# Dynamic response analysis for the eastern North Pacific gray whale population: an alternative approach ${ }^{1}$ 

D.S. Butterworth*, D.L. Borchers** and A.E. Punt**<br>Contact e-mail: dll@maths.uct.ac.za


#### Abstract

Gerrodette and DeMaster (1990) conclude that dynamic response analysis indicates that the gray whale population passed through its maximum net productivity level (MNPL, approximately equivalent to MSY level) between 1967 and 1980. Their conclusion is examined using models for population trends which permit a point of inflection; these are fitted globally to the time series of census estimates available up to 1987-88. A cubic and a logistic model are used. The cubic model results indicate with almost $100 \%$ confidence that the population passed through MNPL within two years of 1973-74. However, both this conclusion and that of Gerrodette and DeMaster are considered to be unreliable. This is because the curves fitted by both analyses correspond to markedly decreasing population sizes over parts of the periods to which they apply. This is inconsistent with plausible population dynamics behaviour, which is itself an underlying pre-requisite for dynamic response analysis methodology. A suggestion is made as to how applications of dynamic response analysis methodology such as that of Boveng et al. (1988) could be adapted to ensure the necessary respect of such constraints. Results of a parametric bootstrap procedure for confidence interval estimation applied to the logistic model indicate that the probability that the population passed through MNPL during the period of the censuses is not large. The census data are scarcely adequate to allow for reliable estimates of the curvature of the population trajectory to be made. The logistic model dynamic response analysis indicates that there is a somewhat greater likelihood that the gray whale population was below rather than above its MNPL in 1990, given the data available at the time.


KEYWORDS: ASSESSMENT; MODELLING; TRENDS; GRAY WHALE; NORTH PACIFIC

## INTRODUCTION

Dynamic response analysis (Boveng et al., 1988; Gerrodette, 1988; Goodman, 1988) is an appealingly simple approach for determining whether a population is above or below its maximum net productivity level (MNPL). This is particularly so in the case of the eastern North Pacific gray whale population. The alternative method of making this determination - fitting simple population models using historic catch data - leads to inconsistencies (e.g. Cooke, 1986; Lankester and Beddington, 1986). In addition, the application of such population models requires some restrictive assumptions, such as time-invariance of carrying capacity (whose violation may perhaps be the reason for the inconsistencies that arise in the simple model fits for the gray whale population - Butterworth et al., 2002). Dynamic response analysis has the advantage that such an assumption is not necessary.

Gerrodette and DeMaster (1990) point out that MNPL is not the same as MSY level (MSYL), which is a function of the sex and age-composition of the harvest. However, the difference in the case of the eastern North Pacific gray whale population is not likely to be large. The question of whether this population is above or below its MSYL has been of particular relevance in IWC Scientific Committee debates about the likely values of MSY rate (MSYR) for baleen whales. If this population is now above MSYL, then the increase rate of $3.2 \%$ per annum (IWC, 1993) evident from preceding censuses (see Table 1b), coupled with the size of the catch over that period (see Table 2), provides an estimated lower bound of some $4 \%$ for MSYR (expressed in terms of total population); however, if the population is still below MSYL, no such bound can be inferred.
${ }^{1}$ A version of this paper was originally presented in 1990.

Gerrodette and DeMaster (1990) present results of an application of dynamic response analysis to the eastern North Pacific gray whale population. The particular methodology they use is that of Boveng et al. (1988), which involves plotting a time series of the second-order coefficients of quadratics (i.e. local curvature estimates) fitted to sequences of censuses of lengths from 6-11 years. They apply this method to the annual census data from 1967-68 to 1979-80 reported in Reilly et al. (1983), shown in Table 1a. They go on to report that the pattern of these coefficients (although few of them are individually significantly different from zero) is indicative of a population that was below MNPL in 1967, but above MNPL by 1980 .

