
Incorporation of Density Dependence and Harvest into a General Population Model for Seals

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INTRODUCTION

Population models constructed in an attempt to simulate the behavior of real populations of seals have historically incorporated convenient and sometimes arbitrary mathematical functions that have mathematically derived equilibria. At present, it is impossible to know what mathematical function best describes the form of the density dependence responses that are assumed operative in nature. Various functions have been applied (Chapman, 1961, 1973; Fowler and Smith, 1973; Allen, 1975; Lett and Benjaminsen, 1977; Eberhardt and Siniff, 1977), but until recently (Fowler, 1981; Chapter 23) no clear patterns have emerged. The various functions do seem to form a continuum ranging from conservative linear functions (Allen, 1975), to nonlinear functions (Eberhardt and Siniff, 1977; Fowler, 1981; Chapter 10). Differences are related to the degree of density dependence expressed at any particular density, with linear functions having a gradual and consistent depressing effect on reproduction or survival when compared to nonlinear functions which concentrate changes into certain ranges of population levels. Therefore, simulation with linear and nonlinear functions should produce a range of types of population responses that should bracket the true population response in nature. Also, many population models assume that the age structure of the harvest has little or no effect on the predictions of the model (but see Chapter 23). In addition, many population models ignore the fact that density dependence may be restricted to specific age classes with reproduction and survival of other age classes being essentially density independent (at least over the observed range of densities). If only those age classes beyond the ages in which reproduction and survival are density dependent are harvested, then it is conceivable that harvest mortality may not give rise to strictly compensatory responses (Brownie et al., 1978). Finally, some population models that incorporate density dependence are based on the assumption that the regulatory mechanisms are operative throughout the entire year. Some evidence exists that this is not the case for Weddell seals (DeMaster, 1978). It appears that, for this species at least, regulatory mechanisms are only operative at specific and predictable times of the year. The purpose of this chapter is to

investigate the ways several factors influence the dynamics of a population of Weddell seals as represented by a collection of assumptions in the form of a population model. These include (1) changing the density-dependent functions from linear to nonlinear form, (2) changing the age at which survival is density dependent (from pups to adults), (3) changing the age structure of the harvest from a harvest of pups to a harvest of adults, and (4) changing the time of the harvest. The latter allows early density-dependent harvest compensation (to be defined later) to occur in one case but not in another.

A PROJECTION MATRIX

A 25×25 projection matrix (Leslie, 1948) may be used for representing a population of female Weddell seals with 25 age classes. As constants, the entries of the top row (age specific reproduction as females born per female) were: $b_0 = b_1 = b_2 = 0$; $b_3 = 0.10$, $b_4 = 0.25$, $b_5 = 0.30$, $b_6 = 0.35$, and $b_7 = b_8 = \dots = b_{24} = 0.38$, as derived from DeMaster (1978), Siniff et al. (1977), and Stirling (1971). Similarly, the subdiagonal entries (age-specific survival) may all be set equal to 0.85 (DeMaster, 1978). Such a matrix model, with constant parameters, produces a constant growth rate and age structure (Leslie, 1945).

A more realistic approach involves a similar model that incorporates some type of density dependence into the transition matrix (Leslie, 1948; Fowler and Smith, 1973; Fowler and Barmore, 1979). Such density dependence is often assumed to be linear (Allen 1975), even though there is growing evidence to support nonlinear functions for large mammals in general (Fowler, 1981; and Chapter 23). In this analysis the following four density-dependent functions were used:

$$P_0 = A - M_0 X_1 \quad (1)$$

$$P_0 = A(1 - e^{-B(X_1 - X_1)}) \quad (2)$$

$$P_i = A - M_1 X_2 \quad i = 1, 25 \quad (3)$$

$$P_i = A(1 - e^{-B(X_i - X_2)}) \quad i = 1, 25 \quad (4)$$

where P_0 = annual pup survivorship

P_i = annual survivorship of seals i years old

A = maximum annual survivorship

M_0 = constant associated with the number of female pups and their survivorship

M_1 = constant associated with the number of females 4 years of age or older and their survivorship

X_1 = number of female pups

X_2 = number of females 4 years of age or older

B = a constant that describes the shape of the curve in equations (2) and (3)

X_k = the maximum number of female pups in the population

X_K = the maximum number of females 4 years of age or older in the population

The following values were used in the 22 simulations summarized in Table 1: $A = 0.85$; $M_0 = 0.000125$; $M_1 = 0.00003594$; $B = 0.02$; $X_k = 350$; $X_K = 1000$. The estimated maximum annual survivorship A is a value derived from the available empirical data (DeMaster, 1978). X_k and X_K were approximated by the maximum number of pups and adult females that have previously been recorded in the McMurdo Sound study area (DeMaster, 1978). The value of B was arbitrarily set equal to 0.02 (Eberhardt and Siniff 1977) and represents a relatively rapid change in the shape of the nonlinear function (Figure 1). M_0 was determined by simulating the population with the nonlinear form of pup survivorship until an equilibrium was reached, and then using the equilibrium values of P_0 and X_1 to solve for M_0 (Figure 1). A similar approach was used to solve for M_1 .

