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INCONSISTENCIES IN READING THE AGE OF HARP SEAL (PAGOPHILUS GROENLANDICUS) TEETH, THEIR CONSEQUENCES, AND A MEANS OF REDUCING RESULTING BIASES

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INTRODUCTION

Ages of harp seals (Pagophilus groenlandicus) are estimated by counting dentinal annuli in tooth sections (Fisher 1954). The accuracy of the method has been validated up to age 12 with known age animals (Øritsland pers. comm.). However, inconsistencies in the ages read for individual teeth frequently occur (Benjaminsen and Øritsland 1975). Estimated age compositions of catches and of the population are important in estimating pup production, mortality rates and mean age of maturity. Hence variability in age determination may have important consequences in estimating abundance, and trends in abundance which ultimately form the basis of scientific advice for management of this species. This paper examines the extent of such errors, the impact on estimates of pup production, mortality rates and mean age of maturity and proposes a means of eliminating the resultant biases.

AGE READING ERRORS

One of the authors (Bowen) investigated age-specific variation of age determination of 202 harp seal teeth by reading each tooth himself in five blind replicates. The sample, collected in April 1979 about 40 km east of Fox Harbour, Labrador, consisted of 68 females and 134 males. A 100 μ section was cut from a lower canine of each specimen at a point slightly below the gingival-enamel junction. Cross sections were examined under polarized light with a 6 to 50 power binocular microscope.

The results are shown in Table 1 which gives the frequency of age read in years against the mean age rounded to the nearest year for each tooth. It is evident that single readings of teeth from a seal aged two or older give unpredictable results. The scatter of ages read increases with mean age read. Close examination of these data indicates that the probability of a single age reading being equal to the mean age reading decreases linearly from almost 1 at age one to about 0.15 at age 23 (Fig. 1). The coefficient of variation of the deviations of read age from mean age is approximately constant, at least up to age 10 (Fig. 2).

Since the number of teeth aged never exceeded 30 in any age group, and in some age groups was as low as 1, Table 1 shows a large number of scattered entries. Table 2 is a smoothed Table of probabilities of reading a tooth from an animal aged i as aged j where i is the row number and j is the column number. These probabilities were derived by subjectively smoothing the empirical frequencies of Table 1 and assuming mean age read is the "actual" size. We shall refer to the body of Table 2 as a matrix P.

The impact of age reading inconsistencies with these probabilities, ignoring sampling variability, is easy to see. If a collection of one million teeth of aged 1 seals and 100,000 of aged 2 seals was read once, the age distribution as read would have 992,000 aged one seals and 106,000 aged two seals and 2,000 aged 3 seals. Thus, the age distribution as read is a smoothing of the actual age distribution of the animals whose teeth were aged.

Again, if sampling fluctuations are ignored, the expected distribution of ages in the sample as read can be determined by matrix multiplication. If the numbers at age (actual) are represented as a row vector and then multiplied on the right by the probability matrix P (= Table 2), then the resulting row vector is the expected age distribution as read. It is this linear connection between the "actual" age distribution and the age distribution as read which enables systematic effects resulting from these ageing errors to be adjusted for. If the matrix P has an inverse (P^{-1}), then multiplication of the age distribution as read by P^{-1} returns to the initial (actual) age distribution. Table 3 is the inverse of the matrix of Table 2.

IMPACT OF AGEING ERRORS

The impact of ageing errors on estimates of vital rates was examined by comparing calculated estimates for examples with an "actual" age distribution and an expected age distribution as read and by simulating the effects of age reading errors.

Winters (1978) estimated natural mortality rates using catch curves for ages 5-17 for samples of male moulting harp seals. For the 1973 sampling year and 1956-68 year-classes, he calculated a slope of catch curve of -.126 leading to an estimated natural mortality rate of 0.109. Carrying out the same calculations using the combined large vessel sample from Lett and Benjaminsen (1977) (see Tables 4 and 5) gave a slope of -0.143 with unadjusted ageing and adjusting that age distribution by P^{-1} resulted in a slope of -0.183 for the catch curve and corresponding natural mortality rate estimate of 0.166. The difference of 0.040 is small but important, since small variations in the natural mortality rate have a substantial impact on calculations of sustainable yield. Since the purpose of this paper is to examine the consequences of age reading variability, not to recalculate all earlier estimates of vital rates for harp seals, the authors have not determined whether all estimates of M would be increased by applying this adjustment. Qualitatively it is clear that the smoothing effect of ageing errors would tend to increase the estimated numbers of the less abundant older age classes thereby underestimating the slope of the catch curve, a difference of one or two percent in general seems reasonable.

The impact on estimates of mean age of sexual maturity using a reproductive sample for moulting seals in April 1953, from area east of Labrador called the front (Fisher 1954). De Master's (1978) formula for the calculation of average age of sexual maturity was used. $X = \ x\ (F(x) - F(x-1))$ when x is age, F is fraction mature at age x in the sample. It was assumed that immature and mature animals of the same age had identical distributions of age reading inconsistencies as in Table 2. The mean age of sexual maturity for the sample as reported by Fisher, and as adjusted for age reading frequencies are shown in Table 6. The adjusted sample has a mean age of maturity of 5.87 if negative numbers in the adjusted age composition are used in the formula or 6.07 if calculated negative adjusted values are set to 0. These values are less than the reported mean age of first maturity of 6.23 for the unadjusted sample. The impact of age reading variability on this sample was examined further, assuming that the sample reported by Fisher represented "actual" ages and determining "read" ages using the probability matrix P. The expected "read" sample is shown in Table 6 under the heading "Fisher times P" it has a mean age of sexual maturity of 6.40. The following five columns represent simulated age readings of the Fisher sample each one corresponding to single, statistically independent readings of teeth from the sample. The calculated mean age of sexual maturity in the simulations varied from 5.35 to 6.63 and averaged 6.19. Large sampling errors due to the small number of animals are evident. If the results of the five simulations are combined, corresponding to reading each tooth five times, the simulated mean age becomes 6.42, which is very close to the expected value. Adjusted values of mean age of first maturity estimates for the individual simulations were very unstable but the adjusted value for the combined sample was 6.24 which compares favourably with "actual" value of 6.23. In this example, age reading errors tend to bias upwards the estimated mean age of sexual maturity by about a fifth of a year. Due to the small number of samples, ageing variation can cause the calcuated mean age to fluctuate widely. In general, age reading variations cause the mean age of maturity to be overestimated due to young, immature animals being aged as older, immature animals, and young, mature animals being aged as older, mature animals. This means that in the crucial ages where maturity is between 30 and 70%, age distributions as read contain too many immatures and too few matures.

D. Rivard calculated the effects of age composition adjustments for survival indices of the 1966-1974 year-classes. Survival indices calculated by Winters (1978) and those calculated by Rivard are shown in Table 7. Survival indices were calculated as follows:

If n_{ij} is the number of seals aged i one year; from Table 4 (unadjusted), individual survival indices were calculated for ages 2 to 8 using the formula

$$S_{ij} = \frac{Nij}{\sum_{i=1}^{25} Nij} \times \frac{\sum_{i=1\,j=1968}^{i=25\,j=1977} Nij}{\sum_{j=1968}^{1977} Nij}$$

Individual estimates of the survival index for each cohort were then weighted by the number of seals in the sample at that age to produce a weighted average survival index for that year-class. These calculations were then repeated after adjusting samples using the matrix P^{-1} of Table 3. Samples used were the total large vessel samples from Lett and Benjaminsen (1977) and from Sargeant (1977).

The calculated survival indices differ from those calculated by Winters since insufficient information was given in his paper to permit exact reconstruction of his results. Figure 3 plots adjusted and unadjusted survival indices as calculated by Rivard against pup kill and shows the predictive regressions of survival index as a function of pup kill before and after adjustment. The unadjusted median year pup production estimate is 423,000 while the adjusted estimate is 398,000.

The survival index for the strong 1968 year-class increased from 1.69 to 1.84, due to the adjustment for ageing inconsistencies, while the survival index for the weak 1969 year-class was adjusted downwards from 0.66 to 0.53. For theoretical reasons, adjustment for ageing inconsistencies tends to increase estimated survival indices for abundant year-classes and reduce those of less abundant year-classes, having little effect on average year-classes. This tends to reduce estimates of pup production. Survival indices based only on two or three young age groups are not affected because of the low rate of ageing inconsistencies for the very early ages. In this example, pup production estimates decreased by 25,000 when the age composition was adjusted, this represents a 6% change.

Roff and Bowen (1980) have developed another estimator of pup production which, like the survival index method, uses variation in the pup harvest and future catches of these cohorts. By the new method, the ratio of catches of two adjacent cohorts in which pup kills are very different is used to estimate p, given as

$$\hat{p} = \sum_{i=1}^{n} \frac{C_{t,\,t+i}}{(C_{t,\,t+i}) + (C_{t+1,\,t+i})}$$

where $C_{t,\,t+i}$ is the catch of cohort t in year t + i and $C_{t+1,\,t+i}$ is the catch of cohort t + 1 in years t + i. Errors in age determination will have a direct influence on the estimation of p and thus pup production. We use the 1967 and 1968 cohorts to illustrate this effect.

