An Analysis of a Hypothetical Population of Walruses

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ABSTRACT

A series of computer simulations of the Pacific walrus population, using a variable Leslie model, were conducted primarily to test the hypothesis that the population increased from about 70,000 in 1955 to about 200,000 in 1975 and, secondarily, to evaluate the reliability of the data available on adult survival rates. Published estimates of the population size, the sex ratio of adults, age at sexual maturity, average reproductive rate, adult mortality, and size and sex/age composition of the annual harvests were incorporated into the model. The results suggested that, either the estimates of size of the 1955 population were too low, or that the survival rates of adults were significantly higher than believed. They suggested further that an increase to 200,000 in 20 yr would have been possible, if the initial population in 1955 had been made up of about 94,000 to 98,000 animals, the sex ratio of adults was 1 male:3 females, and the adult survival was 0.96, with nonlinear density dependence. Such an increase would have been impossible with linear density dependent functions, smaller initial population size, or lower adult survival rates. The maximum sustained yield (MSY) of the hypothetical population, assuming continuation of the current harvest composition at 3 males:1 female, would be between 3 and 5% and should be available when the population is between 59 and 91% of the carrying capacity (*K*), assuming environmental stability. The maximum net productivity (MNP) of this hypothetical population was estimated to be attained at 50 to 84% of *K*.

РЕЗЮМЕ

Моделирование на счетно-решающем устройстве было произведено с помощью «переменной модели Лесли», главным образом, чтобы проверить гипотезу об увелечении численности тихоокеанского моржа приблизительно с 70,000 в 1955 г. до 200,000 голов в 1975 г., а также оценить надежность имеющихся данных о способности выживания взрослых зверей. Опубликованные данные по оценке величины популяции, половому соотношению взрослых, возрасту полового созревания, среднему темпу воспроизводства, смертности взрослых, возрастному составу и ежегодной добычи использовались в модели. Результаты дают основание предполагать, что величина популяции в 1955 г. была слишком низкой или темп выживания взрослых был гораздо выше, чем это считалось ранее. Кроме того, результаты позволяют предпологать, что увеличение до 200,000 голов в течение 20 лет было бы возможным, если популяция в 1955 г. составляла 94 - 98,000 голов, половое соотношение взрослых 1 самец: 3 самки и выживание взрослых - 96% с нелинейной плотностью зависимости. Такое увеличение было бы невозможным с линейной плотностью зависимости, меньшей первоначальной величной популяции, или низким выживанием взрослых. Максимальная ежегодная добыча гипотетической популяции, при сохранении в добыче соотношения 1 самка: 3 самца, будет составлять 3 - 5%. Такой уровень добычи возможен, если при максимальной плотности саморегулирующейся популяции [*K* = 59 - 91%] и стабильности экосистемы. Считаем, что максимальное чистое производство этого гипотетического населения достигается при 50 - 84% *K*.

По оценке автора максимальная чистая продуктивность данной гипотетической популяции может быть достигнута при *K* = 50 - 84%.

INTRODUCTION

In the late 1950's, the size of the Pacific walrus, *Odobenus rosmarus divergens*, population was considered to have been between 40,000 and 70,000 animals (Fay 1957; Kenyon 1960;[2] Fedoseev 1962). Nevertheless, Kenyon (footnote 2) felt that the actual population size in the late 1950's may have been higher than 70,000. Estes (1976),[3] Estes and Gilbert (1978), and Estes and Gol'tsev (1984) supported Kenyon's judgement with evidence that Fay and Fedoseev had underestimated the number of walruses in the American sector of the Chukchi Sea. More recent estimates of the Pacific walrus population have placed it at 140,000 to 200,000 (Estes and Gol'tsev 1984) and 168,000 to 250,000 individuals (Krogman et al. 1978[4]). Estes and Gilbert (1978) concluded that estimates produced from limited aerial surveys should not be considered reliable.

