

A better estimator of mortality rate from age-frequency data

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Abstract: The Chapman–Robson and weighted-regression estimators are currently the two preferred methods for estimation of instantaneous mortality, z , from a cross-sectional sample of age-frequency data. They are derived under the assumption of steady-state population dynamics. Here, a new estimator is developed from a population model that explicitly includes annual variability in recruitment. The new estimator is trivial to implement using existing generalized linear mixed model software. It is vastly superior to both the Chapman–Robson and weighted-regression estimators under a wide range of simulation scenarios in which sources of variability include partial recruitment to the fishery, autocorrelated annual recruitment, variability in annual survival, ageing error, and sampling randomness. All estimators produced confidence intervals that had lower actual coverage than their nominal 95% coverage. Nonetheless, the new estimator had the highest actual coverage, and under some scenarios this was achieved with a narrowest confidence interval.

Résumé : Les estimateurs de Chapman–Robson et par régression pondérée constituent présentement les deux méthodes privilégiées pour l'estimation de la mortalité instantanée, z , à partir d'un échantillon transversal de données de fréquences d'âge. Ils sont établis à partir de l'hypothèse d'une dynamique des populations stationnaire. Un nouvel estimateur est mis au point sur la base d'un modèle de population qui inclut explicitement la variabilité annuelle du recrutement. L'application de ce nouvel estimateur à l'aide de logiciels de modèle de mélange linéaire généralisé est triviale. Il est de beaucoup supérieur aux estimateurs de Chapman–Robson et par régression pondérée pour une grande gamme de scénarios de simulation dans lesquels les sources de variabilité comprennent le recrutement partiel dans la pêche, l'autocorrélation du recrutement annuel, la variabilité de la survie annuelle, l'erreur associée au vieillissement et le caractère aléatoire de l'échantillonnage. Tous les estimateurs produisent des intervalles de confiance qui ont une couverture réelle plus faible que leur couverture nominale de 95 %. Cela dit, le nouvel estimateur présente la plus grande couverture réelle avec, dans certains scénarios, l'intervalle de confiance le plus mince. [Traduit par la Rédaction]

Introduction

Estimation of mortality from a single cross-sectional sample of age-frequency data is commonly called catch-curve analysis. Catch-curve analysis is well suited to situations where additional data about the population (e.g., catch data, annual survey data, fishing or sampling effort) are not available. Recent applications of catch-curve analysis include a study of the relationship between life-history strategies of killifish (*Aphanius fasciatus*) and its habitat (Cavaro et al. 2014), estimation of increased mortality of short-nose suckers (*Chasmistes brevirostris*) due to a parasitic trematode (Markle et al. 2014), and an investigation of intraspecific variation in the life history of the Ballan wrasse (*Labrus bergylta*) (Villegas-Ríos et al. 2013). In addition, the work herein was motivated by the requirement to estimate the natural mortality of several species of unfished surf clam (White et al. 2012) and geoduck (*Panopea zealandica*) for the purpose of setting safe initial total allowable catches for these proposed fisheries.

Catch-curve analysis has a long history in the published literature, going back to the methodology of Heincke (1913). Other popular alternatives include the CR method, named after Chapman and Robson (1960), and the use of linear regression on the log of the age frequencies (Ricker 1975; Seber 1982). These methods are all derived from a common underlying steady-state population model in which recruitment and mortality are assumed constant across all years. Some earlier investigations have examined the performance of these estimators under the steady-state assumption (Jensen 1996; Murphy 1997), but the results of these works are

of little relevance in practice because they include only variability due to sampling error and ignore the substantial variability known to exist in population dynamics (e.g., Myers et al. 1995).

Allen (1997) performed a restricted simulation study to assess the effect of variability in recruitment on the performance of the linear regression estimator, with the parameters of the simulation scenarios set to values pertinent to the population dynamics of crappie (*Pomoxis* spp.). A more extensive simulation study was conducted by Dunn et al. (2002), who explicitly incorporated additional variability in recruitment, annual mortality, and ageing error, for mean values of z ranging from 0.1 to 1.0, concluding that the CR estimator was generally preferred. The simulation study of Smith et al. (2012) assumed that all nonsampling variability could implicitly be encompassed by placing annual variability on expected frequencies-at-age. However, this corresponds precisely to placing variability on recruitment only. Notwithstanding this limitation, they compared the Heincke, CR, and regression estimators under a range of simulation scenarios where particular interest centered on the relevant problem of partial recruitment, that is, the complication that arises when younger ages are only partially available for sampling. This study also evaluated performance of the weighted linear regression (WLR) estimator utilized by Maceina and Bettoli (1998).