Norwegian samples of moulting male harp seals taken in 1970, 1971 and 1973 were used to estimate p (Table 8). The 1967 cohort is represented by ages 3, 4 and 6 and the 1968 cohort by ages 2, 3 and 5. No heterogeneity is detectable (G test) and hence p is estimated by pooling all samples. Unadjusted for errors in age determination, p = 0.29. The 95% confidence limits on the estimated 1967 pup production with this value of p are 353,000 and 595,000.

Adjusting these moulting samples for errors in age determination, p is estimated to be 0.25 (Table 9). The resulting 95% confidence limits on 1967 pup production become 335,000 and 475,000.

THEORY

Observed inconsistencies in age reading can be modelled using probability theory. It is assumed that successive independent blind replicates of age readings for a single tooth would build up an observed probability distribution of age readings for that tooth which converges to a "true" distribution. If each tooth is routinely read only once, the average of these probability distributions over teeth of all seals in a population is a probability distribution of "read" age for a tooth of a given "actual" age chosen at random. It is assumed that age reading variations are statistically independent from tooth to tooth and have the same probability distribution for animals of the same age.

Under these assumptions the distribution of numbers at age as read for a given sample of animals with a given true age is a multinomial distribution. The overall age distribution for a given sample of teeth is the sum of multinomial distributions, one for each "actual" age group. Of course, the "actual" age composition of the sample of seals is also subject to random variation and there is a corresponding variance/co-variance matrix C associated with the distribution of "true ages" of the sample. If a sample of a fixed number of seals is taken at random with replacement from the population, such that each seal of age one and older has the same probability of being included, then the distribution of the "actual" numbers at age within the sample is also a multinomial distribution with probabilities proportional to the abundance of each age group in the ages 1+ population. In practice, the variances and co-variances associated with the actual ages of the sample will be different from the multinomial model, with higher variances due to the way in which samples are collected. Sampling is not completely at random since clusters of animals are included in the age sample. There may also be biases in the sampling procedure, but these are not considered in this paper. The following formulas show the effect of the age reading variation on expected age composition of the sample as read and on the variance/co-variance matrix of numbers at age as read in the sample relative to the "actual" ages.

"Actual" numbers at age in sample = $\underset{\sim}{A}$ (1)

Sample size = $\underset{\sim}{A}.\underset{\sim}{1} = N$ (2)

Expected "Actual" numbers at age in sample $= \alpha$ (3)

Expected "read" numbers at age = $\underset{\sim}{\alpha}\,P$ (4)

Variance/Co-variance matrix of $\underset{\sim}{A} = C$ (5)

Probability of reading "actual" age i as j = P_{ij} (6)

If sample is completely random, $C_{ij} = \underset{\sim}{\alpha}_i \times \underset{\sim}{\alpha}_j \div N \quad i \neq j$ (7)

$$C_{ii} = \underset{\sim}{\alpha}_i \,(1 - \underset{\sim}{\alpha}_i \div N)$$

P' = transpose of P (8)

Variance/Co-variance Matrix of "read" ages of sample A is

$$S_{ij} = -\sum_k P_{ki}\, P_{kj}\, \underset{\sim}{A}_k \text{ if } i \neq j \qquad (9)$$

$$= \sum_k \underset{\sim}{A}_k\, P_{ki}\,(1 - P_{ki}) \qquad i = j$$

Total Variance/Co-variance Matrix as read is

$$CR = P'CP + \Sigma \quad \text{where} \quad \Sigma_{ij} = -\sum_k P_{ki} P_{kj} \underset{\sim}{\alpha}_k \qquad i \neq j \tag{10}$$

$$= \sum_k \underset{\sim}{\alpha}_k P_{ki} (1-P_{ki}) \qquad i=j$$

It is clear that if a matrix P-1, which is the inverse of P exists then multiplying the "read" age distribution by this inverse matrix results in an expected age distribution equal to the "actual" distribution.

$$\underset{\sim}{\alpha} \quad pp^{-1} = \underset{\sim}{\alpha} \tag{11}$$

The effect of this inverse transformation on the variance/co-variance matrix is as shown in the following formula:

$$CA = C + (P^{-1})' \Sigma P^{-1} \tag{12}$$

where CA is the variance/co-variance matrix of the adjusted age distribution.

The above theory is appropriate when each tooth is aged only once and when all teeth with the same "actual" age have the same distribution of probabilities for "read" ages. In fact, some teeth are easier to read than others and this means that the variance/co-variance matrix associated with repeatedly ageing the same sample of teeth is different from the variance/co-variance matrix obtained by taking a larger sample of teeth from the animal population and reading them each once. On the average, the variances of the numbers at age as read tend to be less with multiple readings of the same teeth than with equivalent numbers of age readings of entirely different teeth. The reason for this is the Cauchy-Schwartz inequality as shown in the folllowing formula:

Probability seal k in total population "actual" age i has "read" age j = $_{kj}$, $k = 1,\ldots, M$

Probability a seal chosen at random from all seals age i is read as age j

$$P_{ij} = \frac{1}{M} \sum_k \rho_{kj} \qquad (k = 1 \ldots I) \tag{13}$$

Variance of number read as age i from I seals "actual" age i randomly chosen with replacement and aged once:

$$I \times P_{ij} (1-P_{ij}) \tag{14}$$

Average variance of number read age from a single randomly chosen seal "actual" age j read I times

$$\frac{1}{M} \sum_k I \times \rho_{kj} (1-\rho_{kj}) \tag{15}$$

$$\text{Now } I \times P_{ij} = I \times \frac{1}{M} \sum_k \rho_{kj} \tag{16}$$

$$\text{and } I \times P_{ij}^{2} = I \times \left(\frac{1}{M} \times \sum_{k} \rho_{kj}\right)^{2} \tag{17}$$

$$I \times \frac{1}{M2} \times \left(\sum_{k} \rho_{kj}^{2}\right) \times \left(\sum_{k} 1\right) \qquad \text{Cauchy-Schwartz} \tag{18}$$

$$= I \times \frac{1}{M} \times \sum_{k} \rho_{kj}^{2} \tag{19}$$

Therefore for one tooth read I times, variances ≤ variances for I teeth of same "actual" age read once. It follows, on the average, that variances associated with repeated readings of the same sample are less than those resulting from an equivalent number of single readings of seals from a larger sample with the same "actual" age distribution.

This effect has been neglected in the calculations which follow since it does not impact expected values but only variances and it does not seem practicable, at this point, to classify teeth into easy and hard to read categories apriori. Should this become possible, the methods outlined here could be refined to take advantage of possible extra readings of more difficult teeth.

While the above mathematical formulae are very concise, they do not indicate intuitively the impact of the age reading variation or trade-offs between leaving the biases and removing them at the cost of higher variances. Therefore, we have included a concrete example using ages 1-10 and a truncated version of the P matrix of Table 2. The truncated matrix up to age 10 is contained in Table 10 and its inverse is shown in Table 11. An initial age distribution was chosen based on the 1973 large vessel sample of Lett and Bejaminsen. The number of ten year olds was increased relative to the actual observation in order to suggest the impact of a "plus group". Table 12 shows various quantities which were calculated for this example. It was assumed that each tooth would be read once and two simulations were carried out by the Monte-Carlo method to obtain simulated age distributions as read.

For most ages the expected bias introduced by the ageing inconsistencies was small, of the order of 2 or 3% up to age 5. However, large biases of 11 and 20% occurred for ages 5 and 6 and for ages 7 to 9, biases were of the order of 10%. The increased standard deviation of the adjusted age distribution relative to the age distribution as read was very small for ages 1 to 4 but represented 5% of the mean through ages 5-8 and 10% for age 9. Thus, for some ages, added variation expressed as a co-efficient of variation was greater than the reduction in bias.

In general, it is the exceptionally large and exceptionally small year classes which are substantially systematically influenced by the age reading variability. Age 5 being substantially reduced and age 6 being substantially increased. We note that small numbers of animals and high age reading variability imply that age compositions for ages 12 and older are frequently little better than "random numbers".

Qualitatively, theoretical results agreed with the simulation experiment as shown in Figure 4. Sampling errors associated with the ageing variability are increased by the adjustment but biases are eliminated. From this example, a general rule becomes clear: when the number at age read is large so that sampling errors are small (relatively) and the true age distribution is very uneven so that large biases are introduced by the ageing variability, then the adjusted age distribution is clearly superior to the unadjusted. If the actual age distribution is smooth and the number of ages read is small, then the increase in sampling variability frequently exceeds the decrease in bias associated with the adjustment. In specific instances, the pros and cons can be calculated using the formulas provided above. In any event, whether or not the adjusted numbers are closer to the true value, the systematic effect may have a cumulative importance in analyses such as survival index calculations.