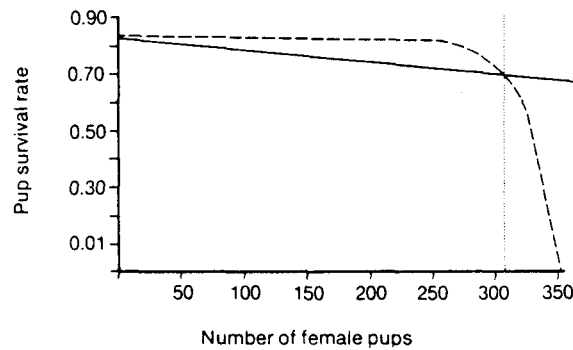


Figure 1 Linear (solid line) and nonlinear (dashed line) relationships between the survival rate for pups and the number of female pups born. The linear form is fit through the initial point (0, 0.86) and the equilibrium point (308, 0.69). Dotted line shows equilibrium level of female pups born.

The simulation was allowed to continue until an equilibrium was reached or until the population went extinct as was done by Fowler and Smith (1973) and Allen (1975):

$$X_{t+1} = L(X_t)X_t - H_t \quad (5)$$

where X_{t+1} = the 25×1 population vector for year $t + 1$

$L(X_t)$ = the 25×25 variable projection matrix expressed as a function of X_t

X_t = the 25×1 population vector for year t

H_t = the 25×1 harvest vector in year t

The original population vector was derived from Stirling (1971) and DeMaster (1978):

Age	Frequency	Age	Frequency
1	232	10	44
2	179	11	37
3	152	12	30
4	130	13	26
5	108	14	22
6	90	15	18
7	75	16	15
8	63	17	12
9	53	18	10

At each iteration of the model, a new population vector is calculated. Appropriate portions of the new population vector are then used to calculate the entries for the projection matrix using various combinations of equations (1)-(4). Thus, the influence of changing the form of the density-dependent function and the age at which survival is density dependent can be investigated. By changing the harvest vector from one containing all pups to a vector of only seals 4 years of age or older (harvest from each age class was proportional to the size of the particular age class), the influence of varying the age structure of the harvest can be investigated.

Equation (5) is representative of a situation where the harvest occurs after the age-specific survival and reproduction have been realized. If the harvest occurs after the rates of survival and reproduction have been determined, there is no chance for further compensation by the nonharvested segment of the population during that unit of time. In other words, there is no increase in the rates of reproduction or survival as a result of the removal of a segment of the population by harvesting. Such reactions, by necessity, can occur only in the next time step. This may or may not be a realistic situation. It is possible that populations may react to the density immediately following harvest (rather than prior to harvest) thus compensating for the harvest in the same time step (a reversal of the situation above). To determine the influence that any such harvest compensation may have on the equilibrium population a simulation that calculated the harvest before the projection was also investigated. This is represented in equation form as:

$$X_{t+1} = L(X_t)(X_t - H_t) \quad (6)$$

In this case, the entries for the projection matrix are calculated from the population vector subsequent to the harvest.

The simulations of female Weddell seal populations, as produced for this study (Table 1), can be broken down into three categories. These are (1) simulations with no harvest (Table 2), (2) simulations in which only pups are harvested (Table 3), and (3) simulations in which only animals 4 years of age and older are harvested (Table 4). Cases 1 and 2 and cases 3 and 4 must necessarily be equivalent in all ways at equilibrium because of the way in which the slope of the linear form of the density dependence was derived. Cases 5 and 6 (Table 2) incorporated both adult and pup survivorship that was density dependent. In these cases, the equilibrium population and number of female pups are not the same. This is because the equilibrium survival rates (P_0/P) are not associated with the same number of female pups and the number of adult females for the linear and nonlinear models.

