero either once or not at all, leading us to conclude that 12 is the minimum number of censuses required for a reliable assessment of the Año Nuevo Island colony.

South Farallon Islands—When four or five censuses are used in regressions on the South Farallon Island pup counts, the coefficients fluctuate between positive values and values which are not distinguishable from zero (Fig. 4). Using intervals of six censuses results in second order coefficients which are all positive and we conclude that we must use at least six censuses for an assessment of this colony.

San Nicolas Island and San Miguel Island—For San Nicolas Island (Fig. 5), the minimum number of censuses providing an unambiguous result is nine. For San Miguel Island (Fig. 6), the minimum number is eight.

Having chosen the appropriate sequence of pup counts for each colony, the actual dynamic response analysis consists of testing the significance of the slope and curvature (Table 1) of the relationship between numbers of pups born and time. The slope coefficients from the linear regressions in Table 1 are significantly greater than zero for all four colonies, reflecting genuine increases in the sizes of the colonies with time. This is a condition which can occur when population sizes are above or below MNPL, so the direction and degree of curvature must be considered to make the determination (Gerrodette 1988). The second order

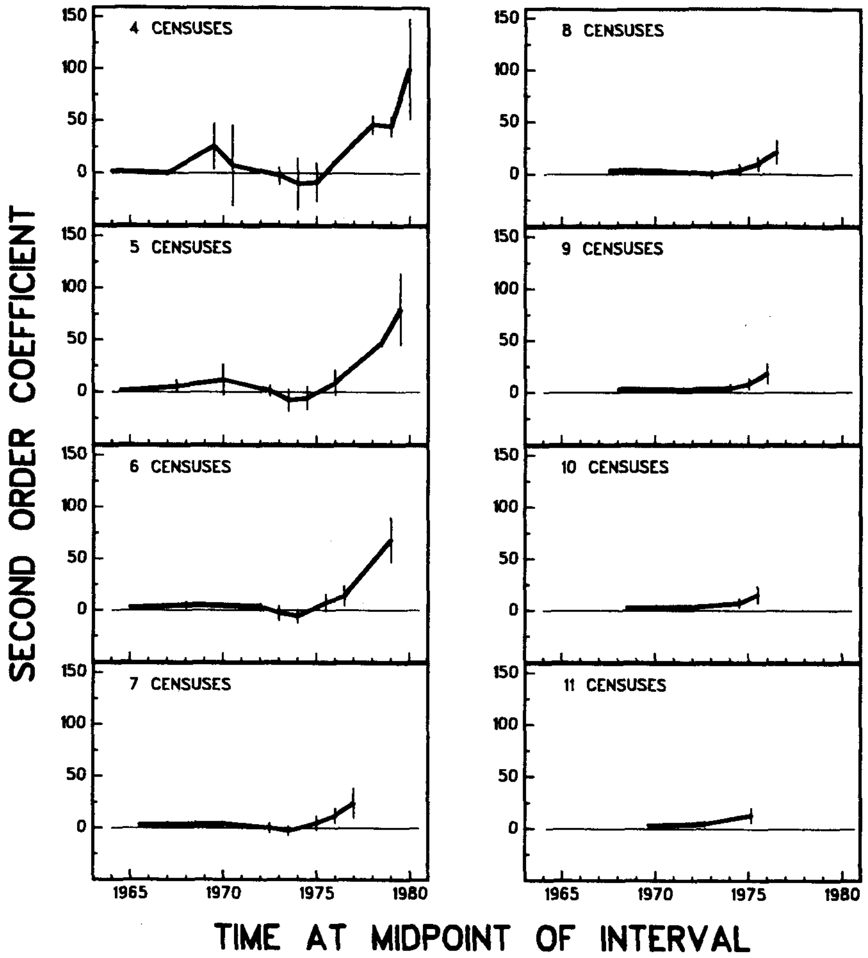

Figure 5. Second order regression coefficients computed from the San Nicolas Island pup count trajectory using intervals of from 4 to 11 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus or minus two standard errors of the coefficients.

coefficients in Table 1 are all greater than zero (at significance levels of 10% or less), reflecting upward curvature in the trajectories. We conclude that all four colonies exhibited growth, on the selected census intervals, like populations below their respective MNPLs.

Discussion

Gerrodette (1988) presented an example of how the decision process of dynamic response analysis could be formalized statistically for a particular set of assumptions about a model for growth, variability in the environment and census uncertainty. Although the method we present could also be cast in terms