The general conclusions from the previous studies were that the Heincke and standard linear regression estimators of z are to be avoided, in favour of the CR and WLR estimators. Smith et al. (2012) found that the relative performance of the CR and WLR

Received 17 April 2014. Accepted 20 October 2014.

Paper handled by Associate Editor Michael Wilberg.

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estimators was dependent on the simulation scenario, particularly the sample size. They considered sample sizes of 200 and 600 and, within the limited range of their simulations, they found the CR preferred on the smaller samples, and WLR preferred on the larger samples. Overall, they recommended use of the CR estimator, as the difference in relative performance was generally slight and the CR estimator had the assurance of a formal derivation (albeit under steady-state conditions), whereas the weighting used by the WLR estimator was ad hoc.

Chapman and Robson (1960) derived the CR estimator by showing that the assumption of steady-state population dynamics results in a geometric distribution for the age frequencies. They also showed that this was equivalent to the age frequencies being Poisson distributed with expected value decreasing geometrically with age. Their work substantially predates the development of the now well-established maximum likelihood framework of generalized linear models (GLMs). Within this framework, the geometric-Poisson equivalence is a special case of the widely known equivalence between Poisson and multinomial models (e.g., McCullagh and Nelder 1989; Millar 2011). Indeed, in the Methods section it is explicitly shown how the steady-state population model can be represented as a Poisson log-linear model and hence how the maximum likelihood estimate of z can be estimated using conventional GLM software.

Moreover, using generalized linear mixed modeling (GLMM), a new estimator of z is derived under the non-steady-state model in which recruitment has annual variation. This new estimator is the negative of the maximum likelihood estimator of the slope coefficient under a random-intercept Poisson log-linear mixed model. It is trivial to obtain using freely available software (see Discussion) and is shown to be generally superior to both the CR and WLR estimators under an extensive range of simulation scenarios. The improvement can be substantial when recruitment variability is moderately high.

Methods

Model of population age frequencies

The population-dynamics model is first presented in general form to allow numbers of age-0 fish and survival to vary with year and (or) age. The steady-state version is then obtained as a special case.

Let $N_{t_0,a}$ denote the number of age-0 fish at the start of year t , and let $s_{t,a}$ denote the proportion of fish surviving from age a in year t to reach age $a + 1$ at the start of year $t + 1$. Let t_0 denote a given year, which in the current context will be the year in which the age-frequency sample was taken. The number of age- a fish in the population at year t_0 is given by the number of age-0 fish at year $t_0 - a$ multiplied by the product of the survival proportions over years $t_0 - a$ to $t_0 - 1$. That is:

$$N_{t_0,a} = N_{t_0-a,0} \prod_{i=0}^{a-1} s_{t_0-a+i,i}$$

If fish recruit to the fishery according to a probability ϕ_a , then with X_a denoting the number of age- a fish available to the fishery at year t_0 , it follows that

$$(1) \quad X_a = \phi_a N_{t_0,a} = \phi_a N_{t_0-a,0} \prod_{i=0}^{a-1} s_{t_0-a+i,i}, \quad a \geq 0$$

If a_0 is the minimum age at which it can be assumed that recruitment to the fishery is effectively 100%, and the number of these recruits is assumed constant over years and denoted N_{a_0} , then

$$X_a = N_{t_0,a} = N_{a_0} \prod_{i=a_0}^{a-1} s_{t_0-a+i,i}, \quad a \geq a_0$$

Furthermore, if survival of recruited fish is assumed constant over both years and age, then this simplifies to

$$(2) \quad X_a = N_a = N_{a_0} s^{a-a_0}, \quad a \geq a_0$$

Since $z = -\log(s)$, taking the natural logarithm of eq. 2 gives

$$(3) \quad \begin{aligned} \log(X_a) &= \log(N_{a_0}) + (a - a_0)\log(s) \\ &= \log(N_{a_0}) + a_0 z - az, \quad a \geq a_0 \end{aligned}$$

Models of sampled age frequencies

Let y_a denote the frequency of age- a fish in a random sample of size n taken at time t_0 from the fishery with age frequencies given by X_a in eq. 1.