Our particular concern is to apply dynamic response analysis to these data in a manner that allows for an easier evaluation of the statistical confidence that can be placed in the Gerrodette-DeMaster conclusion. To this end functions have been fitted which permit a point of inflection to the complete time series of censuses, instead of estimating successive local curvature values and seeing whether these pass through zero. Goodman (1988) mentions this approach, which he terms 'global fitting', but raises two associated problems. First, the range of the data may be inadequate for secure estimation of all the parameters of this global function - for this reason, the parameterisations used in this paper are kept as parsimonious as possible. Secondly, he cautions about possible lack of fit (model mis-specification), with attendant distortion of parameter estimates and their implications. The average of the standard deviations (SDs) of the 13 census estimates in Reilly et al. (1983) is 1,586 (see Table 1a); this compares with an estimated residual SD of 1,536 for an (unweighted) linear regression fitted to these data. If these data contained precise information on complex details of shape, the latter SD would be much higher than the

[^0]Table 1
Gray whale census estimates and SEs. See note in text concerning the SE estimates listed in (b).

| (a) Reilly et al. (1983) |  |  |  | (b) Buckland and Breiwick (2002) ${ }^{1}$ |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Year | Estimate | SE |  | Year | Estimate | SE |
| $1967-68$ | 13,095 | 1,276 |  | $1967-68$ | 13,012 | 879 |
| $1968-69$ | 11,954 | 1,545 |  | $1968-69$ | 12,244 | 461 |
| $1969-70$ | 12,408 | 1,619 |  | $1969-70$ | 12,777 | 502 |
| $1970-71$ | 11,177 | 1,625 |  | $1970-71$ | 11,170 | 795 |
| $1971-72$ | 10,414 | 918 |  | $1971-72$ | 9,841 | 426 |
| $1972-73$ | 14,534 | 1,348 |  | $1972-73$ | 16,962 | 629 |
| $1973-74$ | 14,676 | 1,558 |  | $1973-74$ | 14,817 | 566 |
| $1974-75$ | 13,110 | 1,366 |  | $1974-75$ | 13,134 | 516 |
| $1975-76$ | 15,919 | 1,803 |  | $1975-76$ | 14,811 | 667 |
| $1976-77$ | 16,621 | 1,798 |  | $1976-77$ | 15,950 | 489 |
| $1977-78$ | 14,811 | 2,272 |  | $1977-78$ | 17,127 | 944 |
| $1978-79$ | 13,676 | 1,127 |  | $1978-79$ | 13,300 | 476 |
| $1979-80$ | 17,577 | 2,364 |  | $1979-80$ | 16,581 | 659 |
|  |  |  |  | $1984-85$ | 21,942 | 960 |
|  |  |  |  | $1985-86$ | 20,450 | 685 |
|  |  |  |  | $1987-88$ | 21,113 | 641 |

${ }^{1}$ The values listed above, which were used for the calculations of this paper, were taken from an earlier version of Buckland and Breiwick (2002). There are minor changes to these values in the final version of that paper published in this volume, but the effect of these on the results reported in this paper is negligible.

Table 2
Annual gray whale catches during the period of censuses.
Source: C. Allison, IWC (pers. comm., 16 Jan. 1990).

| Year | Catch |  | Year | Catch |
| :---: | :---: | :---: | :---: | :---: |
| 1967 | 250 |  | 1978 | 184 |
| 1968 | 201 |  | 1979 | 183 |
| 1969 | 214 |  | 1980 | 181 |
| 1970 | 151 |  | 1981 | 136 |
| 1971 | 153 |  | 1982 | 168 |
| 1972 | 182 |  | 1983 | 171 |
| 1973 | 178 |  | 1984 | 169 |
| 1974 | 184 |  | 1985 | 170 |
| 1975 | 171 |  | 1986 | 171 |
| 1976 | 165 |  | 1987 | 159 |
| 1977 | 187 |  | 1988 | 151 |

former; their near equality suggests that model mis-specification is unlikely to be a problem for the analyses of these data that follow.

This paper considers global fits of cubic and logistic functions to the time series of gray whale census estimates up to 1987-88. Confidence intervals (CIs) relating to the year in which the population trajectory shows a point of inflection ( $y^{*}$, corresponding to MNPL) are determined by linear model and (Monte Carlo) parametric bootstrap methods respectively for these two functions. The results are used to assess the statistical confidence which can be placed in the Gerrodette-DeMaster conclusion that dynamic response analysis indicates that the population passed through MNPL between 1967 and 1980.

## DATA AND METHODOLOGY

The gray whale census estimates used in the analyses that follow are given in Table 1. Table 1a lists the estimates reported in Reilly et al. (1983) for the period 1967-68 to 1979-80. These are the data that were used by Gerrodette and DeMaster (1990) in their application of dynamic response analysis. It is therefore appropriate to use this same set for the alternative analyses which follow to re-examine their conclusion. Censuses have been conducted subsequent to 1979-80, and the data from these and the earlier years have
been re-analysed by Buckland and Breiwick (2002). Table 1 b lists Buckland and Breiwick's 'adjusted abundance' estimates for the period 1967-68 to 1987-88; applications of the global fitting methods of this paper to this longer period have all used this more recent dataset.