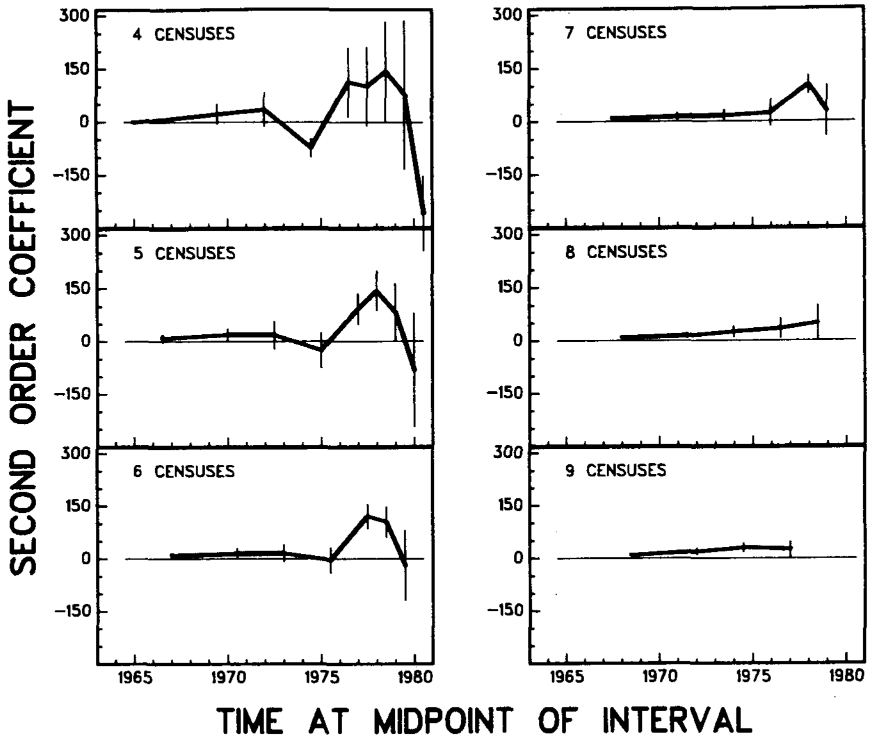

Figure 6. Second order regression coefficients computed from the San Miguel Island pup count trajectory using intervals of from 4 to 9 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus two or minus standard errors of the coefficients.

Table 1. Results from separate linear and second degree polynomial regressions of pups born on time since breeding began, in years. The census interval was chosen by the moving interval method described in the text.

Colony	Census interval	Number of censuses	Linear regression coefficient (std. error)	2nd order regression coefficient (std. error)
Año Nuevo	1969–1980	12	+82.8*** (6.33)	+6.27*** (0.63)
S. Farallons	1977–1982	6	+52.6*** (3.55)	+4.75*** (0.59)
San Nicolas	1970–1982	9	+134*** (25.6)	+18.2** (4.96)
San Miguel	1975–1982	8	+619*** (61.6)	+51.8* (24.4)

Two-tailed Student's t-tests of the hypothesis: coefficient = 0.
*** $P < .01$; ** $P < .05$; * $P < .10$.

of a statistically formal decision process, we attempted simply to minimize the probability of making an incorrect decision, subject to the constraint that the decision should be as current as the data allow.

Our final census intervals, ranging in size from six counts at the South Farallons to 12 counts at Año Nuevo, are similar to the requirements that Gerrodette (1988) found in his simulations (at least 10 censuses for probability of a correct decision to be generally greater than about 0.7). The relative smoothness of the curves in Figure 1 suggests that elephant seal pup counts may be less variable than census data for most species of marine mammals. If so, the data requirements for other species will probably be more stringent.

Recent data from San Nicolas and San Miguel islands (Stewart, unpublished data) and the Farallon Islands (H. Huber, personal communication) are consistent with our conclusion that these colonies are below their MNPLs. Condit and Le Boeuf (1983), however, suggested that the Año Nuevo colony had reached an equilibrium level in 1983 of approximately 1,000 breeding females and predicted that the colony would fluctuate around that level depending on environmental conditions.

The apparent inconsistency between these independent assessments of the status of the Año Nuevo colony draws attention to the trade-off associated with being certain versus being current. We note that increasing the number of censuses in the regression interval reduces the variation in the second order coefficients, but the midpoint of the most recent interval recedes into the past (*e.g.*, Fig. 3). In other words, the assessment becomes less current as more censuses are included. Thus, including 12 censuses in the regressions on Año Nuevo pup counts effectively centers the most recent assessment around 1975, even though we used censuses from Año Nuevo which were made as recently as 1980.

We consider it plausible that a colony such as Año Nuevo might progress from a level below MNPL to equilibrium in a span of about six to eight years. This would suggest that the MNPL was very close to the carrying capacity. In that case, the production curve (dN/dt *vs.* N) would have a peak shifted far to the right (Eberhardt and Siniff 1977, Fowler 1981).

The primary mechanism of density dependent change in the rate of pups born at Año Nuevo is, apparently, limited space on the island for pregnant females to haul-out and give birth (Condit and Le Boeuf 1983). If this is the primary density dependent mechanism at San Nicolas and San Miguel islands, then these colonies may be far below their respective MNPLs and carrying capacities. However, if other density dependent mechanisms (*e.g.*, competition for limited food resources) are operating at these colonies, then MNPLs (and carrying capacities) may be reached before breeding space becomes limiting.

An actual application of dynamic response analysis of population status relative to the MNPL involves a trade-off between the desire to use many censuses for accuracy and the desire to make decisions which are current, and thus based on fewer counts. Our method for choosing an appropriate number of censuses resolves this trade-off by requiring consistency with assumptions about density dependent population growth.

Analysis of the selected census intervals showed that all four colonies were below their respective MNPLs. This conclusion is consistent with independent observations of the conditions of the colonies at the South Farallon Islands, San Nicolas Island and San Miguel Island. However, other studies have suggested that the Año Nuevo Island colony has already reached equilibrium density. The disparity between these results might be reconciled in terms of the time lag between the center of the interval (1975) upon which the dynamic response estimate is based and the apparent time of attainment of equilibrium (1983). This explanation implies a very rapid transition from MNPL to carrying capacity, which however, is consistent with some other speculations about density dependent growth in long-lived animals.

ACKNOWLEDGMENTS

We thank Daniel Goodman for thorough critiques of several drafts. Tim Gerrodette, Jay Barlow, Paul Wade and anonymous reviewer no. 2 provided very helpful comments. This work was supported in part by National Marine Fisheries Service contract 84-ABC-00173.

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Received: June 3, 1986
Accepted: January 4, 1988