Perhaps the best quantitative information available concerning the Pacific walrus population is contained in the American and Soviet harvest data from 1959 to 1975 (Harbo 1961;[5] Burns 1965[6]

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[2]Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25-28 April 1960. Unpubl. rep., 39 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

[3]Estes, J. A. 1976. The reliability of aerial surveys to estimate population abundance of marine mammals. Consideration from a survey of Pacific walrus. Scientific Consultants on Marine Mammals, Bergen, Norway. 31 August-September 1976. [FAO] Advis. Comm. Mar. Resour. Res. ACMRR/80, 13 p.

[4]Krogman, B. D., H. W. Braham, R. M. Sonntag, and R. G. Punsly. 1978. Early spring distribution, density, and abundance of the Pacific walrus (*Odobenus rosmarus*) in 1976. Final report R.U. 14, 47 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

[5]Harbo, S. J., Jr. 1961. Walrus harvest and utilization. Annual project segment report, Federal Aid in Wildlife Restoration. Alaska Dep. Fish Game, Juneau, 25 p.

[6]Burns, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Dep. Fish Game, Juneau, 48 p.

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and unpubl. data; Krylov 1968; F. H. Fay[7]). These data include the retrieved kill and estimated losses from wounding and sinking; for the American harvest, they also include the sex ratio of adults and the number of calves taken. Studies of the reproductive organs from the harvested animals have produced estimates of age-specific rates of fecundity (Fay 1960;[8] Burns footnote 6; Krylov 1968), but these estimates generally have not been accepted due to suspected sampling bias in the harvests and in the assumptions of the estimation process.

To date, then, "relatively" reliable information exists on the size and sex/age composition of the Alaskan walrus harvests from 1955 to 1975, and on the age-specific rates of reproduction. Only the total harvests are known from the Soviet side. The estimates of population size in 1955 to 1975 are questionable, and the estimated rates of natural mortality appear to be unreliable. Nevertheless, these were the best figures available and of sufficient quality for use in a preliminary computer model of the Pacific walrus population.

The primary purpose of integrating the existing estimates of population parameters into the format of a computer model was to test the hypothesis that the Pacific walrus population could have increased in size from 70,000 to 200,000 animals in the 20 yr from 1955 to 1975. Such a model can be used also to estimate unknown parameters, when all others are fixed, and to assess the reliability of any that are in question. In addition, the interrelationships between the various parameters can be examined, and a better understanding can be gained of the relative importance of each to the population.

METHODS

The population model used in this instance was a modification of Leslie's (1945) model, as described by DeMaster (1981); similar models were described by Fowler and Smith (1973) and by Fowler and Barmore (1977).[9] The model assumes that the influence of density dependence on the life history parameters will be within the range of the following two types of functions:

$$Pi = A - c N_x \qquad \text{(linear)}$$

$$Pi = A\,(1 - \exp\,[-b\,(k - N_x)]) \qquad \text{(nonlinear)}$$

where Pi = annual survival of the ith age class
A = maximum annual survivorship
N_x = number of females 4 yr old and older
k = maximum number of females 4 yr old and older
b = constant associated with the shape of the curve
c = constant associated with the slope of the curve.

The initial values for the projection matrix (Tables 1, 2) were derived from the American and Soviet data. Only the female segment of the population was incorporated into the model; the sex ratio was assumed to be constant at 1 male:3 females (Fay 1982). The initial population vector was calculated by solving the following equation for N_0, the number of female calves in the initial population:

$$P = N_0 + .94\,N_0 + (.94)(.90)N_0 + (.94)^2(.90)N_0 + \sum_{x=1}^{36}(.94)^2(.90)(.96)^x$$

where P = 52,500, the number of females in a population of 70,000 walruses. Subsequent age classes were calculated by using the age-specific survival rates from Table 1.

