Bias in Chapman-Robson and least-squares estimators of mortality rates for steady-state populations

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When age-frequency data are insufficient for fisheries scientists to estimate year- or age-specific mortality, they are often pooled to provide a single estimate for all fully recruited age groups. The accuracy of a pooled estimate depends largely on whether or not the sampled population is in a steady state, i.e. a state in which the rates of recruitment and mortality are relatively constant with respect to time and age. Departures from this condition introduce known biases to the estimate of mortality (Ricker, 1975; Jensen, 1984). These departures may be difficult to detect because trends in time-specific recruitment or time- and age-specific mortality can result in a population age structure that is quite similar to that for a steady-state population. For instance, a long-term increasing trend in recruitment could result in a stable age frequency that would indicate a higher mortality rate than was actually occurring (for various scenarios see Ricker, 1975).

Pooled-data estimation techniques that have been applied to age-frequency data for fish populations include "catch curve" least-squares regression analysis (Seber, 1973; Ricker, 1975) and nonregression-based methods developed by Heincke (1913), Jackson (1939), and Chapman and Robson (1960). Of the nonregression-based estimators, the Chapman and Robson estimator is preferred because it is

the least sensitive to sampling error (Robson and Chapman, 1961). Despite the restrictive steady-state requirements, these techniques have been applied to a wide variety of marine animals; recent examples include Atlantic croaker, *Micropogonias undulatus* (Barbieri et al., 1994); blue rockfish, *Sebastes mystinus* (Adams and Howard, 1996); red drum, *Sciaenops ocellatus* (Ross et al., 1995); red porgy, *Pagrus pagrus* (Pajuelo and Lorenzo, 1996); and deep-water shrimp, *Aristeus antennatus* (Ragonese and Bianchini, 1996).

The Chapman-Robson (CR) estimator is based on the probability density function of the geometric distribution and provides a unique minimum-variance, unbiased estimate of survival (S),

$$S = \frac{\sum_{i=1}^{N} x_i}{N + \sum_{i=1}^{N} x_i - 1},$$

where x_i = the number of years the ith fish is older than the age at full recruitment; and

N = the total number of fully recruited fish.

The underlying assumption is that the age of each fish sampled represents a random, independent age observation from a steady-state

population. For age-frequency data that have been truncated to eliminate some older age groups, a slightly biased maximum likelihood estimator of survival (CRt) that can be solved by iteration is

$$\frac{\sum_{i=1}^{N} x_i}{N} = \frac{S}{1-S} - (K+1)\frac{S^{(K+1)}}{1-S^{(K+1)}},$$

where $K + 1$ = the number of fully recruited age groups used (Chapman and Robson 1960).

The least-squares regression (LS) estimator provides an unbiased estimate of $-\log S$ (denoted as Z, the instantaneous total mortality rate) and is based on a linear fit to a log-transformed exponential decay model

$$E(\log N_j) = \log(pN_0) - Zj,$$

where N_j = the number of age j fish in the sample;

N_o = the original number of fish in the population; and

p = the probability that a fish in the population is included in the sample (Seber, 1973).

As required for linear regression, log-abundance data are assumed to be independent and normally distributed with constant variance along the regression line. Concern about violating these assumptions led Chapman and Robson (1960) to recommend that when the LS method is used, the age-frequency data should be truncated to exclude less abundant age groups.

Although both the CR and LS estimator returned very accurate estimates of Z for a suite of exact steady-state age frequencies (Jensen, 1985), the effect of random variation within the sample age frequencies

has not been investigated. Jensen (1996) found that the CR method was less biased and more precise than the LS method when used to estimate mortality from the age structure of pooled, simulated net-hauls of lake whitefish, *Coregonus clupeaformis*. A random sample drawn from a known geometric distribution of ages will have an age distribution that varies stochastically from the true distribution. In this study, I evaluate the effect of sample size, mortality rate, and an age-frequency truncation scheme on the accuracy and precision of the CR (and CRt) and LS estimators when the sample age frequency is drawn randomly from a population of geometrically distributed ages.