Table 13 shows the variance/co-variance matrices associated with the "actual" age distribution assuming random sampling of the herd, the variance/co-variance matrix of the ageing inconsistencies, the contribution of variance in "actual" ages to the co-variance matrix of the age distribution as read, the co-variance matrix of the "read" age distribution, the co-variance matrix of the adjusted age distribution and the increases in variance and co-variances due to adjustment for ageing inconsistencies. Finally, the contribution of ageing inconsistencies to the co-variance matrix of adjusted age distribution is shown. Ageing inconsistencies become about half of the variance of "actual" ages at age 4 and for some older ages are comparable to the variance in the actual ages. For older ages, adjusting for ageing inconsistencies increases the variances of numbers at age estimates by about 50% in this example.

There exists a "stable" age distribution which is not systematically influenced by age reading variations. In mathematical terms, this corresponds to the existence of an eigenvector $\underset{\sim}{V}$ such that

$$\underset{\sim}{V}P = \underset{\sim}{V}$$

If P is given as in Table 2, the V, expressed as proportions to three significant digits reading 25 age groups from left to right with 0.399 at age 1 to 0.000368 at age 25+ is:

0.399	0.200	0.0697	0.0505	0.0459	0.0437
0.0409	0.0351	0.0303	0.0230	0.0177	0.0132
0.00932	0.00683	0.00478	0.00343	0.00231	0.00193
0.00109	0.000686	0.000432	0.000316	0.000216	0.000176
0.000368					

Cross year mortalities calculated for this distribution are unlikely to arise for harp seals since they decline from 0.693 and 1.05 for ages 1-2 and 2-3 to 0.05 for ages 5-6 and then rise over 0.25 for ages 9-10 to 22-23.

ERRORS IN ESTIMATION OF AGE READING PROBABILITY MATRIX P

Must the matrix P be precisely estimated for practical application of the adjustment? Clearly, the adjustment depends on P and the age reading probabilities P depend on the reader as well as varying from year to year. For the adjustment to be usable, it must not be sensitive to small changes in P.

Suppose the matrix P is used for the adjustment of an observed age distribution Y but the "actual" matrix of age reading probabilities is $P + \Delta$. Instead of the correction $X = YP^{-1}$ obtained using P, the correction $X^* = Y(P + \Delta)^{-1}$ corresponds to the "actual" situation. Since the read age distribution is the same,

$$XP = X^*(P + \Delta) \qquad (20)$$

Writing $\delta = X - X^*$ and simplifying,

$$\delta = X\Delta(P + \Delta)^{-1} \qquad (21)$$

(if $P + \Delta$ has an inverse)

For small Δ, $\delta \approx X\Delta P^{-1}$ (22)

Thus, sensitivity of the adjustment to small changes in P is determined by the magnitude of the elements of P^{-1}.

The adjustment $Y(P^{-1} - I)$ differs by $Y\Delta(P + \Delta)^{-1}$ from the adjustment associated with a precisely estimated age reading probability matrix. Thus, the adjustment is justified if YP^{-1} is closer than Y to $Y(P + \Delta)^{-1}$. This is equivalent to comparing the magnitudes of

$$Y \Delta \ (P + \Delta)^{-1} \text{ and } Y (I - (P + \Delta)^{-1}) = Y (P + \Delta - I)(P + \Delta)^{-1} \qquad (23)$$

If Δ is close to a zero matrix, then equation (23) approximates a comparison of

$$Y \Delta \ P^{-1} \text{ and } Y (I - P^{-1}) = Y (P - I) P^{-1}$$

Thus, to a first order approximation, the use of the estimated matrix P is justified if P is a better estimate than the identity matrix (perfect age reading) of the age reading probability matrix.

As an example, we consider the implications of replacing the matrix of Table 10 with an alternative "actual" age reading probability matrix shown in Table 14. The changes are highlighted in Table 15. The adjustment to the inverse matrix on Table 11 is shown in Table 16 and the approximation for "small" Δ is shown in Table 17.

Applying the adjustment $Y\Delta \ (P + \Delta)^{-1}$ to the two simulated age distributions of the example discussed above gives adjustments of

1)	-0.585	0.46	4.21	-3.23	1.87	-9.92	6.6	-0.645	0.565	-3.33
2)	-0.655	0.469	4.22	-3.71	1.92	-9.35	6.88	-0.522	1.04	-4.3

while the approximate formula $Y \Delta \ P^{-1}$ gives adjustments of

1)	-0.594	0.393	4.26	-3.38	2.05	-5.75	6.66	-1.03	0.496	-3.09
2)	-0.665	0.397	4.28	-3.86	2.11	-5.2	6.92	-0.432	0.934	-3.99

In this case, the first order approximation of equation (22) gives a good modification of the impact of changing P. Comparison with figure (4) shows that adjusting with P is better than accepting age as read except for ages 3, 7 and 10+ despite the fact that errors in estimating P are assumed to be almost as large as the difference between P (Table 10) and perfect age reading.

From formula (22) we conclude that it is desirable to reduce errors in estimation of the matrix P to the order of one percent, but P need not be well estimated for this contribution to error to be less than other sources of error. The use of P^{-1} to adjust ages as read is justified if P is a better approximation than perfect aging to the "actual" age reading probabilities.

NUMBER OF AGE READINGS FOR A SINGLE TOOTH

Two obvious questions arise in planning age sampling and age reading programs. One is for a fixed budget - how should resources be divided between collecting samples and ageing repeatedly the same sample? Two, for a given sample, how much reduction in variance can be expected by repeating the readings one, two, three, or more, times.

If these questions are looked at from the point of view of minimizing, or reducing, the variance of a linear contrast of the age distribution vector i.e., the number at some age or some other one-dimensional linear combination of numbers at age for different ages, then the problem can be analysed mathematically as outlined below.

Cost of collecting 1 seal	a
Cost of reading 1 tooth	b
Total budget	B

If n seals are sampled and each tooth is read m times, then

$$an + bnm = B \quad , \quad m \geq 1 \qquad (23)$$

and the variance/co-variance matrix of the adjusted proportion at age is

$$\frac{C}{n} + (P^{-1})' \ \frac{\Sigma 1 (P^{-1})}{nm} \qquad (24)$$

If the variance of a linear combination (contrast in experimental design litterature) is to be minimized,

$$\frac{V'\ CV}{n} + \frac{V'(P^{-1})'\Sigma\ P^{-1}V}{nm} \qquad (25)$$

is minimised where the vector V defines the linear combination.

This is minimised when

$$m = \sqrt{\frac{a}{b}} \times \sqrt{\frac{V'(P^{-1})'\ \Sigma\ \ P^{-1}V}{V'CV}} \qquad (23)$$

Example, minimise variance of numbers at age 5 in previous example

$$m = \sqrt{\frac{a}{b}} \times \sqrt{\frac{133}{235}}$$

$$= 0.75\sqrt{\frac{a}{b}}$$

Since the number of times a tooth should be read to minimize variance under a fixed budget varies as a square root of the ratio of sampling to ageing costs and the square root of the variance ratio of ageing to sampling errors, adequate estimates can be obtained for planning purposes withing knowing precisely what the variances are. The reduction in target variances or co-variances associated with an additional reading of available teeth can be calculated straightforwardly from the following formula:

$$CA = C + \frac{(P^{-1})'\ \ \Sigma\ \ \ P^{-1}}{m} \qquad (24)$$

No matter how many times available teeth are read, the C component remains - corresponding to the "actual" age variance of the sample.

CONCLUSIONS

It has been demonstrated that age reading variations can bias estimates of pup production by as much as 10% and natural mortality rates by a comparable amount. Ageing inconsistencies also tend to result in overestimated mean age of first maturity. The size of these biases is sufficient to have a serious impact on management advice for harp seals in the Northwest Atlantic.

Age reading variability is an important source of variance in estimated age composition. With single readings and historical sample sizes, age compositions above age 12 bear little relation to year class strengths.

A method has been presented which permits read age compositions to be adjusted to unbiased[1] age compositions. The removal of bias is associated with an increase in variance. When age distributions are smooth and samples are small, the reduction in bias is less than the increase in variance associated with the adjustment process while, if the age composition is uneven and numbers sampled are large, the reduction in bias is greater than the increase in variance. Specific instances can be studied using the formulae for means and variances presented above in order to determine whether the adjustment is likely to add more variation than it removes.

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[1] Only bias due to age reading variability is adjusted.

Even if the overall impact on a read age distribution of ageing variability is not large, there is a systematic tendency for abundant year-classes to appear less abundant and weak year-classes to appear stronger. This tendency results in overestimates of pup production from survival index methods, underestimates of natural mortalities estimated by catch curve methods and overestimates of mean age of first maturity. When samples from many years are combined to give estimates as, for example in Winters (1978), the persistent effects of these biases in the same direction are particularly significant since random variation between years is unsystematic and tends to cancel out in such an analysis.

In view of the small number of specimens involved, multiple "blind" age readings for maturity samples are desirable.

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Table 1 Age-specific variation in age determination of 202 harp seal teeth. Each tooth read five times in blind replicates.

