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Abstract

A method is presented for estimating age-specific mortality based on minimal information: a model life table and an estimate of longevity. This approach uses expected patterns of mammalian survivorship to define a general model of age-specific mortality rates. One such model life table is based on data for northern fur seals (*Callorhinus ursinus*) using Siler's (1979) 5-parameter competing risk model. Alternative model life tables are based on historical data for human females and on a published model for Old World monkeys. Survival rates for a marine mammal species are then calculated by scaling these models by the longevity of that species. By using a realistic model (instead of assuming constant mortality), one can see more easily the real biological limits to population growth. The mortality estimation procedure is illustrated with examples of spotted dolphins (*Stenella attenuata*) and harbor porpoise (*Phocoena phocoena*).

Key words: mortality estimation, longevity, survival rates, Leslie matrix, demography, *Callorhinus, Phocoena, Stenella.*

Demographic models are commonly used to study the dynamics of marine mammal populations. Such models are characterized by an explicit representation of age structure. This is desirable for animals, such as marine mammals, which have delayed maturation, long life spans, and for which aging methods are well established. The primary building blocks for demographic models are age-specific birth rates and survival rates.

Of these, age-specific survival rates have been generally more difficult to estimate. Several methods have been used to estimate survival (or mortality) rates from age-frequency distributions. All of these methods depend critically on the assumption that a population is in stable age distribution and is not growing (or, if growing, it is assumed that the rate of growth is constant and is known) (Caughley 1966, 1977). This, of course, limits the usefulness of

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demographic models for estimating the growth rate of a population. Such models are still useful in defining ranges of possible growth rates (Eberhardt 1985, Reilly and Barlow 1986), in establishing rational harvesting strategies (Goodman 1978), or in determining the optimal age structure to promote rapid recovery of a population (Goodman 1980).

Typically, mortality has been estimated as a constant rate across many (or all) age classes. In fact, the pattern of mortality over a typical mammalian life span consists of an initial period of high juvenile mortality, followed by a period of relatively low mortality, and concluding with a period of rapidly increasing senescent mortality (Caughley 1966, Spinage 1972, Siler 1979). In the few instances for which sufficient data are available, marine mammals follow the same pattern (Chapman 1964, de la Mare 1986). Several mortality models have been proposed to fit age-frequency distributions for populations with this pattern (Caughley 1966, Siler 1979, Paranjpe and Rajarshi 1986).

Although survival or mortality rates can be estimated by fitting non-linear survivorship models to age-frequency distributions, there are problems in applying this approach for most populations. Often a population is not in a stable age distribution, or if it is, the age distribution cannot be determined without bias. It is difficult to obtain the large sample sizes that are needed to estimate mortality rates accurately. One or more age classes in a population are often missing or are underrepresented in the sample.

For human demographers, one solution to these problems has been to use model life tables (Gage 1988). A life table based on a population with good data is used to smooth, to interpolate missing values, or simply as a surrogate for the life table of another population with insufficient data. This approach has recently been extended to modeling mortality for Old World monkeys as well (Gage and Dyke 1988). In general, model life tables based on mathematical models (such as Siler's model) are now preferred over the older tabular approach (Gage 1988). For humans, Siler's 5-parameter model has been shown to give better fits than an alternative 4-parameter logit model (Gage and Dyke 1986).

In this paper, we present a simple method of estimating mortality rates based on minimal information: a model life table and an estimate of the longevity of the species. We demonstrate the utility of our approach using data from three marine mammal populations. Age-specific mortality rates are estimated for northern fur seals (*Callorhinus ursinus*). This model is used with two other model life tables (a population of human females circa 1900 and Old World monkeys) to estimate survival rates of other species. The first example, spotted dolphins (*Stenella attenuata*), is used to illustrate how our approach can be used to estimate ranges in current population growth rate given relatively detailed reproductive information and sparse mortality data. The second example, harbor propoise (*Phocoena phocoena*), is used to illustrate how limits can be placed on the maximum possible growth rate given minimal information on mortality and fecundity.

METHODS

Constructing a survivorship model—Siler's competing risk model (Siler 1979) was used as the basis for constructing a general model of survivorship for marine

mammals. In this model, the total risk of mortality at a given age is the sum of an exponentially decreasing risk due to juvenile mortality factors, an exponentially increasing risk due to senescent mortality factors, and a constant risk due to other factors. In this model, the probability of survivorship from birth to age x can be expressed as:

$$l(x) = l_j(x) \cdot l_c(x) \cdot l_s(x), \tag{1}$$

where

$$l_j(x) = \exp[(-a_1/b_1) \cdot \{1 - \exp(-b_1 \cdot x/\Omega)\}], \tag{2}$$

$$l_c(x) = \exp[-a_2 \cdot x/\Omega], \tag{3}$$

and

$$l_s(x) = \exp[(a_3/b_3) \cdot \{1 - \exp(b_3 \cdot x/\Omega)\}]. \tag{4}$$

The survivorship l_c (Eq. 3) represents the constant risk of mortality experienced by all age classes. The survivorships l_j and l_s (Eq. 2 and 4) represent the independent risks of mortality due to juvenile and senescent factors (respectively). The five parameters (a_1, a_2, a_3, b_1, and b_3) allow considerable flexibility in the shape of this function.