The number of females 4 yr old and older (k) in the maximal population of about 200,000 walruses (Fay 1957) was assumed to be 150,000. The constant b was arbitrarily set at 0.002, which represents a relatively rapid change in the shape of the nonlinear function (Eberhardt and Siniff 1977). The constant c was set at 0.0000007, which was calculated directly from the nonlinear model as the slope between the two points described by the survivorship and the population at equilibrium, given an initial survivorship of 0.96 at a population level of 0 (DeMaster 1981). In this way, the simulations with linear and with nonlinear density dependence had the same equilibrium population.

The population model assumed that only animals 4 yr old and older were harvested. The harvest of a particular age class was weighted in proportion to the frequency of occurrence of that age class in the harvest data. Compensatory and additive harvests were represented by the following equations (DeMaster 1981):

Table 1.—Parameters used in the population models, where m_x is the age specific reproductive rate, and p_x is the age specific survivorship.

Age	m_x	p_x	Age	m_x	p_x
0	0	0.94	20	0.22	0.96
1	0	.90	21	.22	.96
2	0	.94	22	.22	.96
3	0	.96	23	.22	.96
4	0	[1].96	24	.22	.96
5	0.10	.96	25	.15	.96
6	.12	.96	26	.15	.96
7	.17	.96	27	.15	.96
8	.22	.96	28	.15	.96
9	.22	.96	29	.15	.96
10	.22	.96	30	.15	.96
11	.22	.96	31	.15	.96
12	.22	.96	32	.15	.96
13	.22	.96	33	.15	.96
14	.22	.96	34	.15	.96
15	.22	.96	35	.15	.96
16	.22	.96	36	.15	.96
17	.22	.96	37	.15	.96
18	.22	.96	38	.15	.96
19	.22	.96	39	.15	.96

[1]Survival from age 4 and older assumed to be density dependent. All other parameters are assumed constant.

Table 2.—Assumed parameters for estimation of adult survival necessary for the population to increase from 70,000 to 200,000 in 20 yr.

Parameter	1955	1975
Female population	52,500	150,000
Total population	70,000	200,000
Sex ratio	1♂:3♀	1♂:3♀
Female kill	1,675	1,675
Total kill	6,700	6,700
Sex ratio of kill	1♀:3♂	1♀:3♂

[7]F. H. Fay, Associate Professor, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. October 1979.

[8]Fay, F. H. 1960. Investigations of the Pacific walrus. Terminal report, Project 26. Arctic Institute of North America, Montreal, Canada, 72 p.

[9]Fowler, C. W., and W. J. Barmore. 1977. A population model of the northern Yellowstone elk herd. *In* R. M. Linn (editor), Proceedings First Conference on Scientific Research in the National Parks, New Orleans, Louisiana, November 9-12 1976. Vol. 1, p. 427-434.

harvest mortality additive:

$$X\ (i+1) = L[X\ (i)—H\ (i)],$$

harvest mortality compensated for:

$$X\ (i+1) = L[X\ (i)—H\ (i)],$$

where $X\ (i)$ = the population vector at time i
L = the projection matrix
$H\ (i)$ = the harvest vector.

Using this model, a series of simulations was computed in which the maximum annual survivorship (A) was increased in each simulation until the population model produced the desired final size. The total kill of females was assumed to be constant over the 20-yr period. The average kill was derived from known harvest data.

RESULTS

The hypothetical population, given a nonlinear density dependent function, increased from 70,000 to 200,000 in 20 yr only when A, the annual survivorship, was set to equal 0.99. This value of A was necessary whether or not the harvest mortality was compensatory. The simulated population, given a linear density dependent function, could not increase from 70,000 to 200,000 in 20 yr, even when A was set at 1.00.