Table 1 Summary of 22 Simulations

Case	P_0	P	Harvest Compensation	Composition of Harvest
1	Linear	—	No	0
2	Nonlinear	—	No	0
3	—	Linear	No	0
4	—	Nonlinear	No	0
5	Linear	Linear	No	0
6	Nonlinear	Nonlinear	No	0
7	Linear	—	No	Pup
8	Nonlinear	—	No	Pup
9	—	Linear	No	Pup
10	—	Nonlinear	No	Pup
11	Linear	Linear	No	Pup
12	Nonlinear	Nonlinear	No	Pup
13	Linear	—	Yes	Pup
14	—	Nonlinear	Yes	Pup
15	Linear	—	No	Adult
16	Nonlinear	—	No	Adult
17	—	Linear	No	Adult
18	—	Nonlinear	No	Adult
19	Linear	Linear	No	Adult
20	Nonlinear	Nonlinear	No	Adult
21	—	Linear	Yes	Adult
22	—	Nonlinear	Yes	Adult

RESULTS OF SIMULATIONS

The results of simulations without harvest (Table 2) show that different density-dependent mechanisms will produce different equilibrium populations. Dif-

Table 2 Results of Weddell Seal Population Simulation in Which There Is No Harvest^a

Case (see Table 1)	Population	X_1	P_0/P	Mean Age	Time to Return (20% reduction)
1. Linear P_0	1701	308	0.6937	5.05	250
2. Nonlinear P_0	1701	308	0.6936	5.06	90
3. Linear P	1790	301	0.8202	4.51	230
4. Nonlinear P	1790	302	0.8201	4.51	50
5. Linear P_0 and P	893	156	0.7708/C.8346	4.76	170
6. Nonlinear P_0 and P	1666	290	0.7715/0.8347	4.76	40

^aSee Table 1 and text for details concerning the nature of the model in each case.

ferent levels of pup production will be associated with these equilibrium populations. The largest difference in equilibrium occurred between cases 4 and 5. When both pup and adult survival are linearly density dependent, the number of pups and adults has to be substantially lower to reach equilibrium than when only one of these density-dependent mechanisms are employed. It is interesting that when only the survival of pups (P_0) is density dependent its equilibrium is less than when only the adult survival is density dependent. This is due to the differences in the composition of the resulting populations in the two cases, as explained in Chapter 23.

Changing the age classes subject to density-dependent survival thus has a predictable effect on the mean age of the equilibrium population. The same is true for the time necessary for the population to return to the equilibrium. When the survival of pups is density dependent, the mean age of the equilibrium population is greater than the mean age of the population when the survival of both pups and adults are density dependent. Also, when survival for all age classes is density dependent, the mean age at equilibrium is greater than when the survival for adults alone is density dependent (see Chapter 21).

Estimates of the time necessary for the population to return to equilibrium were generated by reducing each age class of the equilibrium population by 20%, and then finding how long it took for the population to reach a constant mean age (determined by a predetermined and uniform criterion). The nonlinear models were found to return more rapidly than the linear models because the nonlinear models used in this study have essentially maximum rates of growth until they approach the maximum population, while the linear models have growth rates that are constantly declining as the population increases. The most rapid return took 40 years, while the slowest return took 250 years (Table 2). DeMaster (1978) documented a 50% reduction in the breeding population of the Weddell seal in McMurdo Sound between 1975 and 1976. Stirling et al. (1977) documented a 50% reduction in the number of ringed seals (*Phoca hispida*) in the western Canadian Arctic. Returning from such reductions, of course, would require even more time than indicated by these models.

With a pup harvest as part of the population model, the population giving rise to a maximum sustainable yield (MSYP) and the maximum sustained yield itself

Table 3 Results of Weddell Seal Population Simulation in Which There Is a Harvest of Pups^a

Case (see Table 1)	MSYP ^b	MSYP		Yield (%)	Maximum Population	H_1 max
		Equilibrium	H_1			
7. Linear P_0	938	0.55	17	10	—	—
8. Nonlinear P_0	1396	0.82	43	17	—	—
9. Linear P	1018	0.57	14	8	—	—
10. Nonlinear P	1481	0.83	43	16	—	—
11. Linear P_0 and P	574	0.64	7	7	—	—
12. Nonlinear P_0 and P	1373	0.82	40	16	—	—
13. Linear P_0 compensation	1011	0.59	20	11	—	—
14. Nonlinear P_0 compensation	1665	0.98	52	17	1810	40

^aSee Table 1 and text for details concerning the nature of the model in each case.

^bPopulation giving rise to a maximum sustainable yield (MSY).