Mean age (years)	Read as (in years)																																		n
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
1	150																																		150
2	1	86	3																																90
3	1	2	79	6	2																														90
4			2	42	5		1																												50
5				4	46	5																													55
6				1	4	47	6	1	1																										60
7					1	7	43	3	1																										55
8						2	7	38	9	3	1																								60
9					1		4	4	20	5	1																								35
10							1		5	20	6	3																							35
11								1		2	11	1																							15
12										1	5	17	5	1	1																				30
13								1		1	3	2	11	4		2			1																25
14													2	9	3	1																			15
15													3	1	6	2	1	1	1																15
16											3		1	1	4	16	8			2															35
17									1				2	2		4	3	7	2	4															25
18															2	5	5	13	3	3	3	1													35
19																2	3	2	10	1	5		2												25
20													1		1			2	4	6	5	4	1		1										25
21										1		1						2	2	3	11	4	6		3	1	1								35
22														1					4	1	1	1	1	4	1							1			15
23																		1			1	1				1		1							5
24																1								1		2		1							5
25																			1				1	2	3	1				2					10
26																						1		1		3									5
27																							1		1		2						1		5
:																																			
30																												2	1			1	1		5
Total																																			1010

Table 2

SMOOTHED AGE READING INCONSISTENCIES

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25+
1	0.99	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.02	0.96	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.05	0.90	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	0.01	0.05	0.85	0.07	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	0.01	0.07	0.82	0.07	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.02	0.08	0.78	0.09	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	0.00	0.00	0.03	0.09	0.74	0.10	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	0.00	0.00	0.00	0.04	0.11	0.70	0.11	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	0.00	0.00	0.00	0.00	0.00	0.01	0.05	0.11	0.67	0.11	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.06	0.12	0.63	0.12	0.05	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.07	0.13	0.59	0.13	0.05	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.08	0.12	0.56	0.14	0.06	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.10	0.11	0.52	0.15	0.06	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.03	0.10	0.11	0.49	0.16	0.07	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.03	0.10	0.11	0.46	0.16	0.07	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00
16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.03	0.04	0.10	0.11	0.42	0.16	0.08	0.02	0.01	0.00	0.00	0.00	0.00	0.00
17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.03	0.05	0.10	0.11	0.39	0.16	0.08	0.03	0.01	0.00	0.00	0.00	0.00
18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.04	0.06	0.10	0.11	0.35	0.15	0.09	0.03	0.02	0.00	0.00	0.00
19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.03	0.04	0.07	0.10	0.11	0.32	0.13	0.09	0.04	0.02	0.01	0.00
20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.04	0.05	0.07	0.09	0.11	0.28	0.12	0.10	0.05	0.03	0.01
21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.02	0.04	0.06	0.07	0.09	0.11	0.24	0.11	0.10	0.07	0.05
22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.04	0.05	0.06	0.07	0.08	0.10	0.21	0.10	0.10	0.14
23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.10	0.18	0.10	0.24
24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.10	0.14	0.38
25+	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.03	0.04	0.05	0.05	0.06	0.07	0.08	0.10	0.48

Table 3

INVERSE OF MATRIX

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	1.01	¯0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	¯0.02	1.04	¯0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	¯0.06	1.12	¯0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	¯0.01	¯0.06	1.19	¯0.10	¯0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	¯0.01	¯0.10	1.24	¯0.11	¯0.02	¯0.01	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	¯0.02	¯0.12	1.31	¯0.15	¯0.01	¯0.01	0.01	0.00	0.00	0.00
7	0.00	0.00	0.00	0.01	¯0.04	¯0.15	1.40	¯0.19	¯0.03	¯0.01	0.01	0.00	0.00
8	0.00	0.00	0.00	0.00	0.01	¯0.05	¯0.20	1.50	¯0.23	¯0.03	¯0.01	0.01	0.00
9	0.00	0.00	0.00	0.00	0.00	0.00	¯0.07	¯0.22	1.58	¯0.25	¯0.05	0.01	0.01
10	0.00	0.00	0.00	0.00	0.00	0.01	0.01	¯0.10	¯0.26	1.71	¯0.32	¯0.08	0.02
11	0.00	0.00	0.00	0.00	0.00	0.00	¯0.02	0.03	¯0.13	¯0.31	1.86	¯0.39	¯0.08
12	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	¯0.18	¯0.28	1.98	¯0.49
13	0.00	0.00	0.00	0.00	0.00	0.00	0.01	¯0.03	0.01	0.03	¯0.29	¯0.25	2.16
14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	¯0.02	0.03	0.02	¯0.33	¯0.26
15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	¯0.03	¯0.01	0.02	0.03	¯0.37
16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	¯0.01	¯0.04	¯0.01	¯0.01
17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	¯0.04	0.01	¯0.01	¯0.01
18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	¯0.01	¯0.06	0.03
19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	¯0.05	0.04	¯0.03
20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	¯0.03	¯0.05
21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	¯0.09	0.04
22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	¯0.01	0.02	0.07	¯0.08
23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	¯0.01	0.02	0.07	¯0.11
24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	¯0.03	¯0.02	0.18
25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01

	14	15	16	17	18	19	20	21	22	23	24	25 +
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12	¯0.10	0.05	0.02	¯0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
13	¯0.61	¯0.07	0.02	0.04	¯0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
14	2.35	¯0.76	¯0.11	0.05	0.05	0.00	¯0.02	0.00	0.00	0.01	0.00	0.00
15	¯0.27	2.54	¯0.90	¯0.09	0.12	¯0.06	0.04	0.00	¯0.02	0.00	0.02	¯0.01
16	¯0.40	¯0.30	2.86	¯1.09	¯0.20	0.20	¯0.01	0.01	¯0.01	¯0.02	0.00	0.02
17	¯0.04	¯0.41	¯0.34	3.17	¯1.34	¯0.21	0.19	0.00	0.13	¯0.07	¯0.15	0.11
18	¯0.05	¯0.11	¯0.44	¯0.41	3.69	¯1.51	¯0.60	0.41	¯0.04	0.17	0.03	¯0.13
19	¯0.04	0.02	¯0.22	¯0.48	¯0.56	4.19	¯1.49	¯0.97	0.34	0.28	0.32	¯0.36
20	0.07	¯0.21	0.02	¯0.14	¯0.45	¯0.76	5.04	¯1.77	¯1.66	0.06	1.43	¯0.60
21	¯0.02	0.15	¯0.05	¯0.18	¯0.17	¯0.57	¯1.18	6.37	¯1.70	¯2.31	¯1.75	2.39
22	¯0.05	0.18	¯0.23	¯0.13	¯0.22	¯0.32	¯0.31	¯1.48	7.61	¯1.47	¯6.01	3.43
23	¯0.12	0.06	¯0.07	¯0.07	¯0.13	¯0.19	¯0.38	¯0.62	¯2.28	10.26	¯4.95	¯0.47
24	0.10	¯0.50	0.26	0.12	0.10	0.22	¯0.60	¯0.68	¯0.57	¯4.82	21.97	¯14.73
25+	¯0.01	0.08	¯0.02	¯0.02	¯0.06	¯0.12	0.05	¯0.08	¯0.26	¯0.25	¯2.83	4.53

Table 4

CATCH AT AGE(LARGE VESSELS)

	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
1	226	458	239	239	12	175	360	464	292	232
2	155	58	210	66	9	237	227	223	112	122
3	91	46	45	53	9	188	86	102	60	95
4	47	33	46	19	24	178	65	67	35	78
5	49	45	33	18	9	299	67	57	24	76
6	43	34	30	11	10	81	88	57	13	37
7	75	39	41	10	13	68	21	28	18	20
8	77	51	23	8	9	85	21	23	13	17
9	54	41	35	17	6	42	36	29	11	31
10	56	29	31	16	6	41	21	17	6	10
11	42	27	20	10	4	48	16	28	6	8
12	30	19	26	12	5	30	24	17	5	10
13	32	23	23	8	2	36	23	20	8	15
14	42	26	16	4	2	24	19	15	5	17
15	35	26	24	6	6	37	30	15	5	9
16	34	18	17	6	4	33	16	13	5	13
17	28	24	15	6	3	26	16	13	5	9
18	44	21	17	9	2	24	14	10	3	5
19	38	22	14	6	0	30	12	8	2	3
20	27	20	12	8	5	33	10	6	1	2
21	17	14	8	5	1	18	8	5	1	4
22	24	12	7	9	3	18	9	7	2	2
23	14	11	3	7	1	20	7	5	1	2
24	10	6	4	4	2	15	11	6	0	2
25+	5	7	1	7	0	17	9	5	0	2