Because the natural rate of adult survival probably could not have been as high as 0.99 to 1.00, one must assume that some other component of the model is incorrect. For the reasons given by Estes and Gilbert (1978), the most questionable component is the initial size of the population. Given the entries for the projection matrix from Tables 1 and 2 (excluding initial population size), nonlinear density dependence, and a harvest mortality that was additive, the initial population of females would have had to have been 73,828 (total population 97,828) to have produced the hypothetical final population of 200,000 in 20 yr. If the harvest mortality was assumed not to be additive, an initial population of 70,645 females (total population 94,194) would have been necessary for the increase to 200,000. If the form of the density dependent function was assumed to be linear, initial populations even of these sizes could not have reached 200,000 in 20 yr, given an adult female harvest of 1,675/yr.

In the United States, the Marine Mammal Protection Act of 1972 (MMPA) dictates that marine mammals should be managed at the level of "optimum sustainable population" (OSP). The concept of OSP is interpreted to mean that the population should remain between an upper level imposed by environmental constraints (commonly called K) and a lower level at which the population would produce the greatest annual increment (maximum net productivity = MNP) if the population were not being harvested. To estimate this lower level directly from a population that is being harvested is impossible, but it can be estimated through modeling. Given the age specific rates of births and deaths in Table 1 and the nonlinear density dependent function previously described, the MNP of the simulated population would occur at 84% of K, the equilibrium population (Table 3). For simulations with linear density dependence, the MNP would occur at 50% of K. If we assume that the real MNP is within the range of these two forms of density dependence, the lowest level of the population that would be acceptable under the MMPA would be between 50 and 84% of K.

Current information on the Pacific walrus population suggests that it has increased dramatically since 1955. Within the guidelines of the MMPA, the population could conceivably be managed somewhere between K and the MNP levels. As a starting point, the maximum sustainable yield (MSY) of a specific segment of the population can be estimated, but only if various age and sex specific life history parameters are known. In addition, how these parameters respond to changes in density must be known. Even then, the estimated MSY is only reliable if the environment is relatively constant. To estimate the MSY of adult female walruses, a series of simulations were computed, in which the harvest was continually increased, until the population no longer could sustain it (DeMaster 1981). Using the life history parameters of Table 1 and a nonlinear form of density dependence, the MSY of adult females (females 4 yr and older) would be 5.1% of the total population of females, and would occur at 91% of K (Table 3). If the density dependent function was assumed to be linear, the MSY of adult females would be 2.3%, and would occur at 59% of K. Obviously, we do not know the proper form of the density dependent function, but these results suggest that an adult female harvest of 2 to 5% could be sustained, and presumably would result in the population reaching an equilibrium when it was between 59 and 91% of K.

Table 3.—Comparative dynamic characters of walrus population models with linear and nonlinear density dependence.

Character	Density dependence	
	Linear	Nonlinear
Maximum net productivity (MNP)	50% of K	84% of K
MSY (no compensation)	2,100 adult females	6,800 adult females
Population at MSY_{nc}	59% of K	86% of K
MSY (compensation)	2,200 adult females	7,400 adult females
Population at MSY_c	59% of K	91% of K

DISCUSSION

The exact details of the recovery of the Pacific walrus population are not known, but at least a partial recovery has taken place (Burns footnote 6; Fay footnote 8; Estes and Gilbert 1978; Estes and Gol'tsev 1984). This recovery has occurred in spite of a continual harvest of adults. The average growth rate necessary for a population to double in 20 yr is 1.035, and to triple in 20 yr is 1.056. Such rates of growth are common for many species of marine mammals (Eberhardt and Siniff 1977), but seem somewhat improbable in this instance, considering the low productivity and ongoing harvest of Pacific walruses.

The purpose of this paper was to produce a model that would incorporate the existing data and shed some light on the reliability of the estimate of population size in 1955 and the estimated rate of annual mortality. The results from the various simulations suggest that, either the natural rate of adult mortality is extremely low relative to other pinnipeds (Eberhardt and Siniff 1977), or that the population estimate for 1955 was too low.

