The Utility of Demographic Models in Marine Mammal Management

Jay Barlow

Southwest Fisheries Science Center, National Marine Fisheries Service, PO Box 271, La Jolla, CA 92038, USA

ABSTRACT

Demographic models can be used to estimate population growth rate directly from the stable distributions of age and reproductive state. Two demographic models are considered: the geometric series and Leslie matrix models. Both models are shown to converge to the same estimator for population growth rate, e^r. A method is derived which estimates the sampling variance in e^r using this estimator. The variance of this estimator is calculated for three examples of marine mammal life history and for sample sizes ranging from 500 to 16,000. Even with the largest sample sizes and ignoring numerous sources of additional variability, the sampling variance in estimates of population growth rate is too large to be of practical value in marine mammal management.

INTRODUCTION

Demographic models are used to represent the dynamics of age-structured populations. They can range in complexity from simple 2-age models which consider only 'juveniles' and 'adults', to full Leslie matrix models which typically include one age class for each year of life. Demographic models have had a long history of use in the management of marine mammal populations (Allen, 1981).

Although demographic models have many uses, the most misunderstood (and perhaps the most emphasized) has been the estimation of population growth rates. In this paper I examine this particular use in detail and evaluate whether such models can provide estimates of population growth rates that are useful in the context of marine mammal management.

Several previous studies have investigated the accuracy with which growth rates can be estimated from measurement of demographic parameters. Lenski and Service (1982) and Meyer *et al.* (1986) derive variance estimators based on data that are gathered from a longitudinal study of a cohort. These data, however, are not available for marine mammals. For large whales, the emphasis has been on the accuracy of estimating natural mortality rates from catch-at-age data with independently measured trends in abundance (Tanaka, 1990). De la Mare (1990a) has shown that mortality rates estimated by these methods are not precise. In a more general sensitivity study, de la Mare (1990b) has shown that net recruitment rates are very sensitive to errors in estimating demographic parameters. Here I examine the sampling variance in estimating population growth rates from demographic parameters alone, independent of any information on trends in abundance.

DEMOGRAPHIC MODELS

In this paper I will consider two common demographic models which represent opposite extremes on a spectrum from simple to complex. These models are the geometric series model and the Leslie matrix model (respectively). As is common practice for both models, I will explicitly consider only the female segment of the population.

The geometric series model describes the most basic elements of age structure with only four parameters: the mean survival rate of reproductive females (p), the mean birth rate of reproductive females (m), the age at sexual maturation (α) and the survivorship from birth to the age of sexual maturity (l_α). Given these four parameters, population growth rate (e^r) can be estimated by solving its characteristic equation:

$$1 = (m\, l_\alpha)/(e^{r\alpha} - pe^{r(\alpha-1)}) \qquad (1)$$

Goodman (1984).

The Leslie matrix model typically has many more parameters than the geometric series model. For marine mammals, this model will usually have two parameters (age-specific birth and death rates) for each year of life up to the maximum age attained by the species. This level of resolution has been chosen because it is typical of the level of resolution in age estimation for marine mammals. I use the terminology of Caswell (1989) for a birth-pulse population with postbreeding census. Age-specific survival rates (P_x) form the first sub-diagonal of the matrix and represent the probability of surviving from age class x to age class $x+1$. Age-specific fecundity rates (F_x) form the first row of the matrix and represent the expected number of female offspring born to a female in age class x at time t and which are alive at time $t+1$. Although the population growth rate (e^r) can be estimated by using linear algebra to find the dominant eigen value of the Leslie matrix, it is mathematically equivalent and algebraically simpler to solve the following characteristic equation:

$$1 = \sum_{i=1}^{\beta} e^{-rx} \cdot l_x \cdot F_x \qquad (2)$$

where $l_x = \prod_{i=1}^{x-1} p_i$

and β = maximum age class.

ESTIMATING DEMOGRAPHIC PARAMETERS

Given age-specific fecundity and survival rates, the estimation of population growth rates using demographic models is a simple algebraic exercise. The real problem is in accurately estimating the birth and survival parameters.

Survival rates can be estimated from the age distribution of a population if a number of assumptions are met. The primary assumption is that the population is in a stable age distribution. Although a method has been developed which circumvents this assumption (Fryxell, 1986), this method requires knowledge of both the actual, time-dependent age distribution and the distribution of ages at death. The latter is not available for marine mammal populations. Given a stable age distribution, survival rates

can only be estimated as an 'apparent survival rate' (i.e. the true survival rate divided by the population growth rate). As pointed out by Caughley (1966), true survival rates can be estimated from age-frequency distributions alone only if the population is not growing. Fortunately, it has been shown for the Leslie (Michod and Anderson, 1980) and geometric series (Goodman, 1984) models, that knowledge of the 'apparent survival rate' is sufficient to estimate population growth rate using either model. Although many smoothing models have been proposed for the estimation of the age-specific survival rate, these complications are not necessary when estimating the population growth rate. As will be shown below for both the geometric series and Leslie models, the only relevant survival statistic is the ratio of the number of individuals in reproductive age classes to the number of individuals in the first age class.

