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IMPLICATIONS OF NON-LINEAR DENSITY DEPENDENCE

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ABSTRACT

Ranges of the ratio of maximum net productivity level (MNPL) to carrying capacity (K) are explored in general models for pinnipeds and odontocetes. MNPL/K is used in management of marine mammals but no empirical evidence exists to limit the range of values expected. Density dependent changes in age-specific birth and death rates have been used to infer MNPL/K. Non-linearities in these rates do not translate directly to population growth curves. The simple models demonstrate: (1) density dependence is likely to involve more than a single parameter (such as birth rate), (2) MNPL/K can be greatly reduced from that inferred from one strongly non-linear parameter when changes in other parameters are linear, (3) ranges of MNPL/K depend on biological limits on ranges of fecundity and survival rates, and (4) the magnitude and sign of bias incurred by inferring MNPL/K from functional forms of single parameters cannot be determined. Given current empirical evidence the range of MNPL/K for marine mammals as a group is large. Although MNPL/K should not be inferred from single parameter non-linearities, distributions of MNPL/K values can be generated through models which account for single species ranges for birth and death rates and maximum population growth rate.

Key words: demography, density dependence, logistic, marine mammal, non-linear dynamics, odontocete, pinniped, population dynamics.

Density dependent population dynamic models are used routinely in the management of marine mammals (Gerrodette and DeMaster 1990). Populations are typically managed relative to the population level where the maximum sustainable yield is realized (Donovan 1989) or the population level where net productivity is maximized. Maximum net productivity level (MNPL) is defined as (Gehringer 1976), ". . . the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality." Empirical data

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concerning population growth rates at different population sizes for marine mammals are limited. Population growth is usually represented by deterministic models which describe the future state of a population given the current state. The state is given in terms of numbers of individuals. These population growth models, such as the logistic or various modified logistic models, consider all individuals to be equal with respect to future prospects of birth and death, that is, age structure is not explicitly used in the models.

Although the data for the relationship between population growth and population size are sparse for marine mammals, data on some age-specific birth and death rates are available for a few species. Based on these data, MNPL has been inferred to be above $0.5K$ (Fowler *et al.* 1980, Fowler 1987). From a model using an evolutionary argument, Fowler *et al.* (1980) state: "We would expect a whale population with a maximum specific productivity of 0.04 to show its greatest productivity levels between 88 and 92 percent of its equilibrium level." However, using the relationship from Fowler (1987), with a generation time of 20 yr and a maximum specific productivity of 0.04, would result in MNPL/K of 0.67. The purpose of this paper will be to explore the range of MNPL/K values possible for different combinations of density dependent age-specific changes in birth and death rates. Special attention will be given to biases which could result from inferring MNPL/K from density dependent changes in a single age-specific parameter. Two simple models will be used to explore whether what is known about non-linearities in age-specific birth and death rates justifies acceptance of any particular range of MNPL/K values. The first model is a generalized pinniped model which represents the marine mammal life history with the fastest population growth rate. At the other end of the spectrum, a generalized odontocete model is used to represent life history strategies with slow growth rates.

Empirical evidence—General reviews of empirical evidence for density dependence in large mammals, with separate sections on marine mammals, are presented in Fowler (1987) and Fowler *et al.* (1980). The intent of this paper is not to focus on any particular species but rather to present what general forms may pertain to specific demographic parameters. Fowler (1984) reviews density dependence in marine mammals and finds evidence of regulation for fecundity in nine species, age of first reproduction (AFR) in ten species, juvenile survival in five species and adult survival in one species. These frequencies may reflect ease of gathering data. For example, although adult survival may be density dependent, estimation is difficult and power to detect a change would be low for the amount of change required to affect population growth rates. The lack of empirical evidence makes the form of density dependence for adult survival purely speculative.