The multinomial model

If the sample size n is regarded as fixed, then the statistical distribution of the observed age frequencies, y_a , $a \geq 0$, is multinomial with n trials, each with probability p_a given by the proportion of that age in the fishery. That is

$$(4) \quad p_a = \text{Prob}(\text{Age} = a) = \frac{X_a}{\sum_{j=0}^{\infty} X_j}$$

The Poisson model

If the sample size n is random and distributed Poisson(μ), then the statistical distribution of the observed age frequencies, y_a , is Poisson(μ_a), where $\mu_a = p_a \mu$. This result can be found in Feller (1968).

The multinomial-Poisson equivalence

The multinomial and Poisson models differ according to whether the overall sample size n is fixed or random. The conditions under which the multinomial and Poisson models produce equivalent inference are well established (e.g., Feller 1968; McCullagh and Nelder 1989; Millar 2011). Essentially, if n is random then it can be treated as though it were fixed (and vice versa), provided that no information about parameters of interest is contained in the value of n . In the current context, this is arguably the case. For example, n would be random under an experimental design in which sampling effort was fixed in advance (rather than sample size). If the actual sample size under such a design was 200, then this can be treated as having been fixed in advance, since the value 200 contains no information about z .

The practical consequence of the multinomial-Poisson equivalence is that age-frequency data can be analysed under the Poisson model, regardless of whether the data are actually multinomial (in the fixed n case) or not. The advantage of using a Poisson model is that it falls under the widely used and well-established GLM and GLMM frameworks. In particular, the latter permits annual variability to be incorporated in the dynamics of the age-frequency data.

Chapman-Robson estimator

Chapman and Robson (1960) considered the complication arising from partial recruitment of young fish, but for the sake of convenience they presented the formula for their estimator under the assumption of full recruitment of all fish, that is, $a_0 = 0$. Unfortunately, this has led to some unintentionally misuse of the CR estimator in the published literature, where the CR formula for the $a_0 = 0$ case has been used in situations where the youngest fish in the sample has been several years of age. Here, the estima-

tor is presented for the general case $a_0 \geq 0$. In what follows, it is only the age-frequency data for fully recruited ages that are utilized, and the sample size of these fully recruited fish will be denoted $n_{a_0}^+ = \sum_{a \geq a_0} y_a$. The mean age of (the fully recruited) fish in the sample is then

$$\bar{a} = \frac{\sum_{a \geq a_0} y_a a}{n_{a_0}^+}$$

Under the steady-state age frequencies from eq. 2, the proportion of recruited fish at age $a \geq a_0$ is

$$(5) \quad p_a = \frac{X_a}{\sum_{j \geq a_0} X_j} = \frac{s^a}{\sum_{j \geq a_0} s^j}, \quad a \geq 0$$

Chapman and Robson (1960) utilized these probabilities to specify a geometric model for the age-frequency data. The geometric model is the special case of a multinomial whereby the cell probabilities decay at a geometric rate, as given in eq. 5. Using the theory of mathematical statistics, they obtained the minimum variance unbiased estimator of annual survival:

$$\hat{s}_{CR} = \frac{\bar{a} - a_0}{\bar{a} - a_0 + \frac{n_{a_0}^+ - 1}{n_{a_0}^+}}$$

The CR estimator of instantaneous mortality is then

$$\hat{z}_{CR} = -\log(\hat{s}_{CR})$$

Unbiasedness is not preserved by nonlinear transformations, and consequently \hat{z}_{CR} is a biased estimator of z . In fact, Chapman and Robson (1960) established that no unbiased estimator of z exists and provided a correction for \hat{z}_{CR} to reduce its bias:

$$(6) \quad \hat{z}_{CRc} = \hat{z}_{CR} - \frac{(n_{a_0}^+ - 1)(n_{a_0}^+ - 2)}{n_{a_0}^+ [n_{a_0}^+ (\bar{a} - a_0) + 1] [n_{a_0}^+ + n_{a_0}^+ (\bar{a} - a_0) - 1]}$$