Table 5

ADJUSTED CATCH-AT-AGE

	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
1	225	462	237	240	12	172	359	464	293	232
2	154	53	214	63	9	233	228	221	110	119
3	95	48	42	56	8	191	86	104	62	98
4	45	31	48	17	27	169	64	67	35	78
5	50	48	32	19	7	343—	66	57	25	82
6	36	31	28	10	9	57	103	62	11	35
7	79	36	46	9	14	58	8	23	20	16
8	83	57	15	5	9	97	16	20	13	13
9	45	41	38	19	5	29	43	32	12	41
10	63	27	33	18	6	38	18	10	4	5
11	39	27	12	7	3	55	8	35	5	3
12	17	11	30	16	7	22	28	12	4	6
13	26	21	23	7	¯1	38	22	24	11	19
14	49	28	7	¯2	0	6	12	11	3	21
15	28	27	34	7	10	46	45	14	5	1
16	21	1	10	3	4	32	3	12	5	22
17	5	30	11	2	3	10 -	17	17	8	10
18	81	18	26	14	0	11	16	9	2	2
19	52	29	16	¯2	¯8	45	12	7	1	1
20	20	33	18	14	21	70	7	2	¯1	¯3
21	¯10	12	8	¯5	¯8	¯13	2	0	0	15
22	84	13	16	29	10	4	18	22	11	1
23	37	41	¯11	29	¯6	73	¯10	3	6	¯1
24	11	¯6	34	¯17	26	97	130	52	¯17	12
25+	¯41	¯7	¯25	5	¯20	¯79	¯85	¯38	8	¯7

TABLE 6

FISHER (1954) 1953 APRIL SAMPLE

Age (Years)	Fisher I	Fisher M	Fisher adj. I	Fisher adj. M	Fisher X P I	Fisher X P M	Sim 1 I	Sim 1 M	Sim 2 I	Sim 2 M	Sim 3 I	Sim 3 M	Sim 4 I	Sim 4 M	Sim 5 I	Sim 5 M	Sim Sum. Adj. I	Sim Sum. Adj. M
1	4		4.0	0	4.0	0	4		4		4		4		4		20.1	0
2	1		0.2	0	1.7	0	2		1		3		3		0		5.3	-0.1
3	12		12.4	0	11.6	0.1	12		12	1	11	1	11		13		61.4	2.0
4	13		13.5	-0.7	12.5	0.5	11		11	0	13	0	12		13	1	62.1	-1.9
5	11	6	12.1	6.9	10.1	5.3	10	6	11	4	10	5	11	6	10	6	57.2	31.0
6	2	4	1.0	4.1	2.7	3.9	1	3	4	2	2	4	2	4	2	3	6.4	15.0
7	1	3	0.9	2.9	1.1	3.1	3	3	1	5	1	3	1	2	2	3	8.6	15.6
8		2	-0.3	1.5	0.3	2.3	1	3		3		3		2		3	-0.7	13.3
9		3	0	3.8	0	2.6		3		4		2		4		3	-0.4	19.9
10		2	0	1.6	0	2.2		2		1		2		2		1	0	5.1
$\bar{X}$	6.23		6.07 (x-ve)		6.40		6.63		6.49		6.17		6.31		5.35		Sim Sum 1 to 5	6.42
			5.87 (w-ve)				Adj. 6.33		-6.92		5.97		5.96		5.98		Sim Sum Adj.	6.24

TABLE 7

SURVIVAL INDEX

Year Class	Winters	Unadjusted	Adjusted	Reported Kill (1,000)
1966	0.79	0.75	0.74	235
1967	0.62	0.66	0.53	280
1968	1.65	1.69	1.84	160
1969	0.98	1.13	1.13	237
1970	0.71	0.93	0.91	220
1971	0.91	0.84	0.83	213
1972	1.41	1.29	1.30	120
1973	1.62	1.49	1.51	103
1974	1.68	1.56	1.56	118

TABLE 8

TESTING FOR BIAS IN THE ESTIMATION OF p FOR THE 1967 AND 1968 COHORTS NUMBERS-AT-AGE UNADJUSTED FOR ERRORS IN AGE DETERMINATION

Sample Year	1967 cohort		1968 cohort	
	Age	Number	Age	Number
1970[1]	3	11	2	25
1971	4	15	3	26
1973	6	31	5	89
Total		57		140

[1] Moulting samples from Benjaminsen and Øritsland MS.

$G = 1.73$, $df = 2$, $P\ 0.05$

$p = 57/197 = .29$

TABLE 9

TESTING FOR BIAS IN THE ESTIMATION OF p FOR THE 1967 AND 1968 COHORTS NUMBERS-AT-AGE ADJUSTED FOR ERRORS IN AGE DETERMINATION

Sample Year	1967 cohort		1968 cohort	
	Age	Number	Age	Number
1970	3	12	2	27
1971	4	15	3	29
1973	6	26	5	104
Total		53		160

G = 4.30, df = 2, P 0.05

p = 53/213 = .25

Table 10

SMOOTHED AGE READING INCONSISTENCIES

	1	2	3	4	5	6	7	8	9	10+
1	0.99	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.02	0.96	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.05	0.90	0.05	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	0.01	0.05	0.85	0.07	0.02	0.00	0.00	0.00	0.00
5	0.00	0.00	0.01	0.07	0.82	0.07	0.02	0.01	0.00	0.00
6	0.00	0.00	0.00	0.02	0.08	0.78	0.09	0.02	0.01	0.00
7	0.00	0.00	0.00	0.00	0.03	0.09	0.74	0.10	0.03	0.01
8	0.00	0.00	0.00	0.00	0.00	0.04	0.11	0.70	0.11	0.04
9	0.00	0.00	0.00	0.00	0.00	0.01	0.05	0.11	0.67	0.16
10+	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.06	0.12	0.81

Table 11

INVERSE MATRIX OF AGE-READING INCONSISTENCIES

	1	2	3	4	5	6	7	8	9	10+
1	1.01	¯0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	¯0.02	1.04	¯0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	¯0.06	1.12	¯0.07	0.01	0.00	0.00	0.00	0.00	0.00
4	0.00	¯0.01	¯0.06	1.19	¯0.10	¯0.02	0.01	0.00	0.00	0.00
5	0.00	0.00	¯0.01	¯0.10	1.24	¯0.11	¯0.02	¯0.01	0.00	0.00
6	0.00	0.00	0.00	¯0.02	¯0.12	1.31	¯0.15	¯0.01	¯0.01	0.00
7	0.00	0.00	0.00	0.01	¯0.04	¯0.15	1.40	¯0.19	¯0.03	0.00
8	0.00	0.00	0.00	0.00	0.01	¯0.05	¯0.20	1.50	¯0.23	¯0.03
9	0.00	0.00	0.00	0.00	0.00	0.00	¯0.07	¯0.21	1.58	¯0.30
10+	0.00	0.00	0.00	0.00	0.00	0.01	0.01	¯0.08	¯0.22	1.28

TABLE 12

EXAMPLE OF THEORY

12.a "Actual" Age Distribution of Sample

175 237 188 178 299 81 68 85 42 51

12.b Expected Age Distribution as Read

177.99 240.45 185.83 183.25 266.16 97.61 75.55 78.59 46.46 52.11

12.c ("Actual" - Expected) ÷ "Actual", i.e. relative bias.

-0.017 -0.015 0.012 -0.029 0.110 -0.205 -0.111 0.075 -0.106 -0.022

12.d (Standard Deviation (adjusted) - Standard Deviation (read)) ÷ "Actual" Age Distribution. i.e. increase in coefficient of variation of adjustment.

0.001 0.003 0.009 0.016 0.013 0.042 0.056 0.055 0.103 0.045

12.e Simulated "Read" Age Distributions

1)	181	239	183	180	262	104	68	92	47	48
2)	177	242	189	179	269	90	74	82	41	61

12.f Adjusted Simulated "Read" Age Distributions

1)	178.1	235.6	185.1	174.6	293.8	90.3	53.7	106.7	40.8	45.3
2)	174.0	238.5	191.7	172.6	304.0	70.9	66.7	90.9	30.8	63.9

12.g Sampling Errors

1) Read	3.01	-1.45	-2.83	-3.25	-4.16	6.39	- 7.55	13.41	0.54	-4.11
Adjusted	3.01	-1.40	-2.90	-3.40	-5.20	9.30	-14.30	21.70	-1.20	-5.70
2) Read	-0.99	1.55	3.17	-4.25	2.89	-7.61	- 1.55	3.41	-5.46	8.89
Adjusted	-1.00	1.50	3.70	-5.40	5.40	-10.10	- 1.30	5.90	-11.20	12.9