A recent reanalysis (de la Mare 1992) of some data reviewed by Fowler *et al.* (1980) shows the inability to draw general conclusions about the shape of recruitment functions. The following statements can be made based on empirical data (Fowler *et al.* 1980, de la Mare 1992): (1) marine mammals show density dependent responses, (2) for species for which data are available over a range of population sizes, density dependent responses are not abrupt (knife-edge),

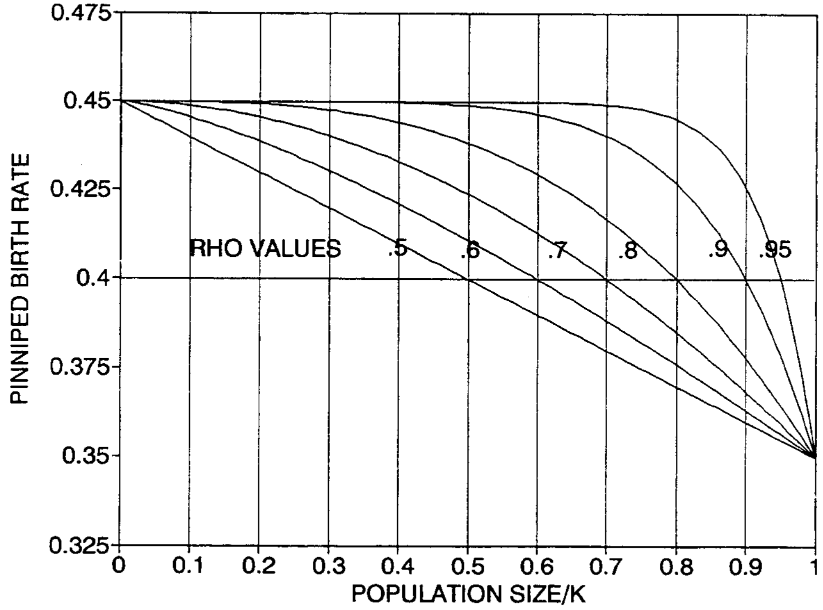

Figure 1. Curves for the Allen equation (Equation 3) for different ρ-values for birth rates for pinnipeds. The horizontal line indicates the point of 50% change in the parameter range. Note the intersections of the functions for different ρ-values with this line.

and (3) density dependent responses have not been shown to be concave (higher rates of change at low density), though the power is low. In this paper, a concave curve is one in which the value for any point between two endpoints is less than the value which would be a linear interpolation. Given the endpoints (0, 1) and (1, 0), a linear relation would yield a y-value of 0.5 when $x = 0.5$. A curve passing through any y-value <0.5 at $x = 0.5$ would be concave. None of the curves in Figure 1 are concave. A theoretical argument has been given by de la Mare and Cooke (1992) that concave responses are possible by allowing spatial variation in the environment. For the purposes of this paper, responses are limited to range from linear to strongly convex (most density dependent response at levels very close to K). Given current quantities and qualities of empirical data, it is not possible to further limit functional forms of age-specific density dependent responses for marine mammals as a group.

Theoretical arguments—Although MNPL is defined in population terms, empirical data exist primarily for age-specific demographic rates. We now consider how each approach is represented theoretically. Density dependent population growth is commonly represented by the generalized logistic equation (Pella and Tomlinson 1969, Gilpin *et al.* 1976) (altered below for discrete growth).

$$N_{t+1} = N_t + (\lambda_{\max} - 1)N_t\left[1 - \left(\frac{N_t}{K}\right)^{\theta}\right] \qquad (1)$$

where N = population size, t = time, K = carrying capacity, $\lambda_{\max}$ = maximum discrete rate of population growth, and θ = shape parameter. Goodman (1980) showed distortion in the population growth curve caused by age structure: a linear change in birth rate caused the population growth curve to be convex. The convex shape of density dependent birth and survival functions argues generally for a maximum growth rate which is greater than $K/2$ ($\theta > 1$).