Materials and methods

I used a stochastic model that allowed for random departures from the exact age distribution of the population to generate the simulated sample age frequencies. Under a known, constant survival rate, a geometric distribution function defines the cumulative probability of a fish from a fully recruited cohort being less than age j as

$$P(age < j) = \begin{cases} 0 & j < 1 \\ \sum_{m=1}^{j}(1-S)S^{m-1} & j \geq 1, \end{cases}$$

where S = the annual survival rate.

For this simulation, age-0 fish are defined as those in their first year of full vulnerability to capture. I sampled individual aged fish from this distribution by choosing a random, uniform number (probability) within the interval from 0 to 1 and determining the age corresponding to this value of the cumulative distribution function. By repeating this process, I was able to draw randomly a specified number of aged fish from a known geometric distribution defined by S. Each generated sample consisted of 100–1,000 individuals drawn independently from geometric distributions defined by Z values between 0.20 and 2.00. One thousand simulations were run for each combination of sample size and Z. For each simulation, a CR estimate of S and an LS estimate of Z were calculated from the sample age frequency. Means of the Chapman-Robson estimates of S were converted to Z so that they could be compared to the means of the LS estimates of Z.

The effect of constraining the right-hand limb of the sample age frequency was investigated by truncating each age-frequency distribution and recalculating mortality. The CRt and the LS estimates were

calculated with these data, and the mean CRt estimates of S were converted to Z. Each truncated age frequency was a subset of a simulation from the complete age-frequency simulations in which all fish that were older than the oldest age group meeting or exceeding a threshold abundance of 5 fish were removed. Although this truncation scheme reduced the effective sample size within each simulation, it accurately reflected the application of a truncation scheme to a real sample.

Results and discussion

Simulations indicated that mean CR estimates of mortality for the complete age frequencies were essentially unbiased. At all Z's and sample sizes examined, the mean CR estimator agreed closely with the true value of Z. All differences between estimated mean Z's and true Z's (relative to the true Z) were <1% (Table 1).

The maximum likelihood estimator developed for use with truncated age frequencies (CRt) showed a negative bias that was greatest when sample size was low. With a 5-fish threshold rule, the mean CRt estimate of instantaneous total mortality was biased −12% at $Z = 0.2$ for a random sample of 100 fish (Fig. 1). At sample sizes of 300 fish or more, bias was reduced to less than about −4% for all Z's (Fig. 1).

The mean LS estimates of Z for complete age frequencies were consistently less than the true instantaneous total mortality rate. This bias was greatest at low levels of Z when sample sizes were small (Table 2). At $Z = 0.2$, the difference between the mean estimated Z and true Z ranged from −16% for samples of 1,000 individuals to −37% for samples of 100. Deviations were much less, −4% to −8%, for all sample sizes when the true Z was 2.0. Bias in the LS estimator was reduced by truncating the sample age frequency. When I used a minimum threshold abundance of five, the negative bias was reduced to less than about 5% at sample sizes of at least 200 fish (Fig. 1).

Precision of the CR and CRt estimators was generally better than that of the LS estimator, especially at low Z's. Although precision improved for all estimators as sample sizes became larger, the coefficient of variation (CV) for the CR and CRt estimators approached 1% for large samples at $Z = 0.2$, whereas the CV for the LS estimator approached only 6–9% (Fig. 2). For all given sample sizes, the precision of the CR and CRt estimators deteriorated as Z increased. The precision of the LS estimator changed little as Z increased, except when the estimator was based on samples of only 100 fish. In general, the CV's for the CR or CRt estimators were less than the

Table 1

Percent deviation from true instantaneous total mortality rate (Z) for the mean of 1,000 Chapman-Robson estimates of Z for each of the given combinations of sample size and true Z. Frequencies for all age groups were used in calculating mortality rates.