TABLE 13

13.a Variance/Co-variance Matrix of "Actual" Ages

153	-29.5	-23.4	-22.2	-37.3	-10.1	- 8.48	-10.6	- 5.24	- 6.36
-29.5	197	-31.7	-30	-50.5	-13.7	-11.5	-14.3	- 7.09	- 8.61
-23.4	-31.7	163	-23.8	-40	-10.8	- 9.11	-11.4	- 5.62	- 6.88
-22.2	-30	-23.8	155	-37.9	-10.3	- 8.62	-10.8	- 5.32	- 6.47
-37.3	-50.5	-40	-37.9	235	-17.2	-14.5	-18.1	- 8.94	-10.9
-10.1	-13.7	-10.8	-10.3	-17.2	/6.3	- 3.92	- 4.9	- 2.42	- 2.94
- 8.48	-11.5	- 9.11	- 8.62	-14.5	- 3.92	64.7	- 4.12	- 2.43	- 2.47
-10.6	-14.3	-11.4	-10.8	-18.1	- 4.9	- 4.12	79.9	- 2.54	- 3.09
- 5.24	- 7.09	- 5.62	- 5.32	- 8.94	- 2.42	- 2.03	- 2.54	40.7	- 1.53
- 6.36	- 8.61	- 6.83	- 6.47	-10.9	- 2.94	- 2.47	- 3.09	- 1.53	49.1

13.b Variance/Co-variance Matrix of Ageing Inconsistencies

6.38	-8.28	-0.0948	0	0	0	0	0	0	0
-6.28	21.5	-13.1	- 1.98	-0.125	-0.0356	0	0	0	0
-0.0948	-13.1	33	-16.2	-3.07	-0.387	-0.0598	-0.0299	0	0
0	-1.98	-16.2	52.7	-27.9	-5.75	-0.564	-0.242	-0.0162	0
0	-0.125	-3.07	-27.9	63.7	-22.6	-7	-2.79	-0.125	-0.0204
0	- 0.0356	-0.387	-5.75	-22.6	46.1	-11	-4.51	-1.47	-0.264
0	0	-0.0598	-0.564	-7	-11	36.4	-12	-4.08	1.63
0	0	-0.0299	-0.242	-2.79	-4.51	-12	35.5	-10.2	-5.67
0	0	0	-0.0162	-0.126	-1.47	-4.08	-10.2	25.8	-9.85
0	0	0	0	-0.0204	-0.264	-1.63	-5.67	-9.85	17.4

13.c Contribution of Variance in "Actual" Ages to Co-variance of "Read" Age Distribution

149	-24.2	-23.5	-23.2	-33.7	-12.4	- 9.58	- 9.96	- 5.89	- 6.61
-24.2	178	-18.7	-29.4	-45.5	-16.7	-12.9	-13.5	- 7.96	- 8.92
-23.5	-18.7	128	- 8.02	-32.2	-12.5	- 9.94	-10.4	- 6.15	- 6.9
-23.2	-29.4	- 8.02	107	- 6.86	- 6.99	- 9.3	-10	- 6.05	- 6.8
-33.7	-45.5	-32.2	- 6.86	152	4.15	- 7.33	-12.1	- 8.68	- 9.86
-12.4	-16.7	-12.5	- 6.99	4.15	44.7	5.78	- 0.953	- 1.76	- 3.36
- 9.58	-12.9	- 9.94	- 9.3	- 7.33	5.78	35.1	7.82	1.58	- 1.18
- 9.96	-13.5	-10.4	-10	-12.1	-0.953	7.82	38.7	7.63	2.75
- 5.89	- 7.96	- 6.15	- 6.05	- 8.68	- 1.76	1.58	7.63	19.1	8.13
- 6.61	- 8.92	- 6.9	- 6.8	- 9.86	- 3.36	- 1.18	2.75	8.13	32.7

13.d Co-variance of "Read" Age Distribution

155	-30.5	-23.6	-23.2	-33.7	-12.4	- 9.58	- 9.96	- 5.89	- 6.61
-30.5	199	-31.8	-31.4	-45.6	-16.7	-12.9	-13.5	- 7.96	- 8.92
-23.6	-31.8	161	-24.3	-35.2	-12.9	-10	-10.4	- 6.15	- 6.9
-23.2	-31.4	-24.3	159	-34.7	-12.7	- 9.86	-10.3	- 6.06	- 6.8
-33.7	-45.6	-35.2	-34.7	216	-18.5	-14.3	-14.9	- 8.81	- 9.88
-12.4	-16.7	-12.9	-12.7	-18.5	90.9	- 5.25	- 5.46	- 3.23	- 3.62
- 9.58	-12.9	-10	- 9.86	-14.3	- 5.25	71.5	- 4.23	- 2.5	- 2.8
- 9.96	-13.5	-10.4	-10.3	-14.9	- 5.46	- 4.23	74.2	- 2.6	- 2.92
- 5.89	- 7.96	- 6.15	- 6.06	- 8.81	- 3.23	- 2.5	- 2.6	44.9	- 1.72
- 6.61	- 8.92	- 6.9	- 6.8	- 9.88	- 3.62	- 2.8	- 2.92	- 1.72	50.2

13.e Co-variance of Unbiased Adjusted Age Distribution

160	-36.7	-23	-22.2	-37.3	-10.1	- 8.48	-10.6	- 5.24	- 6.36
-36.7	222	-49.4	-31	-49.9	-13.7	-11.5	-14.4	- 7.09	- 8.61
-23	-49.4	207	-51.5	-40.5	- 9.77	- 9.21	-11.4	- 5.63	- 6.82
-22.2	-31	-51.5	240	-92.1	-15.1	- 5.97	-10.2	- 5.47	- 6.5
-37.3	-49.9	-40.5	-92.1	348	-66.8	-23.2	-20.2	- 7.25	-11
-10.1	-13.7	- 9.77	-15.1	-66.8	168	-38	-10.1	- 2.93	- 1.79
- 8.48	-11.5	- 9.21	- 5.97	-23.2	-38	151	-47	- 6.62	-0.827
-10.6	-14.4	-11.4	-10.2	-20.2	-10.1	-47	176	-44.2	- 8.25
- 5.24	- 7.09	- 5.63	- 5.47	- 7.25	- 2.93	- 6.62	-44.2	122	-37.8
- 6.36	- 8.61	- 6.82	- 6.5	-11	- 1.79	-0.827	- 8.25	-37.8	88

TABLE 13 (cont'd)

13.f Increase in Co-variance Matrix due to Adjustment for Ageing Inconsistencies

4.55	-6.25	- 0.524	1.06	-3.54	2.28	1.1	-0.632	0.655	0.249
-6.25	23	-17.6	-0.385	-4.33	-3.03	1.44	-0.893	0.869	0.315
-0.524	-17.6	46	-27.2	-5.24	3.15	0.7858	-1	0.516	0.0734
1.06	0.385	-27.2	80.6	-57.4	-2.37	-3.89	-0.0654	0.59	0.299
-3.54	-4.33	-5.24	-57.4	133	-48.3	-8.88	-5.29	1.56	-1.16
2.28	3.03	3.15	-2.37	-48.3	77.5	-32.7	-4.64	-0.299	1.84
1.1	1.44	0.785	3.89	-8.88	-32.7	79.3	-42.7	-4.12	1.98
-0.632	-0.893	-1	-0.0654	-5.29	-4.64	-42.7	102	-41.6	-5.33
0.655	0.869	0.516	0.59	1.56	0.299	-4.12	-41.6	77.3	-36
0.24	0.315	0.0734	0.299	-1.16	1.84	1.98	-5.33	-36	37.8

13.g Contribution of Ageing Inconsistencies to Co-variances of Adjusted Age Distribution

6.79^{E0}	-7.19^{E0}	3.99^{E-1}	1.67^{E-2}	-1.11^{E-2}	2.90^{E4}	4.00^{E-4}	8.64^{E-5}	-4.05^{E-5}	-1.22^{E6}
-7.19^{E0}	2.53^{E1}	-1.76^{E1}	-9.51^{E-1}	5.58^{E-1}	-1.20^{E-2}	-2.04^{E-2}	-4.42^{E-3}	2.02^{E-3}	-7.21^{E5}
3.99^{E-1}	-1.76^{E1}	4.44^{E1}	-2.76^{E1}	-4.36^{E-1}	1.08^{E1}	-1.09^{E-1}	-2.46^{E-2}	-9.45^{E-3}	5.29^{E-3}
1.67^{E-2}	-9.51^{E-1}	-2.76^{E1}	8.45^{E1}	-5.42^{E1}	-4.84^{E1}	2.65^{E0}	5.84^{E-1}	-1.49^{E-1}	-3.65^{E-2}
-1.11^{E-2}	5.58^{E-1}	-4.36^{E-1}	-5.42^{E1}	1.13^{E2}	-4.86^{E1}	-8.72^{E0}	-2.08^{E0}	1.70^{E0}	1.80^{E-1}
2.90^{E-4}	-1.20^{E-2}	1.08^{E0}	-4.84^{E0}	-4.96^{E1}	9.20^{E1}	-3.40^{E1}	-5.20^{E0}	-5.08^{E-1}	1.16^{E0}
4.00^{E-4}	-2.04^{E-2}	-1.09^{E-1}	2.65^{E0}	-8.72^{E0}	-3.40^{E1}	8.60^{E1}	-4.28^{E1}	-4.59^{E0}	1.64^{E0}
8.64^{E-5}	-4.42^{E-3}	-2.46^{E-2}	5.84^{E-1}	-2.08^{E0}	-5.20^{E0}	-4.28^{E1}	9.64^{E1}	-4.16^{E1}	-5.16^{E0}
-4.05^{E-5}	2.02^{E-3}	-9.45^{E-3}	-1.49^{E-1}	1.70^{E0}	-5.08^{E-1}	-4.59^{E0}	-4.16^{E1}	8.14^{E1}	-3.62^{E1}
-1.22^{E-6}	7.21^{E-5}	5.29^{E-3}	-3.65^{E-2}	1.80^{E-1}	1.16^{E0}	1.64^{E0}	-5.16^{E0}	-3.62^{E1}	3.88^{E1}

Table 14

Alternative Age Reading Probability Matrix for Sensitivity Calculations (see text).