In order to establish a general model which would be appropriate over a wide range of life spans, age is normalized by dividing by longevity. Age was re-expressed as a fraction of longevity, Ω, and hence the use of x/Ω in Equations 2, 3, and 4. No rigorous demographic definition exists for longevity, and it is often taken as the maximum age ever recorded for a species (Altman and Dittmer 1972). We use an alternative definition of longevity as the 99th percentile of the age distribution of a sample. Thus, one percent of a sample would be older than the age we define as longevity. In the Appendix we show that our definition is less dependent on sample size than is a definition based on the maximum age observed. In the Appendix we also show that when senescent mortality factors are strong, this parameter, Ω, can be estimated accurately with relatively small sample sizes.

Discrete-time notation—Considerable notational confusion has arisen in discrete-time parameterizations (Goodman 1982); hence, we will be explicit and use the Leslie matrix notation of Caswell (1989) for a birth-pulse population with postbreeding census. We consider only female life history parameters. No mention will be made of male mortality patterns except to say that they may be quite different from female patterns.

Parenthetical notations denote continuous time and subscripts denote discrete time. The survivorship from birth to age x is $l(x)$. The fecundity rate, F_x, is estimated as the product of the probability that a female of age x survives one time step, P_x, and the number of offspring produced by a surviving female (B_x or the crude birth rate). The asymptotic population growth rate, λ, is calculated by solving the discrete-time equivalent of Lotka's equation (eq. 17 in Goodman 1982; eq. 5.16 in Caswell 1989). The frequency of animals in a sample belonging to age class x is denoted by n_x.

Parameter estimation—Parameters of the mortality model were fit using a maximum likelihood approach. At stable age distribution, the probability density function for observing an individual of age x is given by:

$$\text{p.d.f.}(x) = \frac{l(x)}{\int_0^\infty l(y) \, dy}.$$

Because a closed-form solution to the above integral does not exist for the Siler survivorship function, the following approximation was used:

$$\text{p.d.f.}(x) = \frac{l(x)}{\sum_{i=0}^{\omega} l(i)},$$

where ω was chosen as 1.5 times Ω (a point at which $l(\omega)$ is, for all practical purposes, zero). The likelihood function is given by the joint probability of obtaining the observed age-frequency distribution, n. This was estimated as

$$L(n \mid a_1, a_2, a_3, b_1, b_3) = \prod_{i=1}^{\omega} [\text{p.d.f.}(x_i)]^{n_i},$$

where x_i represents the true age of individuals in age class i. The values of parameters a_1 to b_3 were chosen to maximize the natural logarithm of L using the Simplex algorithm (Press *et al.* 1988:289).

Fur seal model—We chose the northern fur seal as the species on which to base a general model of marine mammal survivorship. A wealth of life history information exists for this species over a long time period. We use the fur seal data presented by Smith and Polacheck (1981). Population size was relatively constant during the 1950s, and thus population parameters taken from 1958–1961 should be representative of a population with an approximately stationary age distribution (Smith and Polacheck 1981). (Female fur seals may have been harvested in the 1950s (D. Chapman, personal communication), however those harvests are assumed to be negligible.) Pooling age distributions over a 4-yr period should smooth any deviations from stable age distribution owing to observed annual variation in births (Chapman 1964).

The age frequency distribution for age classes 9 to 20 (Table 1) was estimated from female seals taken by U.S. researchers from 1958 to 1961 (table 1 in Smith and Polacheck 1981). Because juveniles were underrepresented in this sample, age classes 1 to 8 were treated as missing. The expected frequencies in age classes 4 to 8 were calculated using an iterative fitting procedure. First, the expected frequencies in age classes 4 to 8 were estimated based on the 478 animals observed in age class 9 and assuming a survival rate of 0.95 for age classes 4 to 8 (this is one of several estimates proposed by Smith and Polacheck for these age classes). Then the expected frequency in age class 1 was estimated based on observed pregnancy rates of females in age classes 4 to 20. The number in age class 1 was thus the product of age frequencies and crude birth rates over

Table 1. Age-frequency distribution, crude birth rates, fecundity rates and survival rates for northern fur seals, 1958–1961. Estimated age frequencies are given in parentheses. Survival rates were calculated by fitting the 5-parameter version of the Siler survivorship model to the age frequency distribution. Fecundity rates were estimated as the product of these survival rates and the crude birth rates.

Age (years)	Age class x	Age frequency n_x	Birth rate B_x	Survival rate P_x	Fecundity rate F_x
0	1	(2,096)	0.000	0.539	0.000
1	2		0.000	0.702	0.000
2	3		0.015	0.814	0.012
3	4	(646)	0.015	0.885	0.013
4	5	(572)	0.220	0.928	0.204
5	6	(530)	0.395	0.951	0.376
6	7	(505)	0.395	0.964	0.381
7	8	(486)	0.425	0.969	0.412
8	9	478	0.460	0.969	0.446
9	10	447	0.445	0.964	0.429
10	11	434	0.450	0.956	0.430
11	12	429	0.440	0.943	0.415
12	13	387	0.430	0.923	0.397
13	14	362	0.420	0.894	0.376
14	15	336	0.410	0.854	0.350
15	16	293	0.390	0.799	0.312
16	17	233	0.330	0.726	0.239
17	18	142	0.355	0.631	0.224
18	19	97	0.265	0.515	0.136
19	20	59	0.255	0.384	0.098
20	21		0.000	0.000	0.000

age classes 4 to 20. The Siler survivorship curve was then fit to the estimated age distribution, and the expected frequencies in age classes 4 to 8 were re-estimated based on the best fit to the model. The expected frequency in age class 1 was re-estimated, and the fitting procedure was repeated until the expected frequencies in age classes 4 to 8 did not change between iterations.

