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Review of Techniques Used to Estimate the Average Age at Attainment of Sexual Maturity in Marine Mammals

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ABSTRACT

The average age of sexual maturation (ASM) is generally used as a 'K' index to determine whether or not a population is approaching its carrying capacity. If the ASM is increasing, it is inferred that the density *per capita* of resources is increasing and that density-dependent mechanisms are operative. At least five techniques are commonly used to estimate the ASM. These techniques are mean of known-age first-time ovulators, mean deduced from age-specific ovulation rates, regression of age-specific ovulation rates versus age, graphical interpretation of age when 50% of animals have ovulated, and graphical interpretation of age at which the cumulative probability of ovulation equals the cumulative probability of not ovulating. Using hypothetical data, it is shown that different techniques produce different estimates of the ASM. The mean of known-age first-time ovulators is assumed to be the best estimator of the ASM, and other techniques are compared for bias and precision.

INTRODUCTION

The average age at attainment of sexual maturity (ASM) refers to the average age at which females in a population ovulate for the first time. This life history parameter has been used to compare the status of marine mammal populations by assuming that a population which has a higher density will have a greater average ASM. It has been used in population models (see Eberhardt and Siniff, 1977, and Goodman, 1984) that require an estimate of the average age of first birth, which is estimated by adding the average ASM and the average duration of the first gestation period.

The average ASM can be and has been estimated in a number of different ways and from a number of different data sources. Five different estimators are in common use. They are mean age of first-time ovulators (e.g. Bengtson and Siniff, 1981), mean deduced from age-specific ovulation rates (DeMaster, 1978), regression of corpora counts versus age (e.g. Kasuya, 1972), graphical interpretation of a plot of percentage mature against age to determine the age when 50% of females have ovulated at least once (e.g. Perrin, Holts and Miller, 1977), and graphical interpretation of age at which the cumulative probability of ovulating by age x equals the cumulative probability of not ovulating at age x or older (Kasuya, 1972). The purpose of this paper is to compare the estimates of ASM values for each of the five estimators with the same hypothetical data set and to compare the variance of the estimators that utilize age-specific rates of ovulation. It is my intention to show that each estimator will produce a different estimate of the average ASM, and that comparisons made between different populations or the same population over time must be based on estimates of the ASM that are derived in the same manner. This can be a particular problem when comparing the results of one study with published results of another where the method used to estimate the average ASM may not be given.

METHODS

Comparison of ASM estimators

A hypothetical data set of age-specific ovulation rates was derived by assuming the following: annual survivorship of females is constant and equal to 0.90; no animals less than 4 years of age ovulate; 20% of 4-year-olds ovulate; 50% of 5-year-olds that did not ovulate as 4-year-olds ovulate; 70% of all 6-year-olds that did not ovulate as 5-year-olds ovulate; 90% of all 7-year-olds that did not ovulate as 6-year-olds ovulate; and all 8-year-olds that did not ovulate as 7-year-olds ovulate. It was further assumed that animals that ovulated at age x will not ovulate again until age $x+2$, but at these ages all animals will ovulate independent of age. This simulates a reproductive interval of 2 years. The number of animals that ovulate for the first time at age x and the total number of ovulating animals at age x, under these assumptions, are presented in Fig. 1. The age-specific ovulation rates and number of first-time ovulators were used to estimate the average ASM for each of the five techniques.

Sensitivity analysis

A sensitivity analysis was performed on the three ASM estimators that utilize age-specific ovulation rates: the mean deduced from age-specific ovulation rates, the age

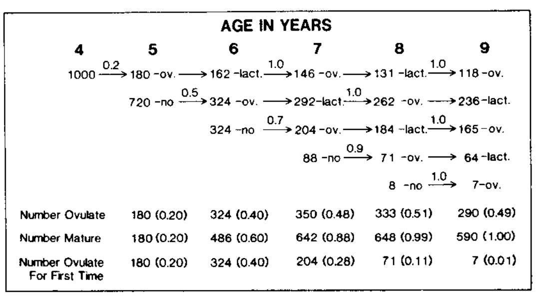


Fig. 1. Summary of hypothetical population of female dolphins. Annual survivorship equals 0.90, and the reproductive interval is 2 years.