Note that the standard error (SE) estimates in Table 1b differ slightly from those given in Buckland and Breiwick (2002). This is because the latter error estimates include a common contribution reflecting the variance of the multiplicative factor used by Buckland and Breiwick to convert 'relative abundance' to 'adjusted abundance' estimates. This variance contribution has not been included in the error estimates reported here. The reason is that (as discussed below) the analysis methods to be used in this paper are concerned only with population trajectory shape, not scale, so that the variance of the multiplicative factor is not relevant to the analyses which utilise the SE information.
The gray whale catches during the period of the censuses are listed in Table 2. These data were provided by C. Allison (IWC) and contain some very minor amendments to those reported in Lankester and Beddington (1986).

Strictly, dynamic response analysis involves determination of the population size corresponding to maximum production. This will not in general correspond to the size at which the population trajectory shows a point of inflection, because the annual harvest, as well as the change in population size, has to be taken into account in assessing production; equivalence occurs only if the annual harvest is constant. The annual gray whale catch over the 1967-88 period has been remarkably steady (mean 176; SD only 23). The greatest deviations of the catch from this mean are +74 and -40 , which are insubstantial in the context of the SEs of the population estimates in Table 1. The analyses of this paper have thus ignored the effects of variations in the annual harvest, thereby reducing the problem to one of estimating the year in which the gray whale population trajectory shows a point of inflection. An advantage of this approach is that it requires only that the population censuses reflect relative (and comparable) indices of population size, rather than unbiased estimates of absolute abundance.

The simplest polynomial function which can show a point of inflection in the trend of relative abundance $(N)$ with time/year $(y)$ is the cubic:

$$
\begin{equation*}
N_{y}=a_{0}+a_{1} y+a_{2} y^{2}+a_{3} y^{3} \tag{1}
\end{equation*}
$$

for which this inflection occurs at time:

$$
\begin{equation*}
y^{*}=-a_{2} /\left(3 a_{3}\right) \tag{2}
\end{equation*}
$$

The particular advantage of fitting such a trend model to the census estimates is that it is linear in its parameters. The assumptions of independence and error distribution normality then allow standard linear model theory to be used to provide parameter estimates and the associated SEs. This applies both to the case when all the censuses considered are given equal weight in the fitting process and when each census is weighted by the inverse of the square of its estimated SE. The SE estimate for $y^{*}$ is of particular interest and is a non-linear function of the model parameters. Nevertheless, this error estimate can be readily calculated using the delta method approximation, applied using the parameter variance and covariance estimates provided by standard packages which perform linear model fits.

A disadvantage of the cubic of equation (1) is that four parameters need to be estimated, with a consequent possible loss of estimation precision. A more parsimonious approach
(with one less parameter) was therefore attempted by fitting the logistic model to the census time series. To avoid problems with statistically unstable parameter estimates, Schnute's (1981) parameterisation of the logistic curve was used for this purpose:

$$
\begin{equation*}
N_{y}=\left[N_{1}^{b}+\left(N_{2}^{b}-N_{1}^{b}\right) \frac{1-e^{-a\left(y-y_{1}\right)}}{1-e^{-a\left(y_{2}-y_{1}\right)}}\right]^{1 / b} \tag{3}
\end{equation*}
$$

i.e. four parameters $a, b, N_{1}=\hat{N}\left(y=y_{1}\right)$ and $N_{2}=\hat{N}\left(y=y_{2}\right)$, where in the special case of the logistic curve the following relations apply:

$$
b=-1 ; a>\left[\ln \left(N_{2} / N_{1}\right)\right] /\left[y_{2}-y_{1}\right]
$$

It then follows that:

$$
\begin{equation*}
y^{*}=y_{1}+a^{-1} \ln (\beta / \alpha) \tag{4}
\end{equation*}
$$

where: $\beta=\left[N_{1}^{-1}-N_{2}^{-1}\right] /\left[1-e^{-\alpha\left(y_{2}-y_{1}\right)}\right]$

$$
\alpha=N_{1}^{-1}-\beta
$$

The calculations were carried out for $y_{1}=1967-68$ and $y_{2}$ equal to the time of the last census considered.

The choice of a logistic curve for fitting purposes is not intended to imply that the dynamics of the gray whale are governed by the associated differential equation. Rather, this curve was chosen because it is one of the simplest forms which possesses the desired general properties for the trend in abundance: plausible past and future limiting behaviour, and a point of inflection.