Alternative model life tables—Although the fur seal model may be an adequate model life table for many pinniped species, it may not be for cetaceans. Unfortunately, insufficient information currently exists to develop a model life table based on actual data for any species of cetacean. Two alternative model life tables were used, based on species with life history traits more similar to cetaceans. The first is a published Siler model based on aggregate data from several species of Old World monkey (Gage and Dyke 1988); parameter values given in Table 2 are equal to their published values multiplied by a longevity of 34 yr. The second model life table was based on human females in the United States circa 1900; Siler parameters (Table 2) were estimated by fitting a tabular life table (Fruehling 1982), scaled to a longevity of 81 yr.

Spotted dolphin example—Spotted dolphins commonly occur with yellowfin tuna in the eastern tropical Pacific. Dolphin mortality has resulted from the activities of the tuna purse-seine fishery in this area, and one spotted dolphin population (the "northern offshore stock," Perrin *et al.* 1979) was estimated

Table 2. Estimates of survival rate parameters for northern fur seals, Old World monkeys, and human females based on the Siler model (Eq. 1). In deriving these estimates, ages were scaled by an estimate of longevity, Ω (18 yr for fur seals, 34 yr for monkeys, and 81 yr for humans).

Species	a_1	a_2	a_3	b_1	b_3
Northern fur seal female	14.343	0.1710	0.0121	10.259	6.6878
Old World monkeys	30.430	0.0000	0.7276	206.720	2.3188
Human female	40.409	0.4772	0.0047	310.360	8.0290

to have decreased to between 29% and 47% of their historical abundance by 1979 (Smith 1983). Based on the ecological concept of density compensation, such populations would be expected to respond to such harvests with increased per-capita growth rates. Here we use measured reproductive parameters and our mortality estimation procedure to estimate possible ranges in the current growth rate of this spotted dolphin population.

Reproductive rates were measured from specimens collected by technicians aboard tuna vessels. The mean age of sexual maturity for females is approximately 12 yr (Myrick *et al.* 1986). Given an 11.5-mo gestation time (Perrin *et al.* 1976), the mean age at first birth is approximately 13 yr if females become pregnant soon after their first ovulation. The fraction of mature females that were pregnant in 1974–1983 samples is estimated as 0.290 (Barlow 1985). Dividing by gestation time (0.958 yr) and assuming a sex ratio of 50% females and a litter size of one (Perrin *et al.* 1976), the crude female birth rate, B_x, is estimated as 0.152 for all mature age classes.

Survival rates could not be calculated directly from age distributions due to apparent biases in sampling (Hohn and Scott 1983). Instead, survival rates were calculated from estimates of longevity and using several possible models for the shape of the survivorship function. Estimates of longevity (the age of the 99th percentile of an aged sample) for spotted dolphins range from approximately 33 yr in the eastern Pacific ($n = 806$, from fig. 2 in Myrick *et al.* 1986) to 45 yr in the western Pacific ($n = 200$, from fig. 16 in Kasuya 1976). To allow for uncertainty in age estimation procedures, both values are considered as estimates of Ω. A range is used for the parameters of the mortality model, including survivorship curves (Fig. 1) based on: (1) the fur seal model, (2) the Old World monkey model, and (3) the human female model.

Harbor porpoise example—Harbor porpoise are often caught and die in coastal gill-nets which are set for halibut in central California (Barlow 1987). For management of this species, it would be useful to know the upper limits on the rate of population growth. No data exist on the age distribution of harbor porpoise in central California, and very few data exist on reproductive rates. We therefore use data collected from other harbor porpoise populations to estimate maximum feasible rates of population growth.

Most of what is known about harbor porpoise life history is based on studies in eastern Canada. Based on tooth layer counts from a sample of 120 males and females from that area, the maximum observed age was 13 yr and the 99th percentile of the age distribution was 10 yr (derived from fig. 3, 4 in Gaskin
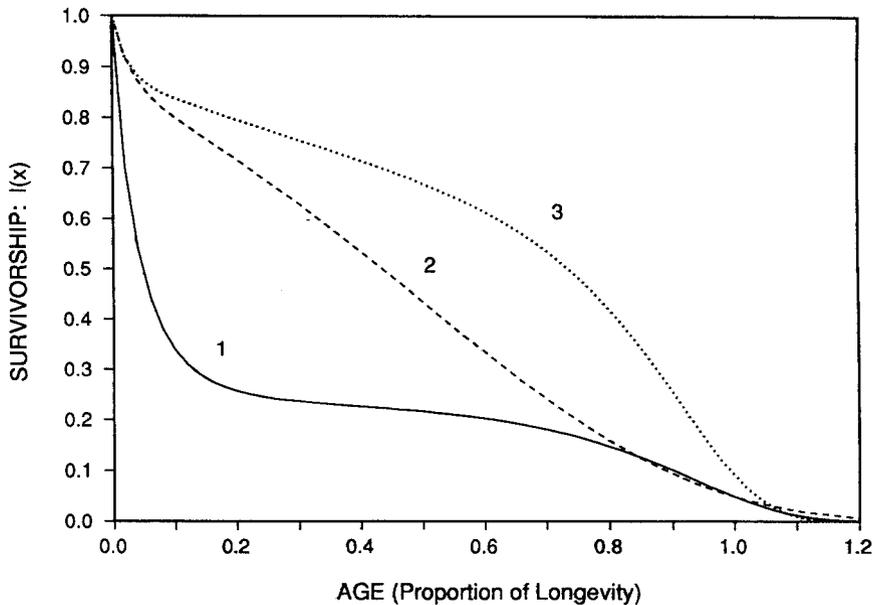
Figure 1. Survivorship curves based on three models: (1) female northern fur seals, (2) larger Old World monkeys, and (3) human females circa 1900. Parameter values for the Siler model (Eq. 1) are given in Table 2. Age is expressed as proportion of longevity, Ω.