Estimating the fecundity parameter(s) of either model is more complicated than simply measuring crude birth rates. In both models, the fecundity term incorporates elements of survival of the mother from census to birth and/or the offspring from birth to census. Methods of estimating Leslie-matrix fecundities (F_x) from field data are discussed by Goodman (1984) and Caswell (1989). The fecundity term in the geometric series model (m) is a weighted average of the age-specific fecundities of the reproductive age classes where the weights are given by the stable age distribution (Goodman, 1984). If the population is in stable age distribution (which is a necessary condition for estimating population growth rates) m can be estimated from a random sample of reproductive females and the appropriate weighting will be implicit.

ESTIMATING POPULATION GROWTH RATES

Substituting the 'apparent survival rate' (i.e. the true rate divided by the population growth rate) in Equations 1 and 2 results in considerable simplification; both can then be represented as direct solutions for e^r.

Geometric Series Model
The characteristic equation for the geometric series model (Eq. 1) simplifies to:

$$e^r = (m\, l_\alpha')/(l - p') \tag{3}$$

where p' = the apparent survival rate

and l_α' = the apparent survivorship to age α

(incorrectly printed as Eq. 33 in Goodman (1984)). The apparent survival rate can be estimated as

$$p' = 1 - (n_{\alpha+}/N) \tag{4}$$

where $n_{\alpha+}$ = the number in reproductive age classes,

and N = the total number in all age classes

(Goodman (1984), from his Eq. 24). The apparent survivorship to age α can be estimated as

$$l_\alpha' = n_{\alpha+}/n_I \tag{5}$$

where n_I = the number in age class 1

(Goodman (1984), from his Eq. 32). Substituting Equations 4 and 5 into 3, population growth rate can thus be represented as

$$e^r = (m\, n_{\alpha+})/n_I \tag{6}$$

The numerator in Equation 6 represents the number of offspring that will be produced by females at time t and which will survive until census at time $t+1$. Assuming that gestation is one year and ignoring the survival aspect of fecundity, the fecundity rate, m, can be estimated as the number of pregnant females, n_p, divided by the total number of mature females, $n_{\alpha+}$. Thus Equation 6 can be re-expressed as

$$e^r = n_p/n_I \tag{7}$$

Leslie Matrix Model
A similar simplification is possible with the characteristic equation for the Leslie matrix (Eq. 2). Again, population growth rate can be expressed in terms of age-class abundances and fecundity

$$e^r = \frac{\sum_{x=\alpha}^{\beta} F_x \cdot n_x}{n_I} \tag{8}$$

(Michod and Anderson (1980), from their Eq. 3). The similarity between Equations 6 and 8 is more than superficial.

The numerator in both represents the number of offspring that will be produced by mature females at time t and which will survive until census at time $t+1$. Again assuming that gestation is one year and ignoring the survival aspect of fecundity, Equation 8 can be reduced to Equation 7. The estimation of population growth rates for both the geometric series and Leslie matrix models has thus converged on a single approach.

The data which will be needed to estimate population growth rate will thus be the number of pregnant females and the number of individuals in the first age class.

VARIANCE ESTIMATION

The estimation of population growth rate has been reduced to the ratio of two elements of a multinomial distribution. This makes the problem of estimating its variance simple. Let q_I be the expected proportion in age class 1 in the population, let q_p be the expected proportion of pregnant females, and let N be sample size of all age and reproductive classes. The sampling variance in e^r can be estimated from the Taylor series approximation for the variance of a ratio (Yates, 1953) using multinomial variance and covariance estimators. Thus

$$var(e^r) = var\left[\frac{n_p}{n_I}\right] = \left[\frac{q_p^2}{q_I}\right] \cdot \left[\frac{1-q_p}{N\cdot q_p} + \frac{1-q_I}{N\cdot q_I} + \frac{2}{N}\right] \tag{9}$$

For simplicity I have glossed-over all the complications involved in estimating fecundity from data on gross percent pregnant. As stated previously, fecundity includes an element of survival. I have assumed that this survival rate is 1.0. The survival part of the fecundity term is typically very difficult to measure and its estimation will add to the sampling variance associated with estimating population growth rates. Furthermore, I have assumed that age and reproductive status can be measured without error. For these reasons the variance estimated here will underestimate the true variance expected from any real sampling plan.