1.00E0	8.67E¯19	0.00E0	0.00E0	0.00E0	0.00E0	0.00E0	0.00E0	0.00E0	0.00E0
1.00E¯2	9.70E¯1	2.00E¯2	0.00E0	0.00E0	0.00E0	0.00E0	0.00E0	0.00E0	0.00E0
0.00E0	4.00E¯2	9.10E¯1	4.00E¯2	1.00E¯2	0.00E0	0.00E0	0.00E0	0.00E0	0.00E0
0.00E0	2.00E¯2	4.00E¯2	8.60E¯1	6.00E¯2	1.00E¯2	1.00E¯2	0.00E0	0.00E0	0.00E0
0.00E0	0.00E0	2.00E¯2	5.00E¯2	8.20E¯1	7.00E¯2	3.00E¯2	1.00E¯2	0.00E0	0.00E0
0.00E0	0.00E0	1.00E¯2	3.00E¯2	8.00E¯2	7.60E¯1	8.00E¯2	3.00E¯2	1.00E¯2	0.00E0
0.00E0	0.00E0	0.00E0	1.00E¯2	4.00E¯2	9.00E¯2	7.40E¯1	8.00E¯2	3.00E¯2	1.00E¯2
0.00E0	0.00E0	0.00E0	1.00E¯2	0.00E0	3.00E¯2	1.10E¯1	6.90E¯1	1.20E¯1	4.00E¯2
0.00E0	0.00E0	0.00E0	0.00E0	1.00E¯2	2.00E¯2	6.00E¯2	1.10E¯1	6.40E¯1	1.60E¯1
0.00E0	0.00E0	0.00E0	0.00E0	0.00E0	1.00E¯2	2.00E¯2	8.00E¯2	1.30E¯1	7.60E¯1

Table 15

Difference between probabilities in Table 14 and Table 10.

0.01	¯0.01	0	0	0	0	0	0	0	0
¯0.01	0.01	0	0	0	0	0	0	0	0
0	¯0.01	0.01	¯0.01	0.01	0	0	0	0	0
0	0.01	¯0.01	0.01	¯0.01	¯0.01	0.01	0	0	0
0	0	0.01	¯0.02	0	0	0.01	0	0	0
0	0	0.01	0.01	0	¯0.02	¯0.01	0.01	0	0
0	0	0	0.01	0.01	0	0	¯0.02	0	0
0	0	0	0.01	0	¯0.01	0	¯0.01	0.01	0
0	0	0	0	0.01	0.01	0.01	0	¯0.03	0
0	0	0	0	0	0.01	0.01	0.02	0.01	¯0.05

Table 16

Change in Adjustment matrix P^{-1} using Table 14 instead of Table 10

1.01E¯2	¯1.03E¯2	2.27E¯4	¯1.05E¯5	¯2.04E¯6	3.04E¯7	1.93E¯7	¯3.91E¯9	¯1.32E¯8	4.34E¯10
¯1.01E¯2	1.03E¯2	¯2.27E¯4	1.05E¯5	2.04E¯6	¯3.04E¯7	¯1.93E¯7	3.91E¯9	1.32E¯8	¯4.34E¯10
1.05E¯4	¯1.05E¯2	1.15E¯2	¯1.29E¯2	1.31E¯2	¯1.01E¯3	¯2.34E¯4	¯1.27E¯4	5.07E¯5	¯9.08E¯7
¯1.05E¯4	1.05E¯2	¯1.14E¯2	1.32E¯2	¯1.24E¯2	¯1.40E¯2	1.55E¯2	¯9.52E¯4	¯3.13E¯4	¯8.83E¯5
1.95E¯8	¯1.95E¯6	1.20E¯2	¯2.40E¯2	1.05E¯3	¯1.39E¯3	1.42E¯2	¯1.54E¯3	¯3.48E¯4	¯3.24E¯5
6.86E¯6	¯6.86E¯4	1.07E¯2	1.19E¯2	2.19E¯3	¯2.57E¯2	¯1.34E¯2	1.75E¯2	¯2.20E¯3	¯2.83E¯4
2.04E¯6	¯2.04E¯4	¯7.34E¯4	1.13E¯2	1.12E¯2	¯5.44E¯4	3.52E¯3	¯3.05E¯2	5.47E¯3	4.05E¯4
2.37E¯6	¯2.37E¯4	¯3.89E¯4	1.23E¯2	6.31E¯5	¯1.34E¯2	2.30E¯3	¯1.69E¯2	1.96E¯2	¯3.26E¯3
¯3.88E¯7	3.88E¯5	¯3.14E¯4	¯1.25E¯3	1.11E¯2	1.14E¯2	1.50E¯2	4.50E¯3	¯5.07E¯2	1.02E¯2
¯1.80E¯7	1.80E¯5	¯5.52E¯5	¯7.61E¯4	¯1.72E¯3	1.15E¯2	7.59E¯3	3.23E¯2	2.38E¯2	¯7.26E¯2

Table 17

Approximation to Table 16 using formula 22 (see below)

1.03E¯2	¯1.05E¯2	2.35E¯4	¯1.39E¯5	1.17E¯6	2.60E¯7	¯6.09E¯8	¯1.57E¯8	1.19E¯9	1.29E¯9
¯1.03E¯2	1.05E¯2	¯2.35E¯4	1.39E¯5	¯1.17E¯6	¯2.60E¯7	6.09E¯8	1.57E¯8	¯1.19E¯9	¯1.29E¯9
2.20E¯4	¯1.09E¯2	1.20E¯2	¯1.36E¯2	1.34E¯2	¯8.24E¯4	¯2.45E¯4	¯1.41E¯4	4.62E¯5	8.47E¯7
¯2.20E¯4	1.09E¯2	¯1.20E¯2	1.38E¯2	¯1.26E¯2	¯1.38E¯2	1.58E¯2	¯1.64E¯3	¯2.19E¯4	¯7.06E¯5
7.98E¯6	¯3.95E¯4	1.25E¯2	¯2.44E¯2	1.67E¯3	¯1.03E¯3	1.39E¯2	¯1.93E¯3	¯2.86E¯4	¯1.96E¯5
1.34E¯5	¯6.66E¯4	1.05E¯2	1.16E¯2	1.97E¯3	¯2.55E¯2	¯1.29E¯2	1.71E¯2	¯1.80E¯3	¯3.32E¯4
1.53E¯6	¯7.56E¯5	¯7.27E¯4	1.09E¯2	1.11E¯2	¯2.45E¯4	3.87E¯3	¯3.01E¯2	4.67E¯3	5.13E¯4
1.84E¯6	¯9.11E¯5	¯6.71E¯4	1.21E¯2	1.14E¯4	¯1.28E¯2	2.88E¯3	¯1.70E¯2	1.83E¯2	¯2.81E¯3
¯2.98E¯7	1.47E¯5	¯5.67E¯5	¯1.13E¯3	1.07E¯2	1.06E¯2	1.44E¯2	4.23E¯3	¯4.79E¯2	9.07E¯3
¯6.49E¯9	3.21E¯7	2.18E¯5	¯1.40E¯4	¯1.26E¯3	1.03E¯2	7.34E¯3	2.96E¯2	2.17E¯2	¯6.76E¯2

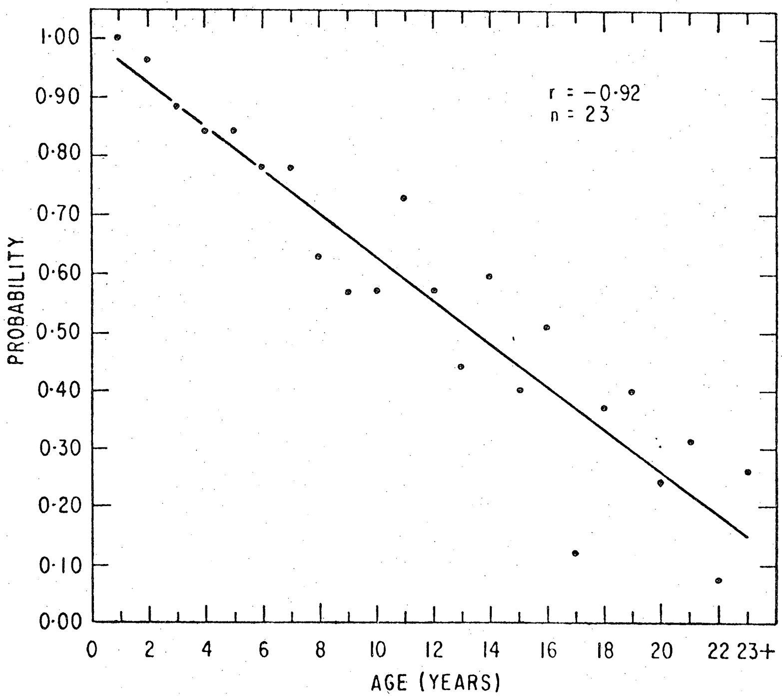

Fig. 1. Probability of a single age reading being equal to the mean age reading as a function of age. (Line fitted by eye.)