Chapman and Robson (1960) also provided the maximum likelihood estimators for s and z :

$$(7) \quad \hat{s}_{ML} = \frac{\bar{a} - a_0}{\bar{a} - a_0 + 1}$$

$$\hat{z}_{ML} = -\log(\hat{s}_{ML})$$

Linear regression estimators

Under the steady-state assumptions, eq. 3 expresses the natural logarithm of the number of recruited fish, $\log(X_a)$, $a \geq a_0$, as a linear function of age, with slope $-z$. If the age frequencies in the sample, y_a , are proportional to the frequencies in the fishery, X_a , then $\log(y_a)$ differs from $\log(X_a)$ by a fixed constant, and hence $\log(y_a)$ will have the same linear relationship with age. Thus, the negative of the slope coefficient from a linear regression of $\log(y_a)$ against a provides an estimator of z , which will be denoted \hat{z}_{LR} . The value of $\log(y_a)$ is not defined when $y_a = 0$, and so only ages with nonzero frequencies are used in the regression.

The weighted linear regression estimator of Maceina and Bettoli (1998) involves two steps. The first step fits the standard linear regression described above, and from this it obtains fitted values for $\log(y_a)$. The second step repeats the regression, but this time

using a weighted linear regression with weights given by the fitted values of $\log(y_a)$ from step one. The negative of the slope coefficient from the weighted regression provides the estimator \hat{z}_{WLR} .

It should be noted that the linear regression estimators of z do not possess the usual desirable properties of such estimators. In particular, they are not unbiased, since the expected value of $\log(y_a)$ is not $\log(X_a)$ because of nonlinearity of the log function.

Poisson log-linear model (GLM)

The Poisson log-linear model is a very standard form of GLM and is widely used in the analysis of frequency data. Letting q denote the unknown sampling fraction, under this model the y_a are assumed to be Poisson with expected value $\mu_a = qX_a$. Using the steady-state equation for $\log(X_a)$ from eq. 3, this can be re-expressed as

$$(8) \quad \log(\mu_a) = \log(q) + \log(N_{a_0}) + a_0 z - az, \quad a \geq a_0$$

Once again, this is a linear model with respect to a , with slope coefficient equal to $-z$ and intercept corresponding to the first three terms on the right-hand side of eq. 8. The important distinction between this and the linear regression methods is that it uses a linear model for $\log(\mu_a)$ rather than a linear model for $\log(y_a)$.

GLMs are fitted using maximum likelihood, and from the Poisson-multinomial equivalence it follows that the GLM estimate from the Poisson log-linear model in eq. 8 is precisely the estimator \hat{z}_{ML} in eq. 7.

Random-intercept Poisson log-linear mixed model (GLMM)

The simulations of Smith et al. (2012) generated data under the scenario of normally distributed annual variability in log-recruitment of age- a_0 fish. That is, values of $\log(N_{a_0})$ were assumed to be normally distributed around an expected value $\log(\mu_{a_0})$. They used a multinomial formulation, and under the equivalent Poisson model it follows from eq. 8 that

$$(9) \quad \log(\mu_a) = \log(q) + \log(\mu_{a_0}) + a_0 z - az + \epsilon_a, \quad a \geq a_0$$

where ϵ_a are independently distributed $N(0, \sigma_R^2)$. This is an example of a GLMM with a random intercept and a fixed slope coefficient with respect to covariate a .

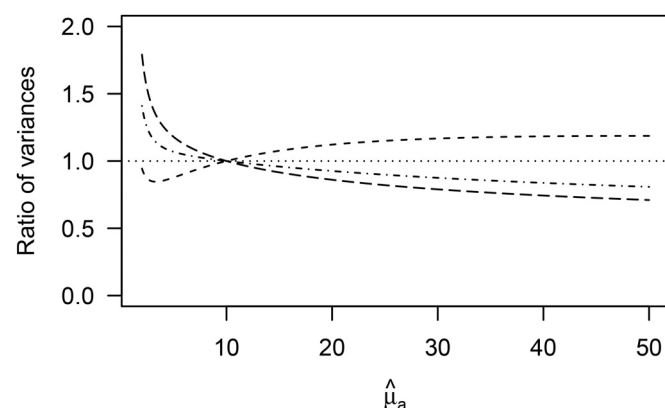
The estimator of z is the negative of the maximum likelihood estimator of the slope coefficient and will be denoted \hat{z}_{MM} . It cannot be expressed explicitly but is readily available using existing GLMM software. By way of example, \hat{z}_{MM} is obtained using the snippet of R code given in the Discussion.