and Blair 1977). Harbor porpoise mature at approximately 3 to 5 yr (Gaskin *et al.* 1984, Read 1989). Most estimates of gestation time rage from 10 to 11 mo for all porpoise species (Gaskin *et al.* 1984). Therefore, a female maturing at age 3 could first give birth at age 4. Simultaneously pregnant and lactating females have been found in samples from several populations (Gaskin *et al.* 1984), indicating that mature females may give birth every year. This is verified by cases where individually recognized females were accompanied by different calves in consecutive years (Watson 1976, B. Taylor, personal communication). In most studies, however, the percentage of mature females that was simultaneously pregnant and lactating is less than 100% (Gaskin *et al.* 1984, Read 1989), indicating an average calving interval of greater than 1 yr.

Upper bounds on the maximum rates of population growth were estimated using the ranges in the above parameters that would yield the largest growth rate. Longevity, Ω, was taken as 10 yr. The age at first birth was taken as 4 yr. The calving interval was taken as 1 yr. Again, a range was used for the parameters of the mortality model; survival rates were estimated based on the same three models used above for spotted dolphins (Fig. 1).

RESULTS

Fur seal—The maximum likelihood fit of the 5-parameter Siler model to the age-frequency distribution for fur seals is shown in Figure 2. The model
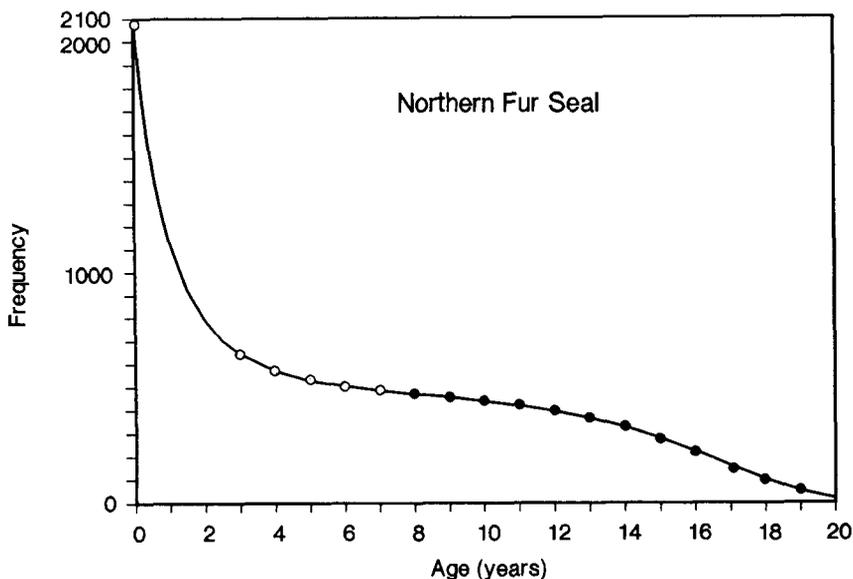
Figure 2. Survivorship curve for female northern fur seals, 1958–1961, based on maximum likelihood fit of the Siler model to an estimated age-frequency distribution. Solid circles represent observed frequencies at age and open circles represent estimated frequencies based on reproductive rates and iterative fitting algorithm (see text).

gave a very good fit to the data ($\chi^2 = 5.65$, df = 12, $P = 0.933$; Kolmogorov/ Smirnov (K/S) test, $P = 0.920$). The parameter values which resulted in the best fit are given in Table 2, and the resulting estimates of survival rates are given in Table 1. Leslie-matrix fecundity rates were calculated as the adult survival rates times the raw pregnancy rates (Table 1). As a check on internal consistency, population growth rates were calculated using these survival and fecundity rates. As expected, the resulting finite rate of population growth (λ = 1.0002) indicates that net growth is effectively zero.

Spotted dolphin—Estimates of current population growth rate for spotted dolphins are given in Table 3 based on three different models of survivorship and based on longevity estimates of 33 and 45 yr. Population growth rates are less than 1.0 for the fur seal model with longevities of 33 or 45 yr and for the monkey model with longevity of 33 yr. Because the offshore spotted dolphin population has been reduced by tuna fishing operations, one might expect that (in the absence of continued fishing mortality) density dependent responses would result in values for life history parameters that yield a growth rate greater than 1.0. The other three combinations of survivorship and longevity result in growth rates greater than 1.0. The maximum growth rate expected given the most optimistic survivorship schedule (that patterned after a human population) and the higher estimate of longevity is 4.2% per year. This approximately equals the maximum rate of increase estimated by Reilly and Barlow (1986) for a

Table 3. Estimates of population growth rate, λ, for spotted dolphins based on current estimates of reproductive rates, three models of survivorship, and two estimates of longevity. Parameters of survivorship models are given in Table 2.