There is a cost in changing from the cubic to the logistic model, however. This is that the logistic model is no longer linear in its parameters, so that non-linear estimation techniques are required. A more serious problem is how to estimate an SE (or CI) for $y^{*}$. This could be obtained from elements of the information matrix, together with an application of the delta method. However, the non-linear nature of the problem means that the resultant CI estimates would be approximate; further, the parameter estimates for such a model fitted to relatively few data often have markedly skewed distributions, so that unless such estimates are precise, the linear approximation of the delta method is unlikely to be accurate. The likelihood ratio approach could be applied in a manner which bypasses the need for the delta method, but the resultant CI estimates would remain approximate because of the non-linearity of the model.
A bootstrap approach was, therefore, adopted to determine the precision of the logistic model $y^{*}$ estimate. [Note: Strictly speaking, Monte Carlo implementations of forms of what is termed a 'conditional parametric bootstrap' procedure were applied (Smith et al., 1993, Table 1) - for convenience, the term 'bootstrap' is used without these qualifications in what follows.] For the case where each census estimate was given an equal weight in the fit, the bootstrap replicate datasets were generated from the fitted logistic curve $\left(\hat{N}_{y}\right)$. Thus, for fits to the 1967-68 to 1979-80 census estimates of Table 1a for example, a re-sampled set $\left\{N_{y}{ }^{S}: y=67-68, \ldots, 79-80\right\}$ where $S=1, \ldots, S_{\max }$ was formed as follows:

$$
\begin{align*}
& N_{y}^{S}=\hat{N}_{y}+\epsilon_{y}^{S} \quad \epsilon_{y}{ }^{S} \text { from } N\left(0, \sigma^{2}\right) \\
& \hat{\sigma}^{2}=\frac{1}{n-3} \sum_{y-67-68}^{79-80}\left(N_{y}-\hat{N}_{y}\right)^{2}, \tag{5}
\end{align*}
$$

where:
$N_{y}$ is the census estimate for year $y$;
$\hat{N}_{y}$ is the fitted logistic curve value for year $y$; and
$n=13$ for this example.
Note that the ( $n-3$ ) term in the denominator of the equation for $\sigma^{2}$ is an ad hoc attempt to adjust for bias in the maximum-likelihood estimate of $\sigma^{2}$, by making allowance for the fact that three parameters are being estimated in the fit. This adjustment would be exact if the model being used was linear in its parameters.

For fits where the census estimates are each weighted by the inverse of their squared SEs, the bootstrap samples were generated directly from the data without reference to the fit itself:

$$
\begin{equation*}
N_{y}^{S}=N_{y}+\eta_{y}^{S} \quad \eta_{y}^{S} \text { from } N\left(0, \sigma_{y}{ }^{2}\right) \tag{6}
\end{equation*}
$$

where $\sigma_{y}$ is the estimate of the SE for census estimate $N_{y}$. The basis for this approach is discussed further in Appendix 1.

In either case, each time series of bootstrap censuses $\left\{N_{y}{ }^{S}\right\}$ is fitted by the logistic model with the same weighting scheme as used for the associated original fit and each bootstrap fit provides a value for the year in which the curve shows a point of inflection $\left(y^{S}\right)^{*}$. The set $\left\{\left(y^{S}\right)^{*}\right.$ : $\left.S=1, \ldots, S_{\max }\right\}$ then constitutes an empirical distribution for the estimate of $y^{*}$; CI estimates follow straightforwardly after ordering this set. For the computations reported in this paper, $S_{\max }=500$.

There is a philosophical difference between the two bootstrap approaches used. Equation (5), for equal weighting, tacitly assumes that the underlying population trajectory is logistic. The approach of equation (6) makes no assumption about the form of this trajectory, but generates equally likely possible time series of censuses by treating each observation as independent; in this context, the logistic curve eventually fitted is regarded only as a convenient functional form with the desired general properties (as detailed above). An advantage of the latter approach is that it avoids the need to make ad hoc adjustments for bias when generating the bootstrap residuals.