The θ-logistic equation does not include age-specific mortality or fecundity, but rather uses a single parameter, discrete population growth rate (λ, where $\lambda_{Nt} = N_{t+1}/N_t$), to predict the next population size given the current population size. For any given set of age-specific birth and death parameters there is a unique population growth rate which satisfies the equation:

$$1 = \sum_{x=AFR}^{\omega} l_x m_x \lambda^{-x} \tag{2}$$

where x = age, AFR = age of first reproduction, ω = oldest age, l = survivorship, m = fecundity, and λ = discrete rate of growth. Population growth is sensitive to different parameters in varying strengths. For example, equal proportional changes (called elasticity, Caswell 1989) in adult and juvenile survival rates will result in different changes to λ. For long-lived animals which have high adult survival rates and typically relatively low maximum population growth rates, λ is most sensitive to changes in adult survival rate (Goodman 1981). Relatively large changes in birth and juvenile survival rates result in rather small changes in λ. For example, consider a case where the survival rate for the first year is 0.50 and is 0.95 thereafter. Let $AFR = 1$, $\omega = 20$, and $m = 0.5$ giving $\lambda = 1.051$. A 10% reduction in adult survival, juvenile survival, and birth rate results in λ values of 0.972, 1.026, and 1.038 or changes of −7.5%, −2.4%, and −1.2% respectively. For this reason it is difficult to intuit how non-linear changes in birth or juvenile survival rates will affect λ and the MNPL. Therefore, simple models will be used to investigate the translation of density dependent changes in birth and death rates into population growth rates.

METHODS

Introduction to the life history models—The translation of several age-specific density dependent functions into a single population growth function is best illustrated with simplified population models. The following parameters characterize the demography: mean fecundity (m), annual adult survival rate (p_a), annual juvenile survival rate (p_j—from age zero to one), AFR, oldest age (ω) and maximum discrete rate of growth ($\lambda_{\max}$). We chose parameter values based loosely on the life history of fur seals (*Callorhinus ursinus*) for the pinniped model (Ragen 1990), and the bottlenose dolphin (*Tursiops truncatus*) for the odontocete model (Scott *et al.* 1990, Wells and Scott 1990). Default values for each parameter were selected to give the growth rate expected at $K/2$ within known ranges for pinnipeds (Ragen 1990) and odontocetes (Scott *et al.* 1990,

Table 1. Default parameters to yield λ at K/2 assuming a linear decrease in per capita growth.

Model	$\lambda(N = K/2)$	m	AFR	p_j	p_a	ω
Pinniped	1.05	0.40	5	0.423	0.960	20
Odontocete	1.02	0.12	10	0.593	0.980	50

Brault and Caswell 1993) (Table 1). Density dependent population growth was achieved by adjusting one or more of the above parameters.

Changes in single parameters—We begin examining the effect of changes in age-specific parameters on population growth rate by changing only a single parameter. The required single parameter changes needed to obtain growth rates from $\lambda = \lambda_{\max}$ to $\lambda = 1$ could then be solved given equation 1. Change between the minimum and maximum parameter values was governed by:

$$X_N = X_{N=K} + (X_{N=0} - X_{N=K})\left[1 - \left(\frac{N}{K}\right)^z\right] \tag{3}$$

where N = population size, K = carrying capacity ($\lambda = 1$), $X_{N=0}$ = the value of the parameter when $N = 0$, $X_{N=K}$ = the value of the parameter at K, and z = shaping parameter. Because z-values are difficult to interpret, we have used a different scale. Let ρ be the N/K value reached when the z-value has changed half its range. Equation 3 can be rearranged to solve for z given the desired ρ-value.

$$z = \frac{\ln(0.5)}{\ln(\rho)} \tag{4}$$

Using Equation 4, we find that if we want a given parameter to have changed 50% of its range when $N/K = 0.9$ then $z = 6.58$. We investigated ρ-values between 0.50 ($z = 1$) and 0.95 ($z = 13.5$). The knife-edge limitation is therefore defined as $\rho = 0.95$, when the parameter has changed 50% of its range in 0.95 (N/K). Equation 3 (Allen 1976) is shown for different ρ-values in Figure 1 for birth rate for pinnipeds.