(MSY) were determined by finding the equilibrium population at various levels of harvest. The largest harvest that the population could sustain was considered to be the MSY. By altering the form of the density-dependent function, the age at which it operates, and the time at which it operates, a range of corresponding MSYP were determined. The MSYP, expressed as a percentage of the equilibrium population (no harvest) was found to vary between 55 and 98 (Table 3). In general, if only the form of the density dependence was changed, simulations with nonlinear density dependence had higher MSYP than the models with linear density dependence. Similarly, nonlinear models tended to have higher MSY values when expressed as a percentage of the total pup production. A unique situation arose with nonlinear models in that some harvest rates actually increased the equilibrium populations (Table 3, case 14). In this case, harvesting 40 pups increased the survivorship of the remaining pups to such an extent that the equilibrium population of the model was 109 seals larger than the equilibrium population with no harvest at all.

Table 4 Results of Weddell Seal Population Simulation in Which There Is a Harvest of Adults^a

Case (see Table 1)	MSYP		
	MSYP	Equilibrium	Harvest
15. Linear P_0	1166	0.69	7
16. Nonlinear P_0	1570	0.92	22
17. Linear P	831	0.46	10
18. Nonlinear P	1437	0.80	24
19. Linear P_0 and P	665	0.74	3
20. Nonlinear P_0 and P	1475	0.89	21
21. Linear P compensation	831	0.46	10
22. Nonlinear P compensation	1486	0.83	25

^aSee Table 1 and text for details concerning the nature of the model in each case.

When the age structure of the harvest is changed from exclusively a pup harvest to a situation in which all seals 4 years of age or older (approximate age of sexual maturity and subsequent return to breeding population: Stirling, 1971; Siniff et al., 1977) are harvested, the MSYP, when expressed as a percentage of the nonharvested equilibrium population, varied between 46 and 92 (Table 4). This is essentially the same as the range of MSYP for the pup harvests. The cases with adult harvests were similar to cases with pup harvests in that those with linear density dependence had lower MSY values and equilibrium populations than those with nonlinear density dependence. The maximum adult harvest occurred in the case where nonlinear density dependence of adult survivorship and harvest compensation were incorporated. In comparing the maximum yields for pup and adult harvests, roughly twice as many pups can be harvest from one age class as adults can be harvested from 21 age classes. This supports

the prediction of Eberhardt and Siniff (1977) that marine mammal populations are extremely sensitive to increases in adult mortality.

The simulations that incorporated pup harvests of various types had MSY values that ranged from 7% (Table 3, case 11) to 17% (Table 3, cases 8 and 14) of the pup numbers. Comparable ranges were even greater when harvest of adults is included in the cases being compared. For all harvest strategies that were examined in this work the MSYP, given as a percentage of the nonharvested equilibrium population, varied between 46 and 98. This analysis suggests that reasonable management decisions must incorporate information concerning the regulatory mechanisms, harvest compensation, time at which density dependence is expressed, and the age structure of the harvest. Specifically, models and predictions for one species should not necessarily be accepted as general guidelines for the management of other species.

DISCUSSION

The Model

The main purpose of this chapter is to demonstrate the effects of different regulatory processes, types of harvests, and harvest schedules. Therefore, the particular hypothetical relationships used to model the regulatory processes can be considered only as rough approximations of what may actually happen. The four types of density dependence in equations (1)-(4) represent a wide range of reasonable types of density dependence. By examining the extremes of a reasonable spectrum of possibilities, minimum and maximum estimates can be produced to create an interval within which the true value will occur.

Other modes of regulation need investigating. Eberhardt (1977), for example, suggests that in addition to the survival of pups, age of first reproduction is a very important mechanism in the regulation of populations of marine mammals. For simplicity, age-specific reproduction was assumed constant in this model. This needs to be investigated. Some of the effects of changing this variable are examined by Fowler and Smith (1973), Fowler and Barmore (1977), and Eberhardt and Siniff (1977), and in Chapter 23. Preliminary modeling in this study suggested that manipulating the age of first reproduction may cause cyclic behavior (see May and Oster, 1976).

The particular nonlinear function used in this work is attractive because it comes close to approximating the concept of a threshold density. That is, survival, for example, is essentially density dependent only when density is above the threshold. Chapman's 1973 presentation of data on northern fur seals (*Callorhinus ursinus*) seems to support the threshold concept because recruitment was found to appear independent of density at low population levels. These are dynamics that conform to the general pattern described by Fowler (1981) and in Chapter 23. In this pattern, most density-dependent change is restricted to a range of levels close to the equilibrium for large mammals.