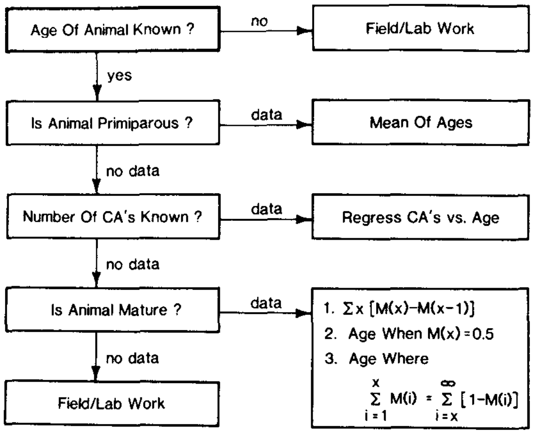


Fig. 2. Summary of which estimators for ASM are used with certain data bases.

where 50% of females are mature (i.e. they have ovulated at least once), and the age where the cumulative probability of previous ovulation equals the cumulative probability of not having ovulated. A series of age-specific ovulation rates were selected at random from a normal distribution, with means equal to the rates given in Fig. 1, and a coefficient of variance equal to 0.025. For each of the 3 estimators, 30 sets of age-specific ovulation rates were generated and estimates of the average ASM derived. This type of Monte Carlo simulation represents a situation where only the sampling variation is being compared. The biological parameters are assumed to remain constant between samples.

Additional consideration

Problems with obtaining precise, unbiased estimates of age were not considered in this review. It was assumed that animals that have been collected can be aged correctly. Problems in identifying corpora and questions of corpora regression and persistence were not addressed. It was assumed that all of the different estimators suffer from these problems, but future efforts should be directed at determining whether all of the estimators are equally sensitive to them. It was also assumed that the mean age of first-time ovulators is an unbiased estimate of the average of ASM. However, sample sizes of ovaries from animals that have ovulated only once are generally small, and estimates based on all ovaries sampled are more common. If counts of total corpora albicantia (CAs) in both ovaries are available, it is possible to regress number of CAs against age. However, if only information on presence or absence of CAs is collected, then one of the three alternative estimators must be used (Fig. 2 summarizes the various analyses and data requirements). Finally, some authors have estimated the length where 50% of all females were sexually mature, and then estimated the ASM from a derived relationship between length and age (e.g. Perrin *et al.*, 1977). This estimator was not considered, as it could not be determined from the data given in Fig. 1.

RESULTS

Comparison of estimators

1. *Mean age of first-time ovulators*

The mean age of first-time ovulators (AFO) is generally accepted as an unbiased estimate of the ASM. However, the sample size for this estimator is often very small, making it relatively imprecise. The mean AFO from the hypothetical population (Fig. 1) is 6.24 years (Table 1). Two advantages of this technique over the other estimators are that it is unbiased and that confidence intervals are easily constructed from the standard formula for the variance of a mean.

2. *Mean deduced from age-specific ovulation rates*

The derivation of this estimator and its variance is given in DeMaster (1978). The mean deduced from age-specific ovulation rates (ASOR) is a positively biased estimator. This is because the estimator evenly weights all of the age classes, when older age classes clearly comprise less of the population than do younger age classes (see Table 1 for formula). Therefore, this bias is progressively worse as the annual mortality rate increases. For an annual mortality rate of 0.10, the mean of ASOR is 6.33 years (Table 1; Fig. 3). If the age structure is known, an unbiased estimate of the ASM can be made with this estimator:

$$\mathrm{ASM} = \sum_{x=0}^{\infty}\left[[M(x)-M(x-1)](x)f(x)\Big/\sum_{x=0}^{\infty}(fx)\right]$$

where $M(x)$ equals the proportion of x-year-old females that are mature, x is the age, and $f(x)$ is the number of animals x years old.