Changes in multiple parameters—In order to reduce the number of permutations of multiple parameters, changes were allowed which met two criteria: (1) parameter values must be biologically reasonable, and (2) changes in z must

Table 2. Minimum and maximum values allowed to maintain biological realism. Birth rate parameters assume a sex ratio of 0.5 and a maximum pregnancy rate of 90%. For the odontocete model calving interval is three years when $N = 0$ and five years when $N = K$.

Model	λ $X_{N=0}$	AFR $X_{N=0}$	AFR $X_{N=K}$	m $X_{N=0}$	m $X_{N=K}$	p_j $X_{N=0}$	p_j $X_{N=K}$
Pinniped	1.10	4	6	0.45	0.35	0.67	0.24
Odontocete	1.04	8	12	0.15	0.09	0.66	0.51

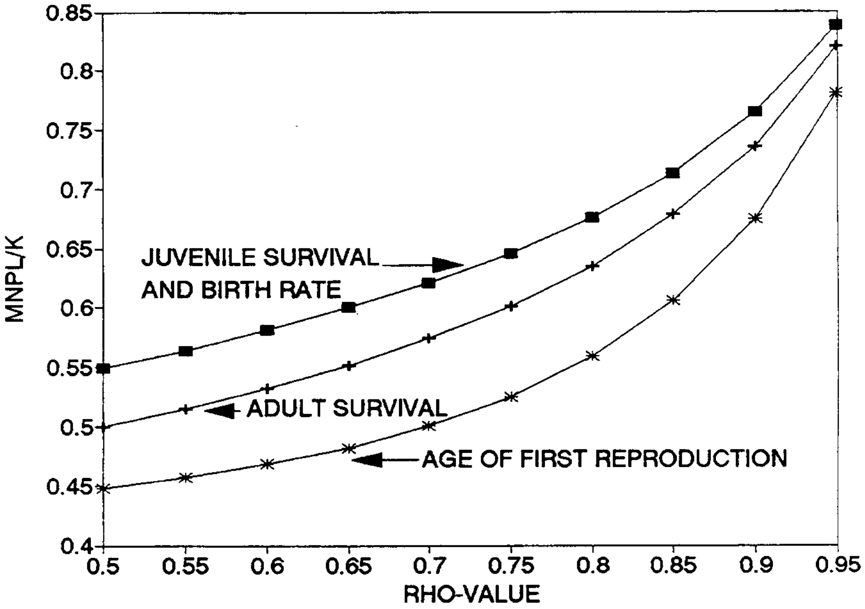

Figure 2. Single parameter changes (Table 1) resulting in a decrease in growth rate from $\lambda = \lambda_{max}$ to $\lambda = 1.0$. Values shown are for the odontocete model. Values for the pinniped model differed by less than 1%.

follow known empirical evidence (*i.e.*, density dependent changes are not knife-edge in form: $0.5 \leq \rho \leq 0.95$). Minimum and maximum values are given in Table 2.

RESULTS

Single parameter changes—Figure 2 shows MNPL for different ρ-values for changes in single parameters as shown in Table 3. Results are shown for the odontocete model as values from the pinniped model never differed by greater than 1%. There are several items to note from this figure. First, as shown by Goodman (1980), not all linear density dependent changes ($z = 1$) produce a MNPL/K at $K/2$ (MNPL/K = 0.5). In particular, juvenile survival and birth rate produce a MNPL/K of 0.55. These two rates are the same because the

Table 3. Demographic parameter values required to achieve specified λ by changing a single parameter from the default values in Table 1, for use in Equation 3.