Survivorship model	Longevity	
	$\Omega = 33$ yr	$\Omega = 45$ yr
Northern fur seal	0.972	0.996
Old World monkeys	0.992	1.020
Human	1.024	1.042

dolphin which first gives birth at 13 yr and which has a calving interval of 3 yr (their fig. 4*b*).

Harbor porpoise—Maximum rates of population growth for harbor porpoise were estimated as 0.917, 0.989, and 1.094 (respectively for the fur seal, Old World monkey, and human survivorship models). If assumptions are met (*i.e.*, longevity is 10 yr and females produce one calf per year starting at 4 yr of age), scaled survival rates must be higher than those of fur seals or Old World monkeys in order for porpoise populations to grow. In the most optimistic case, a population growth rate of 9.4% is possible if survivorship is patterned after a human population.

DISCUSSION

The method of estimating mortality rates for populations based on scaling the survivorship curves of other populations is not meant as a substitute for directly measuring mortality. Rather, it is an attempt to improve the method by which mortality is modeled when such direct measures are not available. We envision the primary use of our approach will be in exploratory modeling such as in our examples of spotted dolphins and harbor porpoise. We do not recommend this approach for estimating the actual population growth rate for any population.

Advantages of age-specific rates—In most previous formulations, demographic models of marine mammals have used survival rates which are constant over all adult age classes (Allen 1981, Breiwick *et al.* 1984, Reilly and Barlow 1986). Although it is usually acknowledged that senescent mortality is expected in mammals, mathematical simplicity has taken precedence over biological reality. This is not a fatal flaw in such studies. As shown by Goodman (1984), population growth rates can be accurately estimated from a model which assumes constant adult survival and fecundity, regardless of the fact that both may show age-specific patterns. Furthermore, Goodman (1984) showed how to estimate one survival parameter that results in essentially the same first-order (*i.e.*, static) behavior as would the full age-specific model. The problem with this approach is that the resulting survival parameter is a theoretical construct which has lost intuitive biological meaning.

The difficulty in dealing with an adult survival parameter which has lost biological meaning is illustrated in the paper by Reilly and Barlow (1986). They estimate maximum population growth rates for dolphins based on a range of estimates of reproductive rates and calf and non-calf survival rates. The major problem they confronted was in determining a realistic upper range for non-calf survival rate. They assumed a maximum age of 50 yr. They showed that survival rates greater than 0.97 resulted in greater than 22% of their populations reaching this maximum age. Although, as they noted, this seems unreasonable, the survival parameter they used is a mathematical abstraction and is not necessarily subject to what seems to be biologically reasonable constraints. Their arguments are, therefore, weak and are based too strongly on their somewhat loosely defined concept of maximum life span.

Biological limits to survival rates are much more apparent using the approach outlined above for spotted dolphins. Senescence appears to be genetically programmed, and thus longevity is largely predetermined. Longevity thus acts as one very obvious biological limit to survival rates. Survivorship curves of mammals all have a similar shape (juvenile risks are high but decrease rapidly; senescent risks increase rapidly). This shape also imposes limits to survival rates. Finally, within the family of shapes which are possible, one can pick a survivorship curve which represents the maximum survival in a protected environment. For the latter we chose the survivorship curve for human females circa 1900 (*i.e.,* during the period of good data collection methods and before the advent of most modern medicines). We believe that this shape reflects an absolute limit to the likely survivorship of any wild population.

Given available information, we cannot evaluate whether the shape of the survivorship curve for the northern fur seal population is truly representative of marine mammals. It was chosen as the only marine mammal species for which data were of the quality and quantity necessary to establish a model. A better approach would be to base a model on a mean survivorship curve from a variety of marine mammals or possibly from a variety of other large mammals with similar life history traits to the species being studied. The life history of dolphins appears more similar to that of humans or elephants (long life span and long interval between offspring) than that of fur seals. We hope that as additional information becomes available for other species, we will be able to specify better a general model of survivorship for marine mammals or, possibly, separate models for pinnipeds and cetaceans. We believe, however, that use of model life tables for marine mammals is a significant improvement over the usual assumption of constant mortality for all age classes.

Scaling by longevity—The idea of scaling survivorship curves to compare species is an old one, dating back at least to the work of Pearl and Parker (1921). In a later paper, Pearl (1922) used a method similar to ours and scaled by the age at which survivorship falls to some small fraction of the first age class. That method was criticized on the basis of high sampling variability (Greenwood 1928). Another method was introduced by Pearl and Miner (1935) based on scaling by the mean duration of life. In the latter paper, the authors were able to note the similarities of life tables for roaches, fruit flies, mice, and

automobiles by plotting all on the same graph. More recently, Eberhardt (1985) suggested the possibility of scaling by the modal age of senescence, as defined by Siler (1979).