True Z	Sample size									
	100	200	300	400	500	600	700	800	900	1,000
0.20	-0.2	-0.1	-0.2	0.1	-0.0	-0.0	0.1	0.2	0.1	-0.0
0.40	-0.1	0.0	0.2	-0.1	0.3	-0.1	0.1	0.2	-0.2	0.2
0.60	-0.3	-0.2	0.0	0.0	-0.1	-0.0	-0.2	0.0	-0.2	0.1
0.80	-0.1	-0.2	0.2	-0.1	0.0	0.2	0.1	-0.0	-0.1	0.0
1.00	0.4	0.2	0.4	-0.1	-0.0	0.1	0.1	0.1	0.0	-0.2
1.20	-0.5	0.2	0.1	-0.0	0.1	0.0	0.2	-0.0	-0.2	-0.1
1.40	-0.3	0.3	-0.1	0.1	0.0	-0.0	-0.1	-0.1	0.0	-0.1
1.60	0.6	-0.1	0.2	0.2	0.2	-0.2	0.1	-0.1	-0.1	-0.1
1.80	-0.2	0.1	0.1	-0.1	0.1	-0.2	-0.1	0.1	-0.2	0.2
2.00	-0.1	-0.0	0.3	-0.1	0.0	-0.2	-0.2	-0.1	0.2	0.2
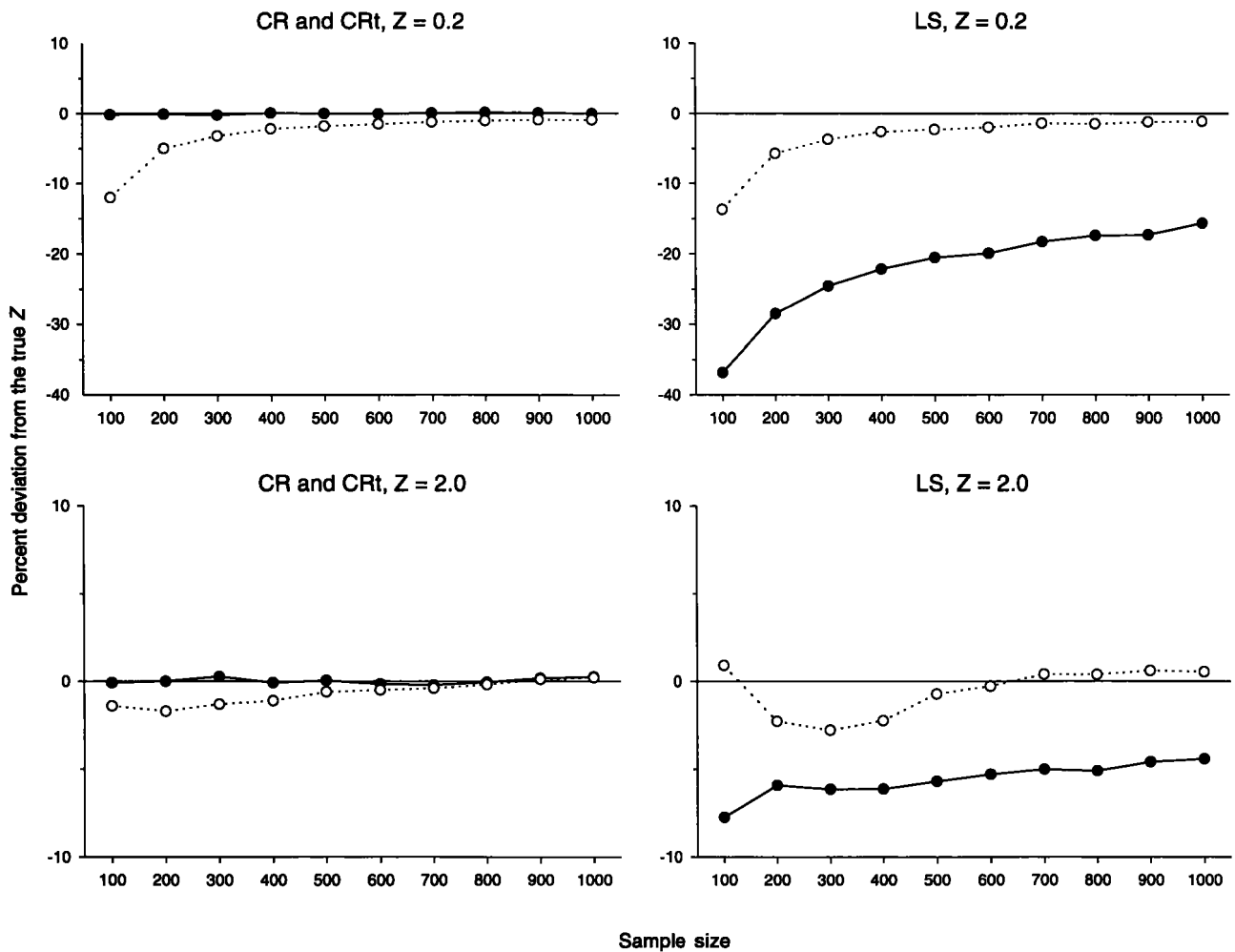
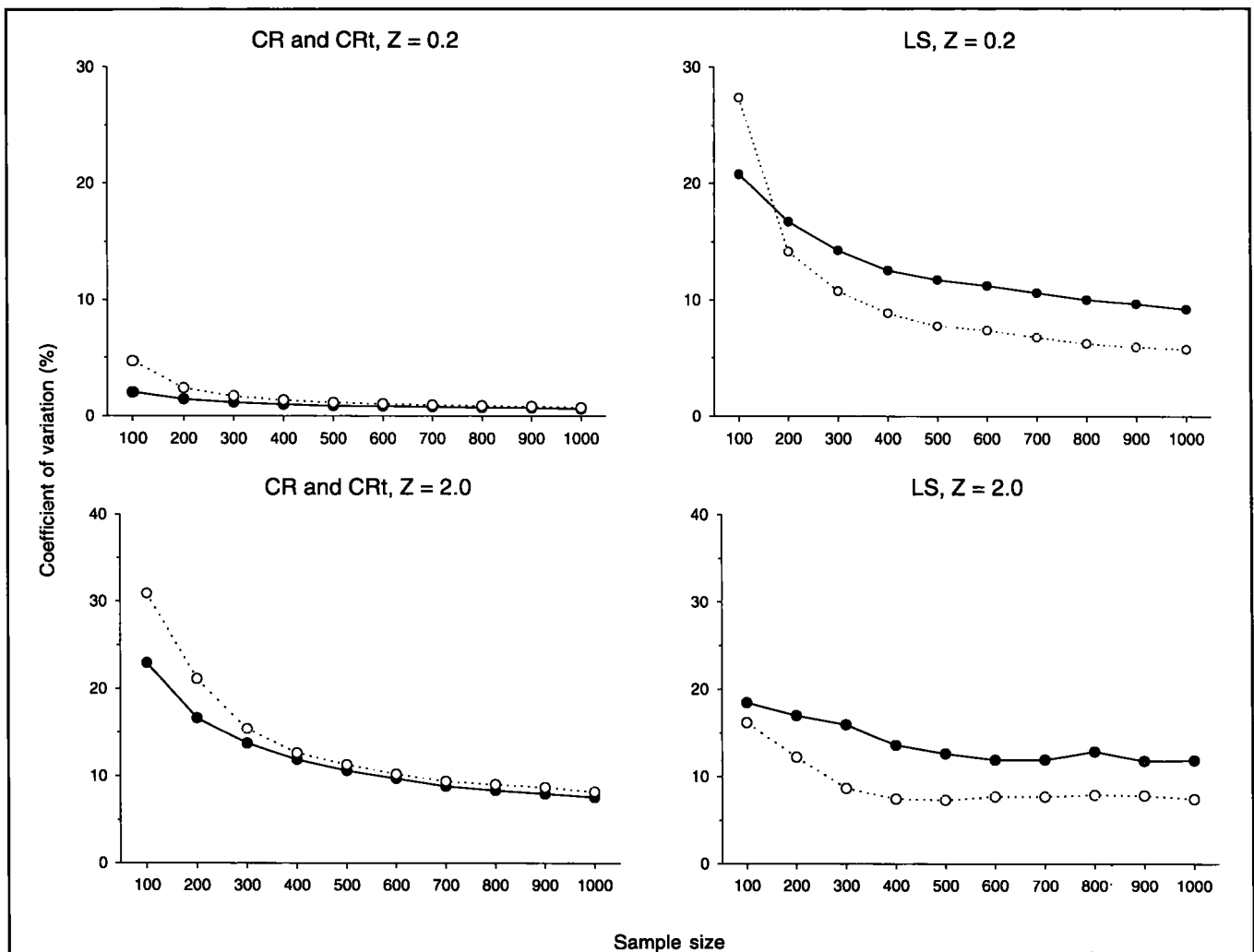## Figure 1