Connection between WLR and Poisson models

A weighted linear regression is appropriate when the variances of the response variables are unequal, in which case the weights are specified to be inversely proportional to the variances. Thus, the WLR estimator is the linear regression estimator under the implicit assumption that the response variable $\log(y_a)$ has variance that is proportional to $1/\log(\hat{\mu}_a)$, where $\log(\hat{\mu}_a)$ is the fitted value obtained from the standard linear regression fitted in step one.

By way of comparison, if the response variable y_a is Poisson distributed, then it follows from application of the delta method (Millar 2011) that the approximate variance of $\log(y_a)$ (conditional on $y_a > 0$) is $1/\hat{\mu}_a$. Under the random-intercept Poisson model, the marginal distribution of y_a cannot be expressed explicitly, but the approximate variance of $\log(y_a)$ (conditional on $y_a > 0$) is of the form $\sigma_R^2 + e^{\sigma_R^2}/\hat{\mu}_a$ (see Appendix A). Without knowing σ_R , this cannot be used to specify a weighting in linear regression.

Fig. 1. Ratio of implicit WLR variance over approximate GLMM variance for $\hat{\mu}_a$ ranging from 2 to 50, for $\sigma_R = 0.25$ (short-dashed curve), $\sigma_R = 0.5$ (dot-dashed curve), and $\sigma_R = 1.0$ (long-dashed curve). The ratios have been standardized to have value of unity when $\hat{\mu}_a = 10$.



A plot of the ratio of the implicit WLR variance, $1/\log(\hat{\mu}_a)$, over the approximate GLMM variance, $\sigma_R^2 + e^{\sigma_R^2}/\hat{\mu}_a$, shows that they are close to proportional over a wide range of values of $\hat{\mu}_a$ for moderate values of σ_R (Fig. 1). In particular, for $\sigma_R = 0.25$ the ratio of the two variances ranged from 0.85 to 1.19 as $\hat{\mu}_a$ ranged from 2 to 50. However, at higher values of σ_R this is no longer the case, and for $\sigma_R = 1.0$ the ratio ranged from 0.71 to 1.79. Thus, it could be that \hat{z}_{WLR} shares some of the properties of \hat{z}_{MM} for moderate values of σ_R .

Simulations

Data generation

To be as relevant as possible, the catch-frequency data used in the simulations included multiple sources of variability and uncertainty that could reasonably be encountered in practice. These included variability in numbers of age-0 fish and annual survival, uncertainty in partial recruitment, and ageing error.

Numbers at age-0

The number of age-0 fish was assumed to vary annually and to be autocorrelated following the specification used in Dunn et al. (2002). For the sake of simulating the population age frequencies, the maximum age was set to the value of 200 and the numbers of age-0 fish used in eq. 1 therefore range over years $t_0 - 200$ to t_0 . It is only the relative values of $N_{t,0}$ that are required for the purpose of generating the simulated data, and without loss of generality they can be generated by a zero-mean (on the log scale) first-order autocorrelated time series of the form

$$\begin{aligned} \log(N_{t_0-200,0}) &= \varepsilon_{t_0-200} \\ \log(N_{t,0}) &= \rho \log(N_{t-1,0}) + \sqrt{1 - \rho^2} \varepsilon_t, \quad t_0 - 200 < t \leq t_0 \end{aligned}$$

where ε_t are independently distributed $\text{Normal}(0, \sigma_\varepsilon^2)$. If one wishes to regard $N_{t,0}$ as an absolute number of age-0 fish, then $N_{t,0}$ could be regarded as numbers in units of millions, for example.