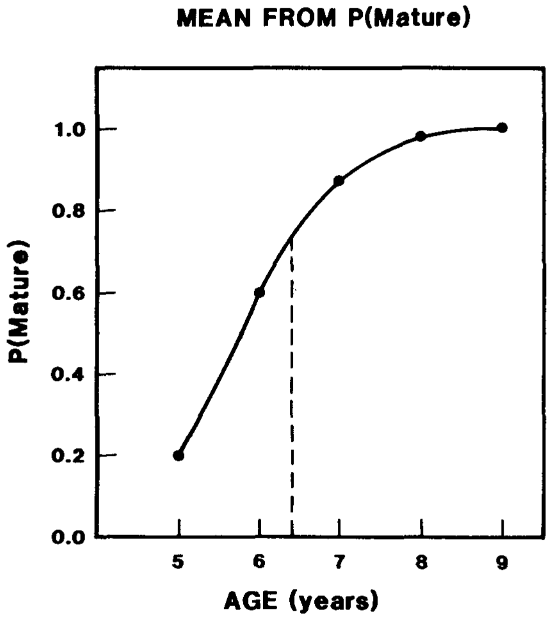
3. *Age where proportion mature equals* 0.50

The age where 50% of the animals are mature (50% age) is a commonly used estimate of the ASM (Perrin *et al.*, 1977; Kasuya, 1976). The estimate is usually made by interpreting a plot of percent mature versus age (see Fig. 4).

Table 1

Summary of five ASM estimators. All estimates of ASM were made with the same data set (Fig. 1). $M(x)$ is the proportion of x-year-old females that were mature, and x is the age in years. In methods 1 and 2, the summation is over all ages

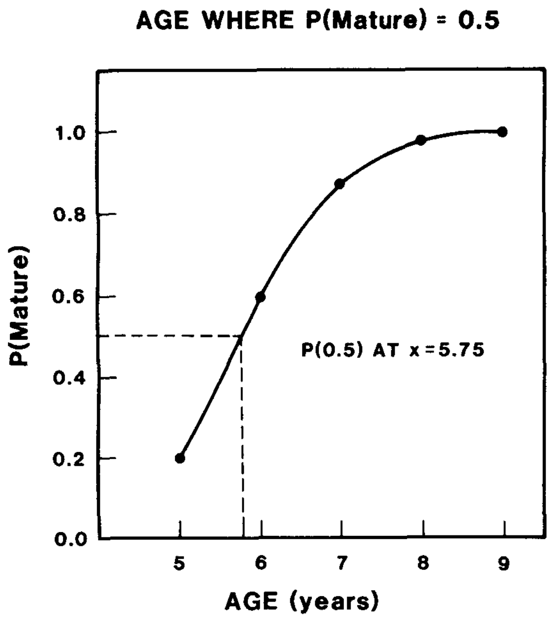
1. Mean of ages:	$\dfrac{\Sigma(\#\text{ ovulate for the first time})\times}{\text{total number in sample}}$	= 6.24 years
2. Mean from P(mature):	$\Sigma[M(x)-M(x-1)]x$	= 6.33 years
3. Age where P(mature) = 0.5:		= 5.75 years
4. Age where	$\sum_{i=1}^{x} M(i) = \sum_{i=x}^{\infty}[1-M(i)]$:	= 5.81 years
5. Regression of # CAs vs age; age where # CAs = 1.0		= 6.77 years



$ASM = \sum x\,[M(x)-M(x-1)] = 6.33$

$= (5)(0.2)+(6)(0.4)+7(0.28)+8(0.11)+9(0.01)$

Fig. 3. Plot of age versus percent mature (ASOR).



$$\frac{0.5-0.6}{0.2-0.6} = \frac{x-6}{5-6}$$

$$x = 5.75$$

Fig. 4. Plot of age versus percent mature (50%).