## RESULTS

The estimates of $y^{*}$ from fitting the cubic model of equation (1) to the census estimates from 1967-68 to 1979-80 and the associated delta method estimates of SE are:
$\begin{array}{lll}\text { Unweighted: } & y^{*}=1973-74+0.4 \mathrm{yrs} & \mathrm{SE}=0.9 \\ \text { Weighted: } & y^{*}=1973-74+0.0 \mathrm{yrs} & \mathrm{SE}=0.5\end{array}$
The fit to the data for the latter case (weighting by $1 / \mathrm{SE}^{2}$ ) is shown in Fig. 1. Gerrodette and DeMaster (1990) used an unweighted fitting procedure for the same data that have been used here (DeMaster, pers. comm.). Although, for reasons discussed in the following section, the weighted procedure is preferred here, the results are relatively insensitive to whichever procedure is chosen.

The results for fitting the logistic model of equation (3) are given in Table 3. They are given for fits to both Reilly et al.'s (1983) estimates for 1967-68 to 1979-80, and Buckland and Breiwick's (2002) estimates for 1967-68 to 1987-88. The weighted fits to these two series are shown in Figs 2 and 3 respectively.

A fit of the full four-parameter Schnute growth curve model (i.e. parameters $a$ and $b$ unconstrained) was carried out for both the unweighted and weighted cases, and compared to the special (three-parameter) case of the logistic model for both datasets. In all cases, a likelihood ratio test indicated that there was no statistical justification for the


Fig. 1. The weighted cubic model fit to census estimates of Reilly et al. (1983) (Table 1a) from 1967-68 to 1979-80 is shown by the dashed line. The dots and associated vertical bars correspond to the actual census estimates and associated $95 \%$ CIs (taken to be $\pm 2$ SEs).


Fig. 2. As for Fig. 1, except that the dashed line corresponds to the weighted logistic model fit.
inclusion of a fourth parameter. This demonstrates that there is no evidence that the choice of the logistic form for fitting purposes is introducing any model mis-specification.

## DISCUSSION

At face value, the two approaches applied here to Reilly et al.'s (1983) census estimates have given startlingly different results. The cubic model suggests, with close to ' $100 \%$
confidence', that these estimates indicate a point of inflection in the population trajectory within two years of 1973-74. This is entirely compatible with the results shown in fig. 2 of Gerrodette and DeMaster (1990). In contrast, the corresponding results for the logistic model shown in Table 3 indicate a probability of less than $10 \%$ that the point of inflection occurs within the period of these first 13 censuses.


Fig. 3. As for Fig. 2 (weighted logistic model fit), except that the fit is now to the census estimates of Buckland and Breiwick (2002) (see Table 1b) for the period 1967-68 to 1987-88.

Table 3
Results of fits of the logistic function to the census time series in respect of the year corresponding to the point of inflection on the curve $\left(y^{*}\right)$. The data in Table 1(a) were used for the fits for the 1967-68 to 1979-80 period, and those in Table 1(b) for the fits for the 1967-68 to 1987-88 period.

|  |  |  | Probability (\%) that y* occurs: |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |

The method of analysis used for assessing the precision of $y^{*}$ for the cubic model could be questioned because it does not exclude the possibility that the point of inflection arises from a convex (viewed from above) followed by a concave curve, which would be unrealistic in a population dynamics context. However, this is a minor concern, and in any case the resolution of the apparently contradictory results from the two models is immediately evident from inspection of Fig. 1.

The rationale underlying dynamic response analysis implicitly assumes that under a constant or zero harvest, the population trajectory will be monotonically increasing. This is not the case for the fitted cubic in Fig. 1, which decreases for the period of both the first three and the last three censuses shown. This is a consequence of the decreases in the actual point estimates from the 1967-68 to 1971-72 (1969-70 excepted) and 1976-77 to 1978-79 censuses. The sizes of the CIs for the census estimates shown in Fig. 1 indicate that these drops are almost certainly stochastic fluctuations; however, the cubic model is using its available degrees of freedom to reflect these drops in the fit which it chooses. Thus, the high precision of the cubic model's estimate of $y^{*}$ is misleading, because it is a consequence of the model allowing unrealistic population behaviour over the early and late parts of the period considered.

For this reason, the cubic model's assessment of $y^{*}$ and its precision is rejected here. For exactly the same reason, the method of analysis used by Gerrodette and DeMaster (1990), which indicated that the gray whale population passed through MNPL between 1967 and 1980, is considered unreliable ${ }^{2}$. The drops in the census estimates between 1967-68 and 1971-72, and between 1976-77 and 1978-79, have the effect of enhancing the second order coefficients in the quadratics fitted to periods including those years, thus apparently strengthening the case for detection of a point of inflection. But the fact that the quadratics fitted over the periods indicated correspond to estimating that population size has decreased for at least parts of those periods also needs to be taken into account. Such population behaviour is inconsistent with the underlying rationale for dynamic response analysis. Future attempts to use the methodology of Boveng et al. (1988) when implementing dynamic response analysis should take care to constrain the parameters of the quadratics fitted to exclude such apparent behaviour. This might be achieved by fitting the logistic model (rather than a quadratic) over short time periods, and then using such fits to estimate the sign and magnitude of the curvature at the mid-point of each corresponding period. Unfortunately, of course, this approach (like any others incorporating the constraints indicated) results in the loss of the convenience and the power of a linear model analysis.