Under the above formulation, $\log N_{t,0}$ has variance of σ_R^2 for all t , and the correlation between successive values is ρ . The values of ρ were fixed at 0.37, and the baseline value of σ_R was taken to be 0.67. These are the median values of the estimated first-order autocorrelations and standard deviations, respectively, in log-recruitment from the meta-analysis of Myers et al. (1995), as tabulated in Dunn et al. (2002). To assess the effect of differing levels of recruitment variability, values of 0.35 and 1.17 for σ_R were also used. These values were chosen because they correspond to 95% probability

intervals of 0.5–2 and 0.1–10 for $N_{t,0}$, respectively. That is, with $\sigma_R = 0.35$, the marginal distribution of $N_{t,0}$ is such that it lies between 0.5 and 2 with probability 0.95.

Partial recruitment

Partial recruitment of young fish to the fishery was modeled by assuming a logistic recruitment ogive, ϕ_a , with 25%, 50%, and 75% recruitment at ages 1, 1.5, and 2, respectively. Under this recruitment ogive, recruitments at ages 3 and 4 are 96.4% and 99.6%, respectively. Instantaneous fishing mortality of an age- a fish is then $f_a = \phi_a f$, where f is the fully recruited fishing mortality, and instantaneous total mortality of age- a fish is then $z_a = m + f_a$, where m denotes instantaneous natural mortality.

Variability in annual survival

Random variability in annual survival was introduced by generating the actual instantaneous mortality at age a in year t as

$$z_{t,a} = z_a + u_{t,a}$$

where $u_{t,a}$ is normally distributed such that $\exp(u_{t,a})$ has mean of unity and coefficient of variation of 0.2, the same value used by Dunn et al. (2002). This formulation may appear unintuitive at first because it does not preclude negative values of $z_{t,a}$. However, this has probability less than 5×10^{-7} . More importantly, it ensures that the expected value of survival of an age- a fish is $s_a = \exp(-z_a)$ and hence that the age frequencies have the same expected values as would arise when there is no random variability in z_a . In contrast, the multiplicative lognormal error implemented by Dunn et al. (2002) results in age- a fish surviving to age $a + 1$ with probability lower than s_a . In particular, for $a \geq a_0$, annual survival would be less than $s = \exp(-z)$, and hence the simulated data will not represent a fishery with instantaneous mortality rate of z .

The sample

With randomly varying values of recruitment and annual survival generated as above, the numbers-at-age of fully recruited fish were generated from eq. 1. A random sample of size n was taken from this population using the multinomial model for the sample age frequencies, y_a^{True} , using the probabilities in eq. 4. The “True” superscript is used to denote that these are the true age frequencies of the individuals in the sample, as distinct from the measured age frequencies.

Ageing error

Let a_i^{True} denote the true age of fish i , $i = 1, \dots, n$. Ageing error was incorporated following the procedure of Dunn et al. (2002). That is, the measured age is

$$(10) \quad a_i = \text{round}(a_i^{\text{True}} \epsilon_i)$$

where $\epsilon_i \sim \text{Normal}(1, \sigma_A^2)$. This corresponds to the measured age having coefficient of variation approximately equal to σ_A . The age-frequency values used in the simulations, y_a , are the frequencies of each age a amongst the n measured ages a_i , $i = 1, \dots, n$.

Results from a meta-analysis of ageing studies (Campana 2001, his figure 5) were used to specify a baseline value $\sigma_A = 0.076$ and extremes of 0.02 and 0.2, corresponding approximately to a 95% coverage interval on ageing errors. In addition, the study of ageing error conducted by Punt et al. (2008) showed a general decrease in σ_A with increasing age, due to a large component of the error arising from uncertainty in the position of the first growth increment on the hard structure being aged. This was included by specifying an ageing error that decreased with the square-root of age, $\sigma_A = 0.2/\sqrt{a}$.

Simulation scenarios

A total of six sets of simulations were performed over a range of scenarios. Simulation 1 used the baseline values for the variability in numbers of age-0 fish and ageing error, $\sigma_R = 0.67$ and $\sigma_A = 0.076$, respectively. Simulations 2 and 3 both used the lower extreme of recruitment variability, $\sigma_R = 0.35$, over the extremes of ageing error, $\sigma_A = 0.02$ and $\sigma_A = 0.2$, respectively. Simulations 4 and 5 were analogous, but using the upper extreme of recruitment variability, $\sigma_R = 1.17$. Simulation 6 used the baseline value $\sigma_R = 0.67$ and the form of ageing error motivated by Punt et al. (2008), $\sigma_A = 0.2/\sqrt{\text{age}}$.