Model	λ	m	AFR	p_j	p_a
Pinniped ($X_{N=K}$)	1.00	0.232	10.510	0.245	0.914
Pinniped ($X_{N=0}$)	1.10	0.643	1.840	0.680	1.000
Odontocete ($X_{N=K}$)	1.00	0.072	22.681	0.355	0.961
Odontocete ($X_{N=0}$)	1.04	0.189	2.875	0.935	0.999

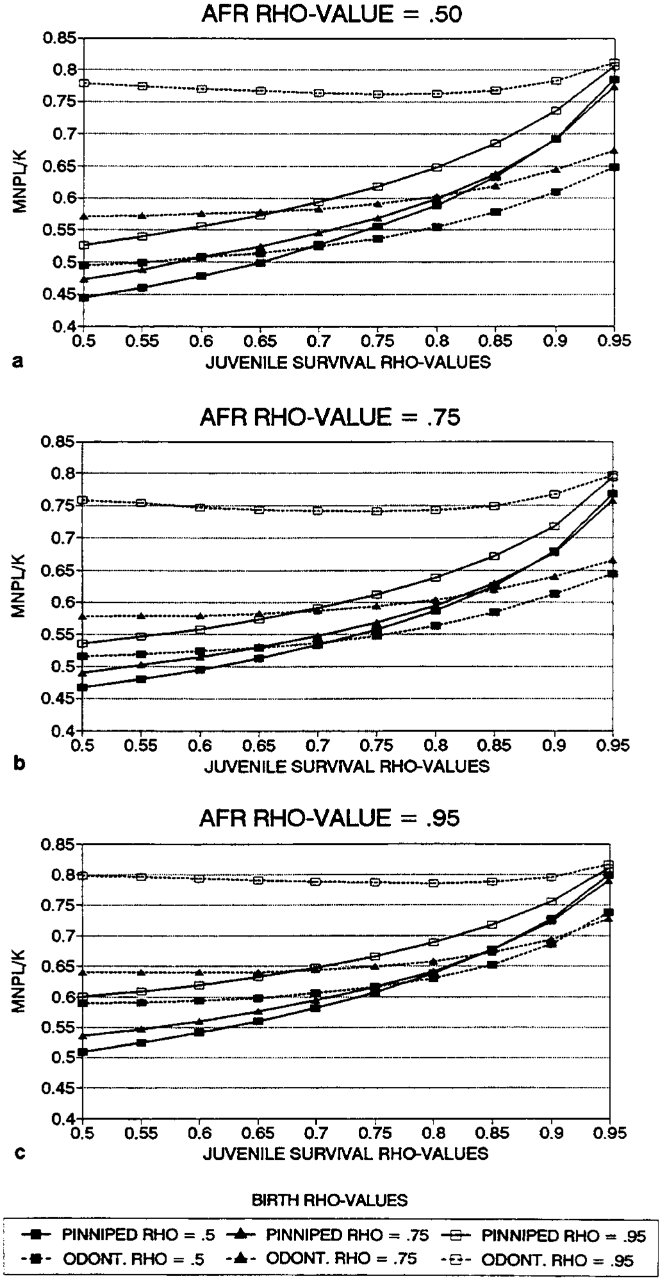

Figure 3. Multiple parameter changes resulting in a reduction in growth rate from $\lambda = \lambda_{max}$ to $\lambda = 1.0$. Figures a, b, and c correspond to *AFR* ρ-values of 0.50, 0.75, and 0.95 respectively. Pinnipeds (solid lines) and odontocetes (dashed lines) are shown for birth ρ-values of 0.50, 0.75, and 0.95. Lines between symbols are given for visual clarity.