Application of the logistic model results in probabilities ranging from $0 \%$ to $31 \%$ that the gray whale population passed through MNPL for the two periods and corresponding sets of census estimates considered (Table 3). Naturally, the confidence with which conclusions can be drawn from such estimates depends on the reliability of the bootstrap methods used to provide distributions for $y^{*}$. Originally it had been our intention to test the procedures of equations (5) and (6) for possible bias, using simulation methods. However, the results in Table 3 are so far removed from $95 \%$ confidence that MNPL falls within the census

[^1]period considered, that the bias in the bootstrap estimators of variance of $y^{*}$ would have to be enormous to reverse these results. This seems such an unlikely possibility that the considerable amount of computer time needed for simulation testing of these estimators for this particular dataset was not felt to be justified.

The poor discriminatory power of dynamic response analysis for the gray whale population which is indicated by the logistic model analysis above is not altogether surprising when the simulation results of Gerrodette (1988) are considered. For example, fig. 3 of Gerrodette (1988) shows the discriminatory power of fitting a quadratic to ten successive population estimates (each with $\mathrm{CV}=0.05$ ) generated from an underlying logistic model. Results are shown for different values (ranging from 0.10-0.20) of the intrinsic growth rate parameter $r$ of the logistic model. The sign of the second order coefficient of the quadratic is used to assess whether the population is above or below MNPL. This figure shows that the discriminatory power decreases as the value of $r$ drops, and for $r=0.10$ the procedure is effectively powerless (almost equally likely to give the incorrect as the correct result) for population sizes greater than 0.4 K . In comparison, for Reilly et al.'s (1983) gray whale data, the effective $r \approx 0.05$ and the census estimates have $\mathrm{CVs} \simeq 0.11$, indicating a decrease in discriminatory power on both counts compared to that shown in Gerrodette's example. Admittedly, three more population estimates are available than the ten which Gerrodette considers in the figure referenced, but these can scarcely compensate for the other negative influences on discriminatory power.

The authors consider the weighted fitting procedure should be preferred to the unweighted one for the applications to Reilly et al.'s (1983) census estimates for 1967-68 to 1979-80. This is because the SEs of the individual census estimates (Table 1a) have very similar magnitudes to those of the residuals in the model fits to the data (note the comparison for a straight line fit discussed earlier in the paper). This suggests that 'observation errors' (in the population-model-fitting sense of this term) totally dominate any errors associated with model mis-specification, so that inverse variance weighting would seem to be the statistically preferable procedure for these data. Accordingly the weighted results were chosen for presentation in Figs 1-2.

For consistency, the weighted result is also the one plotted in Fig. 3, which shows the fit to Buckland and Breiwick's (2002) estimates for 1967-68 to 1987-88. Comparison of the error bars in Figs 2 and 3 indicates that the SE estimates in Buckland and Breiwick's case are certainly not capturing all the variability about the underlying trend (i.e. in terms of the symbols used in Appendix $1 \tilde{\sigma}^{2}<\sigma^{2}$ ). In these circumstances, the weighted procedure will give negatively biased estimates of variance, so that the unweighted results would seem to be the more reliable for these data.

All the results give point estimates of $y^{*}$ and probability levels which indicate a greater likelihood that the gray whale population is currently below rather than above its MNPL (see Table 3). This is more so when the latest three censuses and Buckland and Breiwick's reanalysis are taken into account, although for the reasons explained in the previous paragraph, it is considered that the weighted fit results indicate greater precision than is really the case for the data of Table 1b. The overall impression is therefore that the reliability with which population trajectory curvature can be estimated from the data available, allows a conclusion stated no more strongly than that there is a somewhat greater
likelihood that the gray whale population was below rather than above its MNPL (MSYL) in 1990, given the data available at that time.