Percent deviation from true instantaneous total mortality (Z) for the mean of 1,000 Chapman-Robson (CR) or Chapman-Robson-for-truncated-data (CRt) estimates of survival or least-squares regression (LS) estimates of equivalent Z for different sample sizes when true Z is 0.2 or 2.0. The threshold levels, representing the minimum acceptable abundance for the oldest age used in the calculation of mortality were one fish (—●—) and five fish (—○—).

Table 2

Percent deviation from true instantaneous total mortality rate (Z) for the mean of 1,000 least–squares regression estimates of Z for each of the given combinations of sample size and true Z. Frequencies for all age groups were used in calculating mortality rates.

True Z	Sample size									
	100	200	300	400	500	600	700	800	900	1,000
0.20	−36.8	−28.5	−24.6	−22.1	−20.5	−19.9	−18.2	−17.4	−17.3	−15.6
0.40	−25.2	−20.4	−18.3	−16.9	−14.7	−14.3	−14.3	−13.2	−13.2	−12.3
0.60	−19.6	−17.1	−14.0	−12.9	−12.9	−11.9	−11.5	−11.3	−10.7	−10.6
0.80	−15.8	−14.1	−11.3	−11.0	−10.3	−9.8	−9.6	−9.3	−9.2	−9.7
1.00	−13.6	−10.7	−9.5	−9.3	−8.7	−9.1	−8.3	−7.8	−7.9	−7.9
1.20	−13.0	−9.1	−9.2	−8.4	−7.3	−8.2	−7.5	−7.2	−7.3	−6.8
1.40	−10.8	−9.1	−7.5	−7.9	−6.6	−6.8	−6.6	−6.5	−5.9	−7.1
1.60	−8.8	−7.6	−6.9	−6.2	−6.0	−7.0	−5.9	−5.6	−5.7	−6.1
1.80	−8.3	−6.7	−7.2	−6.4	−5.5	−5.1	−4.4	−5.6	−4.8	−4.9
2.00	−7.7	−5.9	−6.1	−6.1	−5.7	−5.3	−5.0	−5.1	−4.6	−4.4

Figure 2

Coefficients of variation for Chapman-Robson (CR) and Chapman-Robson-for-truncated-data (CRt) estimates of survival or least-squares regression (LS) estimates of equivalent instantaneous total mortality (Z) made from samples of 100 to 1,000 ages generated stochastically under $Z = 0.2$ or $Z = 2.0$. Complete age frequencies (—●—) or those truncated using a 5-fish threshold (—○—) were used.

CV's for the LS estimator when Z was low but were similar or higher when Z was high.

When all fully recruited fish are equally available to a sampling gear, the CR estimator can provide a more accurate estimate of mortality than the LS estimator can. Applying the least-squares estimator to these data clearly violates the linear-regression assumption of equal variances among age groups. When a population is subjected to a low Z, the frequency distribution of log-abundances for older age groups in a sample becomes skewed to the right because log-abundance reaches a lower limit at zero (log of 1; Fig. 3). The frequency distribution of log-abundance then becomes truncated (undefined) past some distance to the left of its mean when zero abundances occur in the untransformed frequencies. The variances of the log-abundances appear to be positively related to age until the log-abundance frequencies become truncated when zero abundances appear in the samples for older age groups.