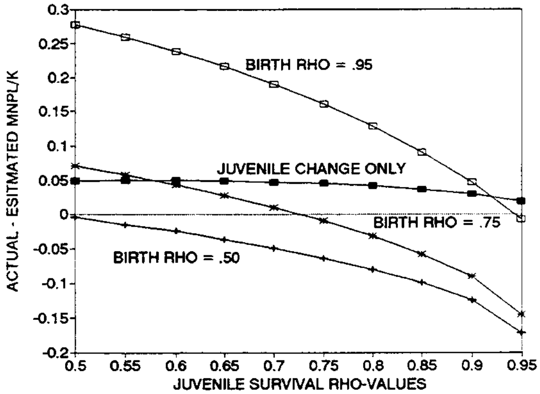

Figure 4. Bias in estimates of MNPL/K from assuming that $\theta = z$-value for juvenile survival. To obtain the actual MNPL/K value, the bias must be added to the value estimated from the z-value. The case shown is for odontocetes where juvenile survival is the only regulating mechanism and for three cases where *AFR* changes linearly ($z = 1$) and birth ρ-values are 0.50, 0.75, and 0.95.

elasticities are the same for these parameters. Recall that elasticity is the response in λ to a proportional change in the parameter. With only one year of juvenile survival, a reduction in juvenile survival or a reduction in birth rate cause the same reduction in the number of individuals recruited into the population. The small range of MNPL/K values for a given ρ-value irrespective of which parameter is being altered is not surprising. Even though λ is more sensitive to p_a, Table 3 reveals that much smaller proportional changes in p_a are required to produce the growth rate change. It may be surprising to note that even strong non-linearities ($\rho = 0.95$) do not produce MNPL/$K > 0.85$. Higher ρ-values will, of course, yield MNPL/K values > 0.85, but such highly concave functions imply no density dependent response until the population is very close to K. There are no empirical data to support such a knife-edge density dependent response. The final item to note is that the change required for a single parameter to accomplish all the density dependent change is often biologically unreasonable and sometimes (in the case of birth rate and *AFR*) biologically impossible. For example, in the pinniped model, AFR ranges from a minimum age (1.84) which is physically impossible to a maximum age (10.51) which is unlikely and was not observed when fur seals were thought to be near K in the 1950s (Scheffer 1955). Because marine mammals produce a single offspring and have a sex ratio of 0.5, values for birth rates cannot exceed 0.5. The maximum value in Table 3 for pinnipeds ($m = 0.643$) is therefore impossible. Similar arguments can be made for the same parameters in the odontocete model.

Changes in multiple parameters—All combinations of *AFR,* juvenile survival and birth rates for $\rho = 0.50$–0.95 were investigated. Results are shown in Figure 3. Note that changes in more than one parameter yield MNPL/K values which are less than those for equal ρ-values for changes in only a single parameter (also found in Fowler *et al.* 1980). The combination of three linear changes for the pinniped model ($\rho = 0.5$ ($z = 1$) for AFR, juvenile survival, and birth rate) actually yields an MNPL/K that is less than 0.5. Comparison of the pinniped model to the odontocete model shows that MNPL/K of the former to be more sensitive to changes in juvenile survival rate ρ-values and the latter to birth rate ρ-values. This is due to the differing magnitude of allowed change in these parameters (Table 2): birth rates vary more for odontocetes and juvenile survival rates vary more for pinnipeds. Thus, the models are sensitive to the minimum and maximum values. Changes in *AFR* ρ-values affect both models similarly when other ρ-values are low but have almost no effect on either when other ρ-values are high.

Consider the scenario where only data concerning juvenile survival were available. If we were to use the z-value from a fit of juvenile survival as the θ in Equation 1 how would our estimated MNPL/K compare to the actual MNPL/K when all birth and death functions are known? Figure 4 gives one example of bias for odontocetes. It can be seen that for a given ρ-value, even the sign of the bias cannot be inferred. The magnitude of the bias depends on the ρ-values of both the juvenile survival and birth rates. Therefore, it is not valid to infer MNPL/K from the functional form of a single demographic parameter. MNPL/K can be estimated either from population size estimates or from complete demographic models.