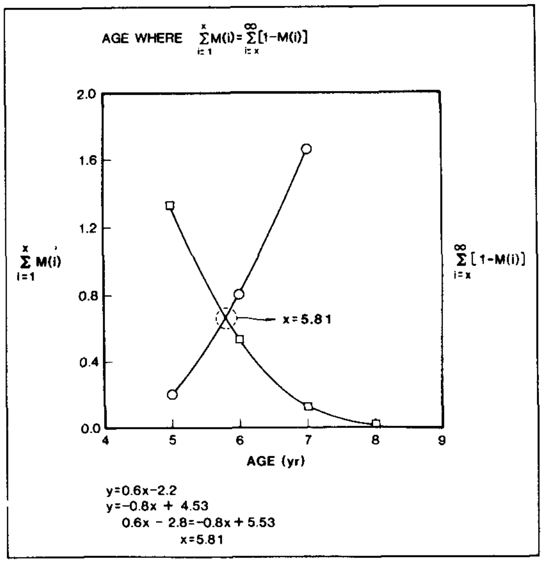


Fig. 5. Plot of terms used to estimate ASM with summation technique.

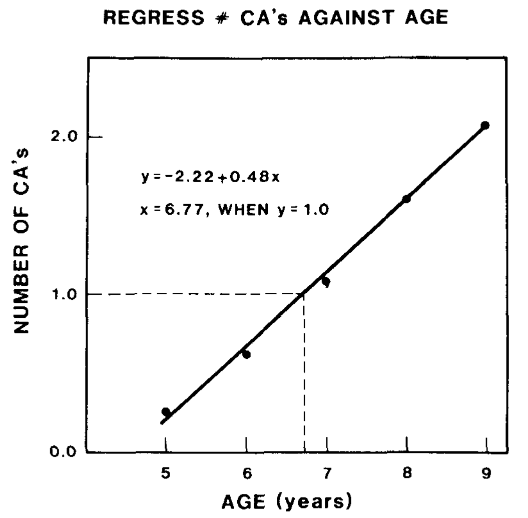
A standardized procedure for modeling the age-versus-percent-mature relationship has not been devised. If the shape of this relationship is symmetric with age, the age where 50% of animals are mature will be similar to the mean of the proportion mature. However, in general this relationship rapidly increases during the early ages and then only slowly increases to unity for the latter ages. In this case the mean AFO will generally be greater than the 50% age. In the hypothetical data set, the 50% age was approximately 5.75 years (Table 1). Variance estimates have not been developed for this estimator of ASM.

4. *Summation estimate*

The fourth ASM estimator (referred to hereafter as the summation procedure) was first described by Kasuya (1972) and subsequently used by Kasuya *et al.* (1974). The summation procedure estimates the ASM as the age where the summation of the proportion mature from birth to the ASM equals the summation of one minus the proportion mature from the ASM to the maximum age (see Table 1 for formula). Kasuya (1972) recommends this procedure over the 50% age method when sample sizes for individual age classes are small. The estimated ASM using the summation procedure and data from Fig. 1 is 5.81 years (Fig. 5). A derivation of this estimator's variance has not been developed, and, therefore, confidence intervals are generally not given. It must also be assumed in using the estimate (and the previous estimate) that a straight line adequately describes the relationship around the ASM.

5. *Regression of the number of CAs versus age*

The final estimator (referred to as the regression estimate) regresses the number of corpora albicantia against age (Fig. 6). The ASM is derived from the regression equation by estimating the age where the number of CAs is greater than zero. In using this technique it is necessary to assume that all ovulations are 'recorded' in the ovaries as



		# CA's				
		0	1	2	3	MEAN
AGE	5	80	20	-	-	0.2
	6	40	60	-	-	0.6
	7	12	68	20	-	1.08
	8	1	39	60	-	1.59
	9	-	12	68	20	2.08

Fig. 6. Plot of number of CAs versus age.