Empirical evidence led Chapman and Robson (1960) to conclude that haul data (catch rates for each age group) had an approximately constant variance when log transformed. However, the results from my simulations indicate that variances for the log-abundances are likely to differ among age groups. The assumption of constant variance is likely to be met only when the sampling gear operates on a few abundant age groups, in which there is no chance of only

periodically encountering an older age group. This led Chapman and Robson (1960) to suggest that these data should be truncated to eliminate the age frequencies beyond the oldest age with a minimum abundance of five fish. Although my findings concur with those of Chapman and Robson, the use of this threshold rule to eliminate older age groups does not completely eliminate all bias in the LS estimator— bias that can be attributed to violations of the assumptions on which the linear regression is based.

For truncated age-frequency data, both estimators gave biased results when small samples were drawn from a population of many age groups (Z=0.2). In these cases, truncation generally resulted in smaller samples that had far fewer age groups than were in the original complete age frequency. At high Z's, age-frequency truncation reduced bias in the LS estimator to less than 5% at all sample sizes and reduced bias in the CRt estimator to less than 2%.

Violations of steady-state assumptions probably impart the most serious biases to pooled estimators of mortality. By simply inspecting a plot of log-abundance versus age for evidence of concavity or for a trend in the linear regression residuals, one can detect gross violations to these assumptions. Subtle biases inherent when the assumptions required by linear regression are not met are more difficult to detect. Both the CR and LS methods can provide very accurate and precise estimates of Z for age frequencies that follow an exact geometric distribution (Jensen, 1985). However, the LS estimator is biased when sample ages are drawn randomly from a steady-state, geometrically distributed population, whereas the CR estimator is not. The LS estimator may be more robust when age samples are not taken randomly (Chapman and Robson, 1960). The CRt and LS estimators generally showed similar levels of bias when the sample age structure is truncated with a minimum frequency criterion of 5 fish. In summary, the CR estimator will provide a more accurate and at least as precise an estimate of mortality as the LS estimator will when a random and complete age-frequency sample can be obtained from a population in steady-state.
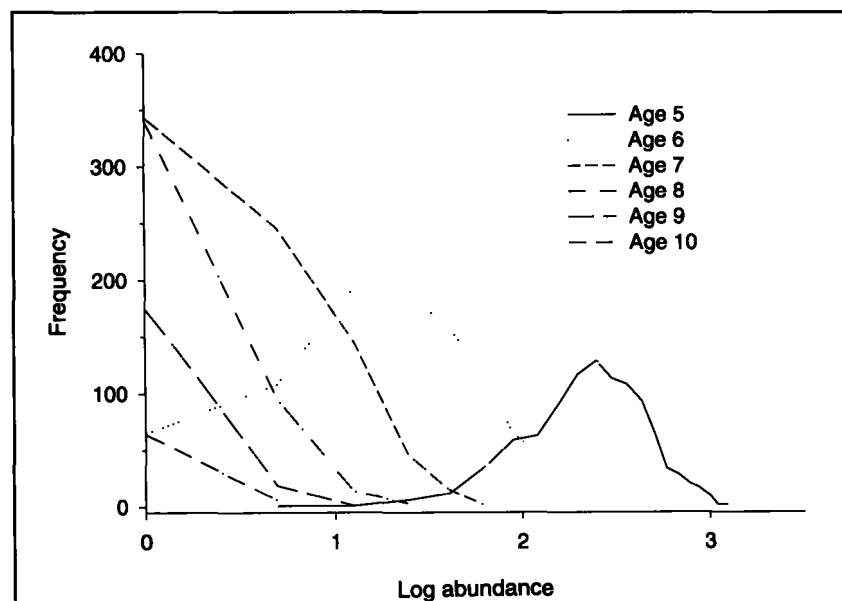
Figure 3

Frequency distributions of log-abundance for ages 5–10 generated stochastically with $Z = 1.0$. Log-abundance of each age group was taken from 1,000 simulations in which samples of 1,000 ages were drawn during each simulation.

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