Discussion

Although it is likely that MNPL is found at values greater than $K/2$, the argument that MNPL should be very close to K (MNPL/$K > 0.8$) is unsupported. The only parameter for which empirical evidence lends credence to strong non-linearities is for juvenile survival in fur seals (Ragen 1990). Even here, many deterministic models have been used to fit the data with values for MNPL/K ranging from 0.43 to 0.93 (Ragen 1990). It is clear that when data are available for marine mammals, one of the primary density dependent regulating mechanisms is age of first reproduction (Fowler 1984). There is no evidence for non-linear change for this parameter (Fowler 1984, Lett *et al.* 1981), though power is undoubtedly low. As shown in Table 3, biological constraints make the likelihood of this parameter being the sole regulatory mechanism unlikely. It is therefore likely that population growth is regulated by several mechanisms, only some of which may be non-linear (Smith and Polacheck 1981). When several parameters change in a density dependent fashion, the result is that MNPL/K is less than that achieved by only a single non-linear growth rate regulating mechanism. If z-values for all parameters are high, MNPL/K values differ very little from values estimated for MNPL/K assuming $\theta = z$. On the other hand, disparities can be large if some parameter changes are linear.

The generalized pinniped and odontocete models were chosen to bracket the range of population growth rates observed in marine mammals. It may be argued, however, that these choices do not bracket the range of possible MNPL/K

values. Fowler (1988) argues that MNPL/K is related to rate of increase per generation. The generalized models have similar rates of increase per generation. To investigate the influence of rate of increase per generation on the conclusions of this paper, we chose the most extreme outlier in Fowler's work: *Stenella.* This genus has a similar rate of increase to the odontocete model but a shorter generation time. Choice of parameter ranges were from Chivers (1992). Results were very close to the odontocete model and did not compromise the conclusions from the generalized models.

Non-linearities in population regulation mechanisms which lead to linear decreases in per capita growth rates (MNPL/K = 0.5) have been noted in several laboratory systems (Barlow 1992, Kerfoot *et al.* 1985). Further, Barlow's experiment with guppies (*Poecilia reticulata*) (1992) showed highest sensitivity to density dependent somatic growth. Although mammals express determinate growth, AFR seems to be an important regulatory mechanism which may link body growth rate to population growth (Lett *et al.* 1981).

Unfortunately, we are only a little closer to defining likely ranges of MNPL/K. It seems likely that $0.5 < \mathrm{MNPL}/K < 0.85$. For a given species, the range may be able to be reduced. For example, if we know that for fur seals z-values were $z = 1$, $1 \leq z \leq 3$, and $3 \leq z \leq 9$ for *AFR,* birth and juvenile survival rates respectively, then $0.58 < \mathrm{MNPL}/K < 0.73$. A much more realistic fur seal model (Ragen 1990) calculated a distribution of MNPL/K from simulations using permutations of possible ranges of demographic values and z-values. MNPL/K occurred at highest frequency between 0.60 and 0.65 (corrected values; Ragen, personal communication). Unfortunately, there are few species for which we have the quantity of data available as for the fur seal.

Eberhardt (1977) proposed a general model for self-regulation in long-lived species which gave an order for age-specific density dependent responses. Such rigidity in growth regulation was questioned by a comparison of population dynamics of three species of Antarctic seals (Siniff 1984). These species, living in proximity to one another, showed varied responses which were attributed to different reactions to environmental variance. Thus, even within the Antarctic ecosystem and among closely related species, marked differences in density dependent age-specific birth and death rate responses exist. The deterministic equations discussed in this paper assume no environmental variance. Clearly, populations must evolve to respond to the stress caused by environmental changes. Marine environments change markedly over short time periods (El Niño events, fluctuations in prey availability in cold water regimes, *etc.*). Some marine mammal species are relatively fixed in space due to breeding or feeding requirements while others may be free to move over large distances to locate resources. It seems an act of faith to believe that all the likely different density dependent age-specific regulatory mechanisms would result in a narrow range of MNPL/K values. The exercise in this paper has demonstrated that even if dynamics were deterministic, without knowledge about all the density dependent age-specific birth and death rates, a single value of MNPL/K cannot be inferred. Distributions of MNPL/K for each species given a range of parameter estimates may be more appropriate considering the current amount and quality of data.

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