The model described in this paper was based on numerous assumptions for which substantive data are few and, in some cases, questionable. In all of the simulations, I assumed that the sex ratio of the adult population remained constant at 1 male:3 females, based on Fay's (1982) derivations from shipboard visual and aerial photographic surveys of the Pacific walrus population. Further information on herd composition and how it varies throughout the year is needed for improvement of the estimate of adult sex ratio. Simulations in which the sex ratio is assumed to be 1:2 and 1:1 also should be computed. The effect of these would be to increase the difference between the estimated and required population in 1955, given the life history values of Table 1. Increasing this difference will only strengthen the argument that either the 1955 population estimate was too low or that estimates of adult survival were too low. Second, I have assumed that the environment of the walrus remained relatively constant. Although human perturbation (other than hunting) probably has been minimal over the past 20 yr, natural perturbations may have occurred and not been recognized.

In all of the simulations where a harvest took place, I assumed that the sex ratio of the harvest was 3 males:1 female, and that a constant number was taken each year. Data concerning the sex ratio of the harvest supports a 1:3 ratio (Burns footnote 6; Fay footnote 8), but the numbers taken were not constant; rather, they declined from about 9,000 in 1955 to about 3,000 in 1969, and have been rising slowly since then to about 7,000. The effects of these changes on the population probably were insignificant, if the initial harvests were low enough to allow the population to increase (which, apparently, it did).

Data on the kinds of density dependent factors influencing this population were not available at this writing. Simulations which incorporate density dependent reproduction or calf survival should be computed.

Evidence from Weddell seals, *Leptonychotes weddelli*, suggests that reproduction may be relatively unaffected by changes in density, because the time of reproduction does not coincide with the seasonal onset of poor feeding conditions (DeMaster 1981), and this may be the case for walruses as well. One could assume that all independent walruses will be affected equally by food shortages, and that younger individuals will not be more disadvantaged than the older ones in obtaining food. The advantages usually invoked for older pinnipeds, such as greater experience with the area, better diving capabilities, and outright dominance, may not apply under conditions where all feeding is done in relatively shallow waters, the distribution of the ice dictates which areas can be utilized, and a major portion of the adult males may not be feeding in the same areas where the subadults and adult females feed. Obviously more information is needed on these points.

Throughout this paper, a distinction has been made between natural mortality and mortality due to harvests. One problem that arises in estimating mortality rates from age composition of the harvest is that mortality from both sources is combined. Furthermore, estimates of mortality derived from samples of populations that are growing will be biased upward (Payne 1977). Burns (footnote 6) suggested that adult male mortality was about 13%/yr, based on the age fecundity from the harvest. If the Pacific walrus population was growing at about 5%/yr, the estimate of survival from age composition will be negatively biased (Payne 1977). When corrected as:

$$S = e^{(\ln .87 + \ln 1.050)} = .91$$

where S = annual survivorship, the better estimate for adult male mortality would be 9%/yr. Again, this includes both natural and hunting mortality. If the Pacific walrus is polygynous (Fay et al. 1984), and the harvest of males is greater than that of females, the rate of natural mortality for adult females should be less than the total mortality for adult males, rather than greater as indicated by Burns (footnote 6). Therefore, the male mortality rate of 13% (Burns footnote 6) should exceed the maximum for adult females, the actual rate probably being much lower.

All of the simulations in which the population increased as rapidly as hypothesized (3 to 5%/yr) required that natural adult survivorship be above 95%, given the known level of harvest. The model suggests that the Pacific walrus population was theoretically capable of increasing from 70,000 to 200,000 in 20 yr, but to have done so, the sex ratio of the population would have had to have been strongly weighted to females. Information on the current sexual composition of the population would, therefore, be extremely useful for better understanding of the population dynamics of this species.

Finally, the model suggests that the MNP of a population varies considerably with the type of density dependence that is operative. This has been demonstrated also for MSY values (DeMaster 1981). MNP values for marine mammals commonly are assumed to lie between 50 and 60% of K. More realistic estimates of MNP will require information on the age at which density related changes take place in life history parameters, and on the form of the relationship between life history parameters and density of the population.

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