## CONCLUSIONS

Conclusions from the cubic model analysis of this paper, and from the analysis by Gerrodette and DeMaster (1990), that the gray whale population passed through MNPL ( $\simeq$ MSYL) between 1967 and 1980 are unreliable. This is because the curves fitted by both analyses correspond to markedly decreasing population sizes over parts of the periods to which they apply; this is inconsistent with plausible population dynamics behaviour, which underlies the rationale for dynamic response analysis. Care should be taken to implement dynamic response analysis in a manner that respects such plausibility constraints.

The census data available up to 1987-88 are scarcely adequate to allow for reliable estimates of population trajectory curvature to be made. Fits using the logistic model indicate a somewhat greater likelihood that the gray whale population was below rather than above its MNPL in 1990.

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## REFERENCES

Boveng, P., DeMaster, D.P. and Stewart, B.S. 1988. Dynamic response analysis. III. A consistence filter and application to four northern elephant seal colonies. Mar. Mammal Sci. 4:210-22.
Buckland, S.T. and Breiwick, J.M. 2002. Estimated trends in abundance of eastern Pacific gray whales from shore counts (1967/68 to 1995/96). J. Cetacean Res. Manage. 4(1):41-8.
Butterworth, D.S., Korrûbel, J.L. and Punt, A.E. 2002. What is needed to make a simple density-dependent response population model consistent with data for eastern North Pacific gray whales? J. Cetacean Res. Manage. 4(1):63-76.
Cooke, J.G. 1986. On the net recruitment rate of gray whales with reference to inter-specific comparisons. Rep. int. Whal. Commn 36:363-6.
Gerrodette, T. 1988. Dynamic response analysis. II. Evaluation of dynamic response analysis in a simulated no-harvest case. Mar. Mammal Sci. 4:196-209.
Gerrodette, T. and DeMaster, D.P. 1990. Quantitative determination of optimum sustainable population level. Mar. Mammal Sci. 6(1):1-16.
Goodman, D. 1988. Dynamic response analysis. I. Qualitative estimation of stock status relative to maximum net productivity level from observed dynamics. Mar. Mammal Sci. 4:183-95.
International Whaling Commission. 1993. Report of the IWC Scientific Committee Special Meeting on the Assessment of Gray Whales, Seattle, 23-27 April 1990. Rep. int. Whal. Commn 43:241-59.
Lankester, K. and Beddington, J.R. 1986. An age structured population model applied to the gray whale (Eschrichtius robustus). Rep. int. Whal. Commn 36:353-8.
Reilly, S.B., Rice, D.W. and Wolman, A.A. 1983. Population assessment of the gray whale, Eschrichtius robustus, from California shore censuses, 1967-80. Fish. Bull. 81(2):267-81.
Schnute, J. 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38:1120-40.
Smith, S.J., Hunt, J.J. and Rivard, D. 1993. Risk evaluation and biological reference points for fisheries. Can. Spec. Publ. Fish. Aquat. Sci. 120 vi-vii.

## Appendix 1

## A BASIS FOR THE PARAMETRIC BOOTSTRAP APPROACH OF EQUATION (6)

At first sight, it might appear that the approach of equation (6) would provide positively biased estimates of variance, because it would seem that bootstrap noise is being added to, rather than replacing the real noise about the underlying trend.

To show that this is not the case, the equivalence of the approaches of equations (5) and (6) is demonstrated for the simple case of estimating the standard error of the mean from a sample drawn from a normal distribution, i.e.:

Data: $\quad\left\{y_{i}: i=1, \ldots, n\right\}$ where $y_{i}$ from $N\left(\mu, \sigma^{2}\right)$
Estimator: $\hat{\mu}=y=\left\{\sum_{i=1}^{n} y_{i}\right\} / n$
The requisite variance is known for this case:

$$
\begin{equation*}
\operatorname{var}(\mu)=\sigma^{2} / n \tag{A.2}
\end{equation*}
$$

and would be estimated by:

$$
\begin{equation*}
\operatorname{vâr}(\mu)=\hat{\sigma}^{2} / n \tag{A.3}
\end{equation*}
$$

## The parametric bootstrap approach of equation (5)

A large number $\left(S_{\max }\right)$ of datasets $\left\{y_{i}{ }^{S}: i=1, \ldots, n\right\}$ is generated, where:

$$
\begin{aligned}
& y_{i}^{S}=\hat{\mu}+\in_{i}^{S} \\
& \in_{i}^{S} \text { is from } \mathrm{N}\left(0, \hat{\sigma}^{2}\right) \\
& S=1, \ldots, S_{\max }
\end{aligned}
$$