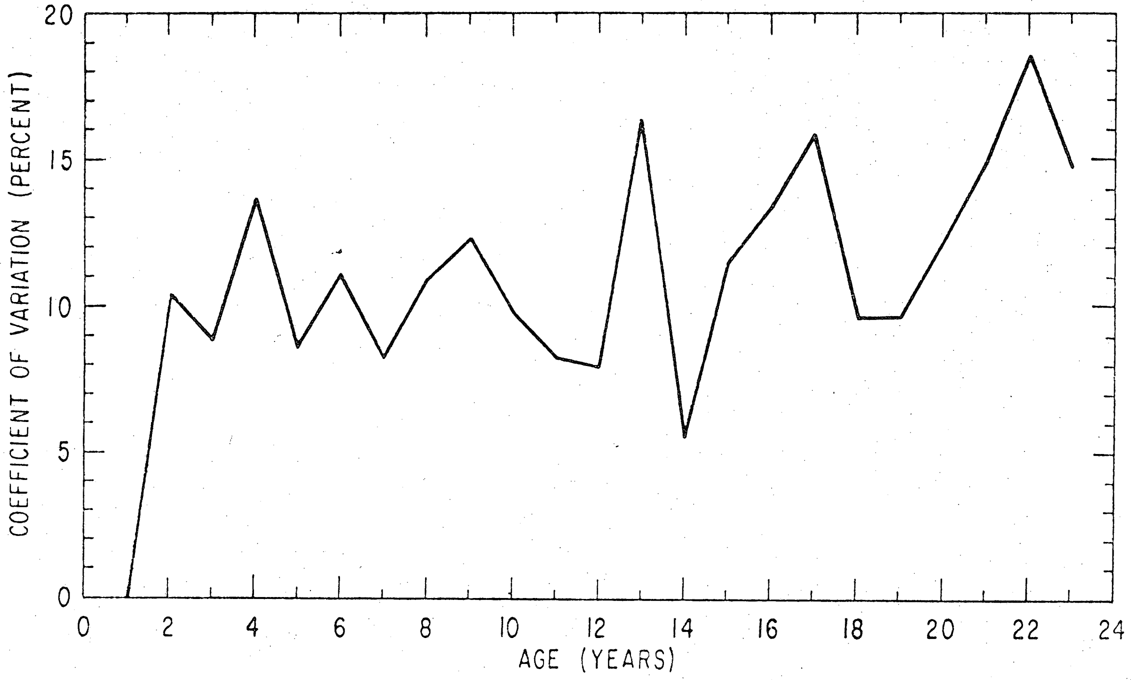

Fig. 2. Coefficient of variation as a function of mean age read.

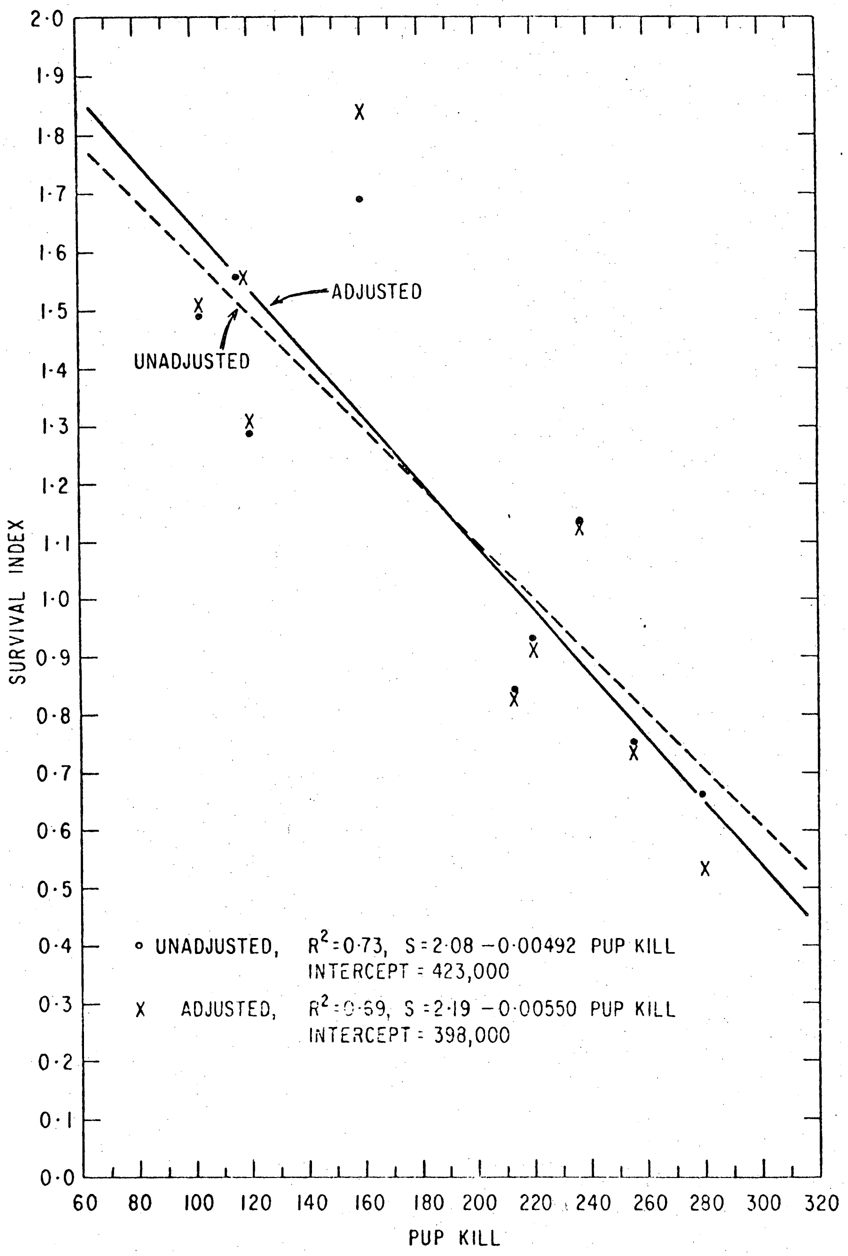

Fig. 3. Effect of ageing errors on estimated pup production using the survival index method.

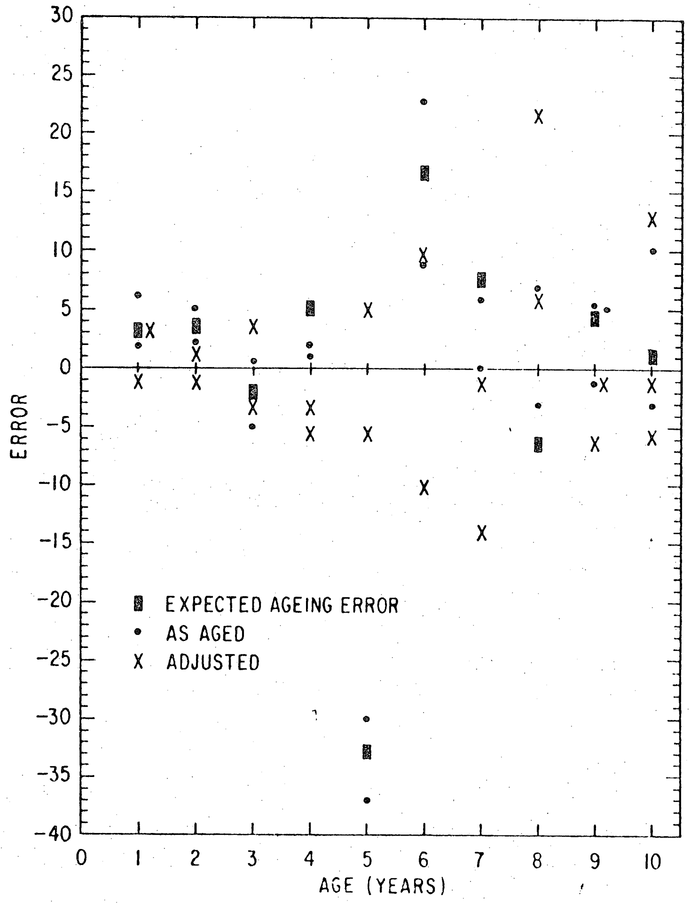

Fig. 4 Example showing simulated effects of age reading variations and adjustments (see text).