MONTE CARLO SIMULATIONS

A simple simulation is used to test Equation 9 and to examine the distribution of estimated population growth rates. I assume that the population can be sampled

randomly with respect to age and reproductive condition. I draw random samples from a hypothetical population of females and record (1) the number in the first age class and (2) the number of pregnant females. For each sample, population growth rates are estimated from Equation 7. Thus, in this simulation I assume that all errors in estimating population growth result from random sampling of a multinomial distribution.

The expected fraction of the female population in each of the two categories given above is dependent on both the age-specific fecundities and survival rates. Consequently, the simulations require some assumptions about the life history of the species. Three model life tables will be used as representative examples in the simulation. Case I is a generalized marine mammal with an adult survival rate of 0.9, a mean adult fecundity rate of 0.21, an age of sexual maturity of 6 years, a survivorship from birth to sexual maturity of 0.506 and a population growth rate of 1.000. Case II is the same generalized marine mammal except with a mean fecundity of 0.45 and a population growth rate of 1.065. Case III is modeled specifically after the spotted dolphin (*Stenella attenuata*) with age specific fecundity and survivorship as illustrated in Fig. 1 and with a population growth rate of 1.024. The expected frequency of individuals in the first age class, all other immature age classes, the mature pregnant and the mature not-pregnant groups are given in Table 1 for each of the three examples.
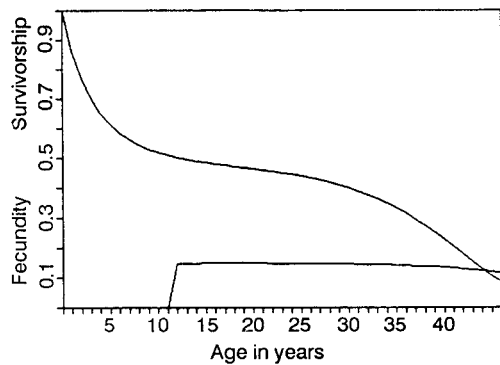

Fig. 1. Age-specific survivorship and fecundity rates used to model the spotted dolphin (from Barlow and Boveng 1991) in Case III of the simulation study.

To simulate sampling from a real population, samples were drawn randomly from the multinomial distributions given in Table 1. Samples sizes of 500, 1,000, 2,000, 4,000, 8,000 and 16,000 females were drawn for each of the three sample life tables. Population growth rates were calculated from each sample, and sampling was repeated 1,000 times to estimate the mean and variance of the estimated population growth rates.

RESULTS

The distributions of estimated population growth rates from the simulations are given in Figs 2 to 4 for the three life table examples (all based on a sample size of 4,000 females). In all three cases, the mean growth rate is in reasonable agreement with the expected mean growth rate, but the range of estimated growth rates is wide and

Table 1

Expected proportion of females that are in each of four age-reproductive classes (in year class 1, in other immature age classes, pregnant with a female fetus, and mature but not pregnant with a female fetus) for a population in stable age distribution.

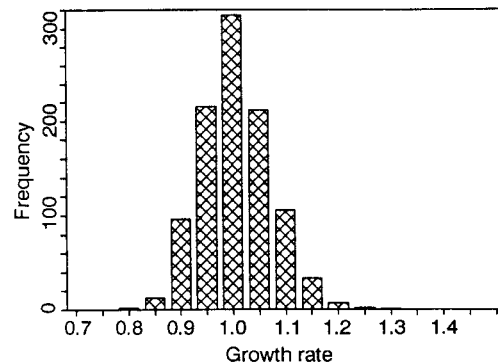| Life table example	Age class one	Other immature ages	Mature and pregnant	Mature not pregnant
Case I	0.118	0.313	0.118	0.451
Case II	0.177	0.404	0.188	0.230
Case III	0.072	0.430	0.074	0.424

Fig. 2. Frequency distribution of estimated population growth rates for Case I based on 1,000 samples of 4,000 females.
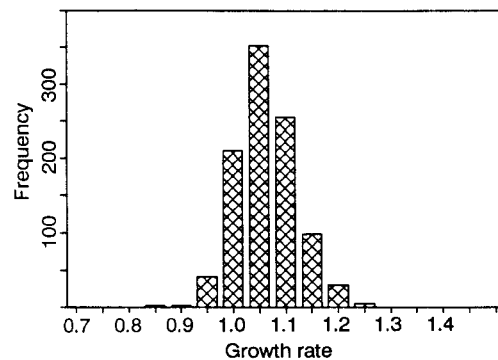