Models Without a Harvest

This analysis indicates that mechanisms that have relatively small effects on the growth rate of a population indeed may regulate those populations. However, the time necessary for this regulation to occur may be longer than the period during which environmental conditions are constant enough to allow for a constant equilibrium population. Because the minimum time necessary for the population to return to the equilibrium (after a 20% reduction in the population) was 40 years in this work, it seems unlikely that seal populations would ever reach a stationary age distribution (age distribution where age structure is constant). If it is assumed that declines can occur much more rapidly than increases (Stirling et al. 1977; DeMaster, 1978; Siniff et al., 1977; Payne, 1977), it may be that populations of pinnipeds will commonly be found to be increasing to a level their resources can maintain. However, periodically populations may rapidly decline, possibly owing to changes in some aspect of the physical environment. This type of growth pattern needs to be considered as far as future methodologies and research (see Fowler, 1981).

Considering the predictable manner in which the mean age of a population responded to various types of density dependence, it may be possible to use the change in the mean age of the population as it grows to infer something about the age class for which density-dependent mechanisms are operative. That is, if the mean age of the population increases as the population increases, it is most likely that density-dependent factors are affecting the younger age classes or the birth rate (see Chapter 21), and vice versa. This approach may not be particularly sensitive because of the relatively wide confidence interval around the mean age that is generated from a distribution of ages. However, such a technique has been used successfully with southern elephant seals (*M. leonina*: Laws, 1960) to determine the number of bulls to be culled. Further studies of this population parameter should be conducted.

Models Incorporating Harvest

The incorporation of age-specific harvests into a general population model seems to be necessary in light of the findings in this study and as shown in Chapter 23. The fact that the maximum sustainable yield of adult female Weddell seals was only 1.7% in the most liberal population model in this study suggests that harvests as low as 20 seals from a population of 1000 adult females may be critical. Since 1964, an average of 30 adult females have been harvested from the McMurdo population of Weddell seals in the Antarctic. This population contains roughly 1000 adult females. The 1977-1978 harvest of this population was roughly 35 adult females (combined take of United States and New Zealand). The gradual decline of this population since 1967 may be, in part, a result of this adult harvest (DeMaster, 1978).

On the other hand, harvesting 17% of the female pup production could be sustained by this same simulated population. It is even conceivable that some

harvests may temporarily increase populations. A similar mechanism has been suggested for black bears (Kemp 1974).

Analyses that have incorporated factors similar to those discussed in this chapter have been presented by Stirling et al. (1976), Allen (1975), and Chapman (1961). Stirling et al. (1976) simulated brown bear and polar bear populations with a fixed age-specific rate of reproduction and survival. Although it is not possible to generate MSY values with their model, a type of sensitivity analysis can be generated. The authors found that various population projections were extremely sensitive to manipulations that affected the mortality of adult females.

Chapman (1961) estimates the MSY of 3-year-old male northern fur seals (*Callorhinus ursinus*) with two different types of density-dependent rates of recruitment. Both models are nonlinear, with one model producing an MSY of 45%, when the population of pups is 68% of the maximum population of pups. The other model produces an MSY of 46%, when the population of pups is 72% of the maximum pup population. The estimated MSY of 3-year-old fur seals is much greater than the estimated MSY of pup Weddell seals in this chapter. This is primarily because the intrinsic growth rate for fur seals is much larger than for Weddell seals. However, the population at which the MSY occurs for fur seals is bracketed by the estimates of the MSY population produced in this chapter for Weddell seals.

CONCLUSIONS

It is difficult to generalize from these results because of the hypothetical nature of the model and because each manipulation was associated with a unique MSY and equilibrium population. Estimates of the MSY were found to be higher for nonlinear than linear models, higher for pup harvests than adult harvests. These results are consistent with the general patterns described in Chapter 23. Models that incorporated harvest compensation produced higher MSY than models that did not.

The management of populations of pinnipeds is confounded by difficulties in assessing population levels, regulatory mechanisms, and controlling factors. The recent criticisms of the concept of MSY (Larkin, 1977) and the current use of the concept of optimum sustainable population (OSP) (Marine Mammal Commission, 1975) seem to stem from an awareness of how sensitive current MSY estimates are to changes in the marine community (particularly of fishery stocks) and changes in the age structure of the harvest. In the future, the population models that are used to estimate MSY values must incorporate these factors. Changes in the community structure will necessarily alter the equilibrium population of seals, and adjustment procedures need to be established. Perhaps initial carrying capacity estimates should be compared with current carrying capacity estimates. Perhaps, the effect of varying environments may have to be incorporated in future models by determining MSYs (stated as a percentage) in

advance, but then delaying the determination of the quotas until an assessment of the current populations are made. Finally, the idea that one general model will predict maximum harvest rates and equilibrium stocks for many or all seals seems doubtful. For each species, the regulating mechanisms, and controlling factors must be identified before MSYs can be derived. In addition, the age structure of any proposed harvests must be incorporated in management oriented models because this is critical in determining the MSY for any particular population.

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