None of the previous approaches used to scale survivorship curves were appropriate for our study. Rescaling based on the modal age of senescence was not chosen because it requires prior fitting of a Gompertz model to the senescent phase of a survivorship curve (Siler 1979). We desired a method that would allow us to rescale age prior to fitting a survivorship curve. Rescaling based on the mean duration of life was not chosen because this can be greatly affected by the juvenile mortality phase. We wanted a method that would be anchored more strongly at the other end of the age scale and which would thus retain the expected relationships between juvenile, adult, and senescent phases of life. The method used by Pearl (1922) was not quite appropriate either, because it assumed that samples were taken from a cohort study. Given a sample from an age frequency distribution it is not possible to estimate the age at, say, 1% survivorship unless the survivorship curve is first estimated.

Instead of the age at 1% survivorship, we chose a scaling factor based on the 99th percentile of an aged sample. This statistic is likely to have similar properties to the former (proposed by Pearl 1922). Contrary to arguments made by Greenwood (1928), our simulation studies (Appendix) show that this statistic can be accurately estimated with small sample sizes. Because senescent mortality is a dominant force in mammalian life tables and because it increases so rapidly, we expect this result to hold for any mammal population in which some of its members live long enough to experience senescence. Our approach may fail for some populations in which harvesting truncates the age distribution before senescence, as may be the case for harvested deer populations (Barlow and McCulloch 1984, Eberhardt 1985). We have not investigated the problem of estimating longevity from non-stable age distributions; however, if senescence is strong, we do not believe that this is a significant problem.

Using prior expectations in estimating mortality rates—We have concentrated our attention on situations (1) where large quantities of data exist and a full Siler model can be fit (*e.g.*, the fur seal) or (2) where very little data exist and a model life table is substituted (*e.g.*, the spotted dolphin and harbor porpoise). A third situation arises when some data exist, but not enough to reliably fit a 5-parameter model. In such situations one would like to combine the information in the available data with the information contained in the model life table to obtain a realistic survivorship curve. We propose three possible methods for estimating mortality rates in such situations.

The simplest method would give equal weight to both the actual data and the model life table. Assume that the actual data is the age distribution of *n* individuals taken randomly from a stable population. The expected stable age distribution for *n* individuals is calculated from the appropriate model life table and is combined with the observed age distribution. The Siler model is then fit to the combined age distribution.

A second alternative would be to fit only a portion of the Siler parameters based on the actual data. The remaining parameters could be held constant at

whatever values are specified in the model life table. The most variable parameter could be fit first (*e.g.*, the juvenile mortality parameter a_1), and the goodness of fit could be evaluated. Additional parameters could be added in a stepwise fashion until the improvement in the goodness of fit is no longer significant.

A final alternative would be to use an empirical Bayesian approach (Iversen 1984) with the Bayesian prior distribution defined by the model life tables. Rather than use a single model life table, the prior expectations of mammalian survivorship could be represented as a probability distribution for each of the 5 parameters in the Siler model. Because this model is rather over specified (Siler 1983), covariances between the parameters would also have to be considered. The result of this approach would be a probability distribution of survival rates which is a function of both the data and the prior distributions. As more data are included, the importance of the prior distributions will diminish.

Future research is planned to investigate each of the above approaches for estimating survival rates.

LITERATURE CITED

ALLEN, K. R. 1981. Application of population models to large whales. Pages 263–276 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York, NY.

ALTMAN, P. L., AND D. S. DITTMER, eds. 1972. Biology data book, Second edition, Vol. I. Federation of American Societies for Experimental Biology, Bethesda, MD.

BARLOW, J. 1985. Variability, trends, and biases in reproductive rates of spotted dolphins, *Stenella attenuata.* Fishery Bulletin 83:657–669.

BARLOW, J. 1987. An assessment of the status of harbor porpoise populations in central California. Administrative Report LJ-87-06, available from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA. 35 pp.

BARLOW, J., AND C. Y. McCULLOCH. 1984. Recent dynamics and mortality rates of the Kaibab deer herd. Canadian Journal of Zoology 62:1805–1812.

BREIWICK, J. M., L. L. EBERHARDT AND H. W. BRAHAM. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). Canadian Journal of Fisheries and Aquatic Sciences 41:484–496.

CASWELL, H. 1989. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, MA.

CAUGHLEY, G. 1966. Mortality patterns in mammals. Ecology 47:906–918.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, Chichester, U.K.

CHAPMAN, D. G. 1964. A critical study of Pribilof fur seal population estimates. Fishery Bulletin 63:657–669.

DE LA MARE, W. K. 1986. On the estimation of mortality rates from whale age data, with particular reference to minke whales (*Balaenoptera acutorostrata*) in the Southern Hemisphere. Report of the International Whaling Commission 36:239–250.

EBERHARDT, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

FRUEHLING, J. A., ed. 1982. Sourcebook on death and dying. Marquis Professional Publications, Chicago.

GAGE, T. B. 1988. Mathematical hazard models of mortality: an alternative to model life tables. Americal Journal of Physical Anthropology 76:429–441.

GAGE, T. B., AND B. DYKE. 1986. Parameterizing abridged mortality tables: the Siler three-component hazard model. Human Biology 58:275–291.

GAGE, T. B., AND B. DYKE. 1988. Model life tables for the larger Old World monkeys. American Journal of Primatology 16:305–320.

GASKIN, D. E., AND B. A. BLAIR. 1977. Age determination of harbour porpoise, *Phocoena phocoena* (L.), in the western North Atlantic. Canadian Journal of Zoology 55: 18–30.