Fig. 3. Frequency distribution of estimated population growth rates for Case II based on 1,000 samples of 4,000 females.

appears skewed. Mean and standard deviations of population growth rates are given in Table 2. Estimates of standard deviation based on Equation 9 are generally in good agreement with the simulation results, but for smaller sample sizes, growth rates and standard deviations are consistently lower than for the simulation (possibly linked to the truncation of third and higher-order terms in
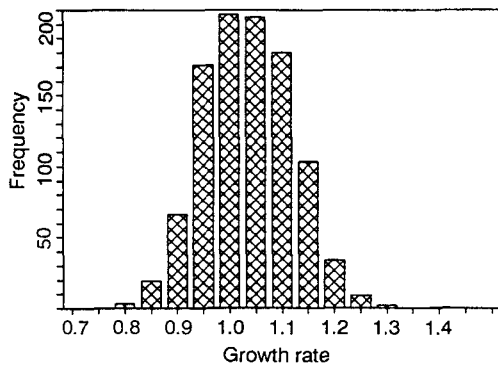
Fig. 4. Frequency distribution of estimated population growth rates for Case III based on 1,000 samples of 4,000 females.

Table 2

Standard deviations of growth rates estimated from Equation 9 and from Monte Carlo simulation. Simulation results are based on 1,000 replicates of the given sample size.

| Life table example	Sample size	Analytical growth rate	Standard deviation	Bootstrap growth rate	Standard deviation
Case I	500	1.000	0.184	1.029	0.193
	1000	1.000	0.130	1.012	0.137
	2000	1.000	0.092	1.004	0.095
	4000	1.000	0.065	1.005	0.067
Case II	500	1.065	0.157	1.073	0.163
	1000	1.065	0.111	1.060	0.109
	2000	1.065	0.079	1.059	0.079
	4000	1.065	0.056	1.064	0.056
Case III	500	1.024	0.241	1.059	0.258
	1000	1.024	0.170	1.042	0.177
	2000	1.024	0.120	1.031	0.123
	4000	1.024	0.085	1.035	0.084
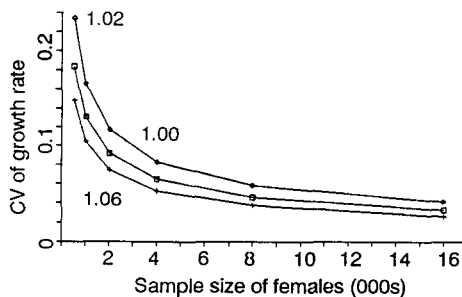
Fig. 5. Analytically derived estimates of the coefficients of variation in population growth rates as a function of sample size for each of the 3 cases used in the simulation. From top to bottom, Cases III, I, and II.

deriving Equation 9). Coefficients of variation in annual growth rate, e^r, are illustrated as functions of sample size in Fig. 5.

DISCUSSION

Results indicate that even under the most optimistic scenario, extremely large sample sizes are required to accurately estimate population growth rates. Even with a sample size of 4,000 females, biologically implausibly high growth rates were frequently estimated. These results were based on the assumption that random sampling was the only source of error. Many other important sources of variation were ignored. If those other sources of variation were included, the situation could only be worse. It is unlikely that unbiased samples could be collected from a sufficient number of individuals for this approach to be useful in managing marine mammal populations.

Although coefficients of variation of less than 10% are typically considered good in ecological studies, values less than 1% are probably necessary for estimates of population growth to be useful in the management of harvests. The reason for this is that it is the annual increment (e^r-1), not e^r, that is of interest in determining harvest rates. When population growth is small, a CV of 1% in e^r can be equivalent to a CV of 100% in e^r-1. This level of accuracy would provide little useful information and clearly should not be used as a sole basis for determining acceptable harvest rates.

The sample sizes required to estimate population growth rates to within 1% were outside the range of values that I considered. It is easy to see from Fig. 5 that the required sample would be much greater than 16,000 females. There are many practical reasons why such large samples may be unobtainable. It should be remembered that in taking such a sample, it is likely that an equal number of males would have to be caught and examined (i.e. a total sample of much greater than 30,000 animals). The cost of obtaining such a large sample using unbiased collection methods would be staggering. Furthermore, the method is very sensitive to the ratio of reproductive females to females in year-class 1. Because juveniles usually segregate from adults, an unbiased estimate of this ratio may not be obtainable at any cost.