permanent scars and that the ovulation rate is constant with age. The technique has a disadvantage in that it is positively biased whenever the reproductive interval is greater than 1 year. This is because animals with reproductive intervals greater than 1.0 often have the same number of CAs in consecutive years. This tends to make the age where the average number of CAs is equal to 1.0 greater than the average age of first-time ovulation. Also, variation in attaining maturity must be taken into account when fitting an ovulation-rate curve (see Perrin and Reilly, 1984). Using the data in Fig. 1, the regression estimate of the ASM is 6.77 years (Table 1). Confidence intervals can be derived with standard procedures for estimating the variance around the regression line, but this will provide an underestimate of the variance of the ASM.

Sensitivity Analysis

The results of the sensitivity analysis indicate the three techniques are equally precise (Table 2). In other words, one estimate does not have a relatively smaller confidence interval than another. Perhaps different results would be obtained with a simulation if the coefficient of variation were larger. This should be explored in the future.

Table 2

Summary of three different ASM estimators, where identical data set was used to calculate the means, confidence interval, and coefficient of variance

ASM estimator	$\bar{x} \pm 2$ S.E.	C.V.
ASOR	6.34 ± 0.196	0.0079
50% age	5.75 ± 0.164	0.0071
Summation	5.81 ± 0.180	0.0079

DISCUSSION

The ASM of a population is currently used to compare the 'status' of different populations. This assumes that the ASM is dependent on density *per capita* of resources. When used in this manner, there is a clear advantage in using those estimates that have accompanying variance estimates (AFO, ASOR, and the regression estimate). However, in those cases where the ASM is used as a discrete parameter in a population model, this advantage is no longer paramount. In such cases, one needs to consider the relative bias of each estimator. For two of the estimators, the direction of the bias will be known. That is, estimates based on ASOR and regression will usually be positively biased relative to the AFO estimator. The bias of the two graphical techniques is not consistent but depends on the form of the relationship between age and percent mature. In general, these estimators will underestimate the true mean. In making management-oriented decisions it may be necessary to consider what the expected bias is. In most cases, an overestimate of the true mean will result in a lower estimate of the replacement yield.

CONCLUSION

The point of this paper is not to encourage the sole use of any one technique in estimating the mean age at attainment of sexual maturity. In making statistical comparisons between populations, one seems to be limited to one of three estimators for which variances can be easily derived.

Authors should be encouraged to be consistent in their usage of ASM statistics. I recommend that the following guidelines be followed:

(1) age-specific ovulation rates should be given,
(2) the procedure used to calculate the ASM should be stated explicitly, and
(3) ASMs from different population should not be compared unless the same/estimation technique was used, or comparison should be suitably qualified.

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REFERENCES

Bengtson, J. L. and Siniff, D. B. 1981. Reproductive aspects of female crabeater seals (*Lobodon carcinophagus*) along the Antarctic Peninsula. *Can. J. Zool.* 59(1): 92–102.

DeMaster, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. *J. Fish. Res. Bd Can.* 35(6): 912–15.

Eberhardt, L. L. and Siniff, D. B. 1977. Population dynamics and marine mammal management policies. *J. Fish. Res. Bd Canada* 34: 183–90.

Goodman, D. 1984. Statistics of reproductive rate estimates, and their implications for population projection. (Published in this volume.)

Kasuya, T. 1972. Growth and reproduction of *Stenella coeruleoalba* based on the age determination by means of dentinal growth layers. *Sci. Rep. Whales Res. Inst., Tokyo* 24: 57–79.

Kasuya, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. *Sci. Rep. Whales Res. Inst., Tokyo* 28: 73–106.

Kasuya, T., Miyazaki, N. and Dawbin, W. B. 1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 26: 157–226.

Perrin, W. F., Holts, D. B. and Miller, R. B. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. *Fish. Bull., US* 75: 725–50.

Perrin, W. F. and Reilly, S. B. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. (Published this volume.)