GASKIN, D. E., G. J. D. SMITH, A. P. WATSON, W. Y. YASUI AND D. B. YURICK. 1984. Reproduction in the porpoises (Phocoenidae): implications for management. Reports of International Whaling Commission (Special Issue 6):135–148.

GOODMAN, D. 1978. Management implications of the mathematical demography of long lived animals. Contract report prepared for the Marine Mammal Commission. NTIS PB-289678. 80 pp.

GOODMAN, D. 1980. Demographic intervention for closely managed populations. Pages 171–195 *in* M. E. Soulé and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, MA.

GOODMAN, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. American Naturalist 119:803–823.

GOODMAN, D. 1984. Statistics of reproductive rate estimates, and their implications for population projection. Reports of the International Whaling Commission (Special Issue 6):161–173.

GREENWOOD, M. 1928. "Laws" of mortality from the biological point of view. Journal of Hygiene 28:267–294.

HOHN, A. A., AND M. D. SCOTT. 1983. Segregation by age in schools of spotted dolphin in the eastern tropical Pacific. Abstract, Fifth Biennial Conference on the Biology of Marine Mammals, Boston, MA. November 27–December 1, 1983.

IVERSEN, G. R. 1984. Bayesian statistical inference. Sage Publications, Inc., Beverly Hills, CA.

KASUYA, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Scientific Report of the Whales Research Institute 23:73–106.

MYRICK, A. C., JR., A. A. HOHN, J. BARLOW AND P. A. SLOAN. 1986. Reproductive biology of female spotted dolphins, *Stenella attenuata,* from the eastern tropical Pacific. Fishery Bulletin 84:247–259.

PARANJPE, S., AND M. B. RAJARSHI. 1986. Modelling non-monotonic survivorship data with bathtub distributions. Ecology 67:1693–1695.

PEARL, R. 1922. Experimental studies on the duration of life. VI. A comparison of the laws of mortality in *Drosophila* and in man. American Naturalist 56:398–405.

PEARL, R., AND J. R. MINER. 1935. Experimental studies on the duration of life. XIV. The comparative mortality of certain lower organisms. Quarterly Review of Biology 10:60–79.

PEARL, R., AND S. L. PARKER. 1921. Experimental studies on the duration of life. I. Introductory discussion of the duration of life in *Drosophila.* American Naturalist 55:481–509.

PERRIN, W. F., J. M. COE AND J. R. ZWEIFEL. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata,* in the offshore eastern tropical Pacific. Fishery Bulletin 74:229–269.

PERRIN, W. F., P. A. SLOAN AND J. R. HENDERSON. 1979. Taxonomic status of the "southwestern stocks" of the spinner dolphin, *Stenella longirostris,* and the spotted dolphin, *S. attenuata.* Report of the International Whaling Commission 29:175–184.

PRESS, W. H., B. P. FLANNERY, S. A. TEUKOLSKY AND W. T. VETTERLING. 1988. Numerical recipes: the art of scientific computing. Cambridge University Press, Cambridge, U.K.

READ, A. J. 1989. Incidental catches and life history of harbour porpoises *Phocoena phocoena* from the Bay of Fundy. Ph.D. dissertation, University of Guelph, Canada. 121 pp.

REILLY, S. B., AND J. BARLOW. 1986. Rates of increase in dolphin population size. Fishery Bulletin 84:527–533.

SILER, W. 1979. A competing-risk model for animal mortality. Ecology 60:750–757.

SILER, W. 1983. Parameters of mortality in human populations with widely varying life spans. Statistics in Medicine 2:373–380.

SMITH, T. D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fishery Bulletin 81:1–13.

SMITH, T., AND T. POLACHECK. 1981. Reexamination of the life table for northern fur seals with implications about population regulatory mechanisms. Pages 99–120 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York, NY.

SPINAGE, C. A. 1972. African ungulate life tables. Ecology 53:645–652.

WATSON, A. P. 1976. The diurnal behavior of the harbour porpoise (*Phocoena phocoena* L.) in the coastal waters of the western Bay of Fundy. M.Sc. thesis, University of Guelph, Canada. 93 pp.

APPENDIX

Sensitivity of Ω to sample size—A sample of n ages (X_i: $i = 1, 2, 3, \ldots,$ n), drawn at random from a population with a particular age distribution and ordered such that $X_{i-1} < X_i < X_{i+1}$, is set of "order statistics" for age. In a sample of 100 ages, the 99th order statistic could be called the "99th percentile" because 99 percent of the sample values are smaller than or equal to the value of the 99th order statistic. The maximum order statistic of a sample (of any size) could be called the "100th percentile" because 100 percent of the sample ages are less than or equal to the maximum age.

For a sufficiently simple age distribution, such as one resulting from an age-constant mortality rate, the sampling properties of the order statistics and percentiles could be determined analytically. However, for more complex survivorship functions like those represented by the Siler model, computer simulation is a more tractable technique to investigate sampling behavior.

Figure 3 shows the results of simulated sampling from the age distribution of a hypothetical population which is stable and stationary and subject to the fur seal model survivorship schedule. For a particular sample size, represented on the X-axis, 250 random samples were drawn from the hypothetical age distribution. The mean of the largest ages is represented in Figure 3 as the "100th percentile" with error bars to indicate ± 1 standard deviation of the observed largest values. The curve labelled "99th percentile" represents the expected values for our parameter Ω, again with ± 1 standard deviation (based on 250 samples independent of those used to estimate other percentiles). The analogous curve for the 95th percentile is also shown.