The estimate from the $S$ th bootstrap dataset is:

$$
\begin{align*}
\mu^{8} & =\left\{\sum_{i=1}^{n} y_{i}^{8}\right\} / n \\
& =\left\{\sum_{i=1}^{n}\left(\mu+\epsilon_{i}^{8}\right)\right\} / n  \tag{A.4}\\
& =\hat{\mu}+\left\{\sum_{i=1}^{n} \epsilon_{i}^{8}\right\} / n
\end{align*}
$$

and the average of these estimates is:

$$
\begin{align*}
\bar{\mu} & =\left\{\sum_{s=1}^{s} \mu^{s}\right\} / S_{\max } \\
& =\tilde{\mu}+\left\{\sum_{i=1}^{n} \sum_{S=1}^{s} \epsilon_{1}^{s}\right\} /\left\{n S_{\max }\right\}  \tag{A.5}\\
& \rightarrow \mu \text { for } S_{\max } \text { large }
\end{align*}
$$

Thus, for large $S_{\max }$, the bootstrap method of equation (5) provides an estimate:

$$
\begin{align*}
\operatorname{var}_{\text {eq }[5]}(\mu)= & \left\{\sum_{S=1}^{S}\left(\mu^{S}-\bar{\mu}\right)^{2}\right\} /\left\{S_{\max }-1\right\} \\
& \approx\left\{\sum_{S=1}^{S}\left(\mu^{s}-\bar{\mu}\right)^{2}\right\} / S_{\max }  \tag{A.6}\\
& =\left\{\sum_{S=1}^{S}\left[\sum_{i=1}^{v} \epsilon_{i}^{S}\right]^{2} / n^{2}\right\} / S_{\max } \\
& =\dot{\sigma}^{2} / n \text { as } \operatorname{cov}\left(\epsilon_{,}^{S}, \epsilon_{j}^{s}\right)=0 \text { unless } i=j
\end{align*}
$$

which is the required result (see equation A.3).
The parametric bootstrap approach of equation (6)
In this instance, the datasets generated are $\left\{y_{i}{ }^{S}: i=1, \ldots, n\right\}$ where:

$$
\begin{aligned}
& \tilde{y}_{i}^{S}=y_{i}+\eta_{i}^{S} \\
& \eta_{i}^{S} \text { is from } N\left(0, \tilde{\sigma}^{2}\right) \\
& S=1, \ldots, S_{\max }
\end{aligned}
$$

The estimate from the $S$ th bootstrap dataset is:

$$
\begin{align*}
\bar{\mu}^{8} & =\left\{\sum_{i=1}^{n} \bar{y}_{i}^{s}\right\} / n \\
& =\left\{\sum_{i=1}^{n}\left(y_{i}+\eta_{i}^{s}\right)\right\} / n \quad\left[\text { write } y_{i}=\bar{y}+\left(y_{i}-\bar{y}\right)\right] \\
& =\left[\sum_{i=1}^{n} \bar{y}+\sum_{i=1}^{n}\left(y_{i}-\bar{y}\right)+\sum_{i=1}^{n} \eta_{i}^{s}\right] / n  \tag{A.7}\\
& =\bar{y}+0+\left\{\sum_{i=1}^{v} n_{i}^{5}\right\} / n \\
& =\hat{\mu}+\left\{\sum_{i=1}^{n} n_{i}^{s}\right\}^{s} / n
\end{align*}
$$

Equation (A.7) has exactly the same form as equation (A.4), because the contributions from the real noise:

$$
\left[\sum_{i=1}^{n}(y,-\bar{y})\right]
$$

cancel, so that under the same arguments as used above:

$$
\begin{equation*}
\operatorname{vâr}_{e q(6)}(\mu) \simeq \tilde{\sigma}^{2} / n \tag{A.8}
\end{equation*}
$$

Thus, if $\tilde{\sigma}^{2}$ (corresponding to the variance estimate associated with each data point) is equivalent to $\sigma^{2}$ (measuring the variance about the underlying trend - a constant in this illustration), the bootstrap approaches of equations (5) and (6) are identical for this case. A similar exercise demonstrates that they are also identical for the case of linear regression.


[^0]:    * Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch 7701, South Africa.
    \# Current address: RUWPA, Mathematical Institute, North Haugh, University of St Andrews, St Andrews, Fife, KY16 9SS, UK.
    ${ }^{+}$Current address: School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195-5020, USA.

[^1]:    ${ }^{2}$ Our assessment of unreliability concerns their methodology when applied to this particular case; it will not necessarily hold in general.