Although based on Fig. 5, the utility of demographic estimates of population growth rate already looks dismal, it is important to consider the sources of variation that were ignored in the simulation. Perhaps the biggest source of error will come from biases in sampling. In previous attempts at obtaining unbiased samples of minke whale populations, Kishino et al. (1989) found that different age groups segregated into different characteristic group sizes and in different geographic areas. Random sampling of groups of different size is difficult because the ability to find groups varies with group size. Correction for the geographic segregation of age groups is difficult because it requires knowledge of the density of animals in each geographic stratum. Assuming that all these potential biases can be corrected, the correction process itself will introduce an additional source of sampling variance. Errors in the estimation of age and reproductive status are unavoidable. Assuming that this type of error can be measured, correction will again add additional sources of variation. Yet another problem is that populations may not be in stable age distribution. A long time series of samples would be required just to determine if this important assumption has been met.

The direct estimation of population growth rate is not the only use of demographic models. Demographic models have already been useful in estimating the upper limits on population growth of marine mammals (Reilly and Barlow, 1986; Barlow and Boveng, 1991). Also, the method of using stable age distributions is not the only method of estimating demographic parameters. Buckland (1990) and Barlow (1990) investigate alternative methods based on longitudinal studies of individually identifiable whales. The point of this study is not to denigrate the general value of demographic data. My main point is that one should have realistic ideas about what sample sizes are needed to estimate population growth rates using demographic models. Seldom, however, have the sample size requirements of demographic models for any purpose been tested **before** researchers go out and start collecting data. Data are collected in the optimistic anticipation that they will be useful when plugged into a demographic model. Often a simulation study such as the one presented here would have revealed the task was hopeless with any reasonable sample size. Tremendous expense could be saved, and we would not deceive ourselves into thinking that we were collecting all the information needed to make intelligent management decisions. Proper experimental design with a full analysis of all potential sources of error should be standard procedure before embarking on any large-scale research project.

ACKNOWLEDGEMENTS

REFERENCES

Allen, K.R. 1981. Application of population models to large whales. pp. 263–75. *In:* C.W. Fowler and T.D. Smith (eds.) *Dynamics of Large Mammal Populations.* Wiley and Sons, New York. xviii+477pp.

Barlow, J. 1990. A birth-interval model for estimating cetacean reproductive rates from resighting data. *Rep. int. Whal. Commn* (special issue 12):155–60.

Barlow, J. and Boveng, P. 1991. Modelling age-specific mortality for marine mammal populations. *Mar. Mammal Sci.* 7(1):84–119.

Buckland, S.T. 1990. Estimation of survival rates from sightings of individually identifiable whales. *Rep. int. Whal. Commn* (special issue 12):149–53.

Caswell, H. 1989. *Matrix Population Models: Construction, Analysis and Interpretation.* Sinauer Associates, Sunderland, Massachusetts. 328pp.

Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47:906–18.,

de la Mare, W.K. 1990a. A further note on the simultaneous estimation of natural mortality rate and population trend from catch-at-age-data. *Rep. int. Whal. Commn* 40:489–92.

de la Mare, W.K. 1990b. Inferring net recruitment rates from changes in demographic parameters: a sensitivity analysis. *Rep. int. Whal. Commn* 40:525–9.

Fryxell, J.M. 1986. Age-specific mortality: an alternative approach. *Ecology* 67(7):1687–92.

Goodman, D. 1984. Statistics of reproductive rate estimates, and their implication for population projection. *Rep. int. Whal. Commn* (special issue 6):161–73.

Kishino, H., Kato, H., Kasamatsu, F. and Fujise, Y. 1989. Statistical method for the estimation of age composition and biological parameters of the population. Paper SC/41/SHMi3 presented to the IWC Scientific Committee, May 1989 (unpublished).

Lenski, R.E. and Service, P.M. 1982. The statistical analysis of population growth rates calculated from schedules of survivorship and fecundity. *Ecology* 63(3):655–62.

Meyer, J.S., Ingersoll, C.G., McDonald, L.L. and Boyce, M.S. 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. *Ecology* 67(5):1156–66.

Michod, R.A. and Anderson, W.W. 1980. On calculating demographic parameters from age frequency data. *Ecology* 61:265–9.

Reilly, S.B. and Barlow, J. 1986. Rates of increase in dolphin population size. *Fish. Bull., US* 84(3):527–33.

Tanaka, S. 1990. Estimation of natural mortality coefficient of whales from the estimates of abundance and age composition data obtained from research catches. *Rep. int. Whal. Commn* 40:531–6.

Yates, F. 1953. *Sampling Methods for Censuses and Surveys.* Hafner Publishing Co. Inc., New York. 401pp.