As seen in Figure 3, the 99th percentile of a random sample from the fur seal model is less sensitive to sample size and less variable than the maximum age (100th percentile). Further decreasing the percentile rank to 95 results in even less sensitivity to sample size. However, we chose the 99th percentile as a scaling value because percentile ages of lower rank will be more heavily influenced
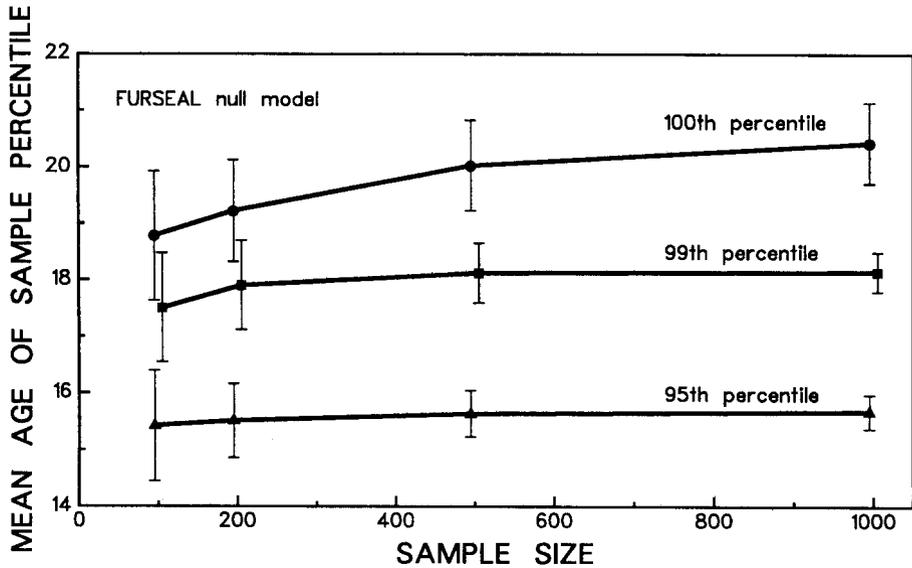
Figure 3.   Mean values for selected percentile ranks in samples of various sizes from the "fur seal model" age distribution. Means and error bars (± 1 standard deviation) were computed from 250 samples at each sample size.
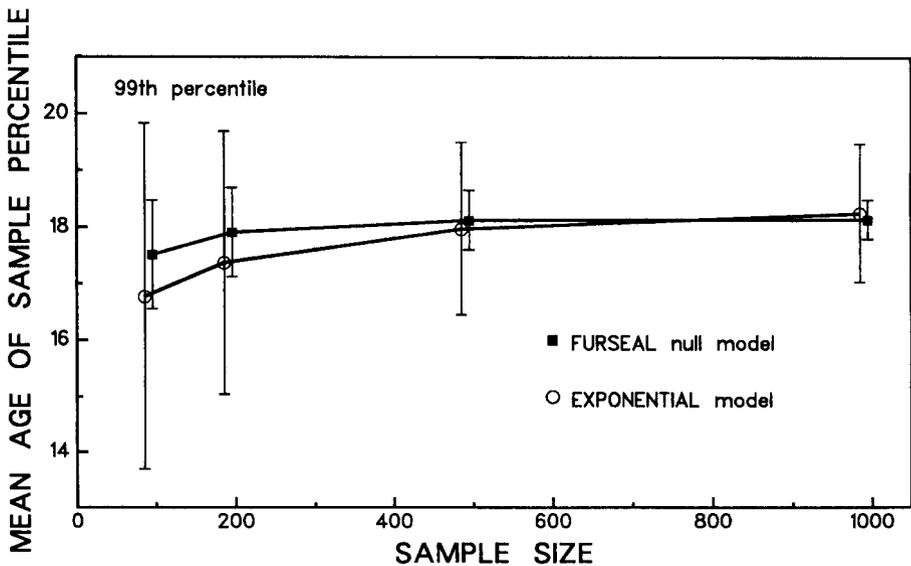

Figure 4.   Mean values of the 99th percentile ages versus sample size for a survivorship schedule with increased senescent mortality (fur seal model) and a schedule with constant mortality (exponential model). Means and error bars (± 1 standard deviation) were computed from 250 samples of each sample size.

by mortality patterns early in life. We also believe that the 99th percentile will be less sensitive to deviations from stable age distribution than would be a lower percentile. Thus, it is desirable to base the scaling on as large a fraction of the life span as possible.

Effect of senescent mortality—To illustrate the effect that senescent mortality factors have on the age distribution (and consequently on the sampling properties of Ω), we compared a constant mortality model with the fur seal model (Fig. 4). Both models had age distributions with the 99th percentile equal to 18 yr. The fur seal model, which exhibits senescent mortality, results in estimates of Ω which are less sensitive to sample size and much less variable than those obtained by sampling the exponential age distribution (which is not subject to increasing mortality due to senescence).

Conclusion—Although these examples do not constitute general proofs, we believe that the results will hold for most survivorship schedules characteristic of marine mammal species. The 99th percentile of a sample will be less sensitive to sample size (for samples of 100 or more) than the maximum age and will have lower variance. Senescent increase in the mortality rate will serve to stabilize the sampling properties of any of the higher order statistics (or percentile ranks) for age.