All simulations were performed for the sample sizes of $n = 200$ and 600. It was assumed that natural mortality and fully recruited fishing mortality were equal, and fully recruited total mortality of $z = m + f$ ranged from 0.1 to 1.0. This distinction between natural and fishing mortalities is relevant only to the population dynamics of partially recruited fish.

Five thousand simulations were performed under each simulation scenario, and four summary measures of estimator performance were calculated. The first three of these were expressed as a percentage of the true value of z . The measures were (i) percent bias, (ii) percent root-mean-square error (RMSE), where mean-square error is calculated as the sum of squared-bias and variance of \hat{z} over the 5000 simulations, (iii) percent half-width of the nominal 95% confidence interval (determined from the estimated standard error of \hat{z}), and (iv) actual coverage of the nominal 95% confidence interval.

Estimation details

Calculation of estimators

Implementation of the CR and WLR estimators followed the recommendations from the simulation study of Smith et al. (2012). In particular, the bias-corrected CR estimator \hat{z}_{CRc} was employed. The difference between \hat{z}_{CR} and \hat{z}_{CRc} is approximately $(1 - e^{-z})^2 / n_{a_0}^+ e^{-z}$ (Chapman and Robson 1960), which, over the range of z values considered here, has maximal value of $1.09/n_{a_0}^+$ and is negligible relative to the variance of \hat{z}_{CRc} .

Smith et al. (2012) considered several options for determining the choice of the value of the minimum age of full recruitment a_0 . These options included use of a formal χ^2 test derived by Chapman and Robson (1960), but simpler choices of a_0 were ultimately found to be superior. The WLR estimator was found to have the best performance with a_0 chosen as the modal age (age of highest catch), while the CR estimator performed best with a_0 chosen as the modal age plus 1. The GLM and GLMM estimators also used this choice of a_0 owing to their underlying commonality with the CR estimator via the equivalence of the multinomial and Poisson models underlying these estimators. When the modal age was not unique, the smallest modal age was used.

The GLM and GLMM estimators are obtained by fitting the respective model to the age frequencies, y_a , $a = a_0, \dots, \infty$. In practice, it is necessary to use a sufficiently high upper bound on age, a_{max} . From preliminary simulations, it was found that taking a_{max} to be twice the maximum age in the age-frequency sample was sufficient. So, for example, if the maximum measured age was 18 years, then a_{max} would be 36 and y_a , $a = 19, \dots, 36$ would all be set to zero. A line of R code to implement this simple data manipulation is provided in the Discussion.

Calculation of standard errors

The WLR estimator is obtained from a weighted linear regression, and hence the estimated standard error of the slope coefficient is the standard error estimate for \hat{z}_{WLR} . Chapman and Robson (1960) provided an approximate variance formula for \hat{z}_{CRc} under the steady-state population model. However, in the presence of variable population dynamics, this variance is an underestimate. Following the implementation of Smith et al. (2012), the estimated variance was corrected for overdispersion, where overdispersion

was calculated using the usual Pearson χ^2 statistic for goodness of fit to count data. To avoid use of sparse data in the calculation of the Pearson χ^2 , only ages with an expected frequency of at least unity were used in calculation of overdispersion.

The Poisson log-linear model also provides an estimate of the standard error of the maximum likelihood estimate of the slope coefficient and hence of \hat{z}_{ML} . Analogously to the CR method, this also needs to be corrected for overdispersion because of possible additional variability, and once again the Pearson χ^2 was used. The random-intercept Poisson log-linear mixed model includes additional variability, and the estimated standard error of the slope coefficient was used directly as the estimated standard error of \hat{z}_{MM} .

Results

Overall, the random-intercept Poisson log-linear estimator, \hat{z}_{MM} , had superior performance in terms of RMSE than the other three estimators over all of the simulation scenarios (Figs. 2–7). The improvement was substantial for the baseline simulation (Fig. 2) and even more so when σ_R was high and σ_A was low (Fig. 5) or decreasing with age (Fig. 7).

The estimator \hat{z}_{MM} was generally the least biased, though all estimators showed a tendency to be negatively biased. For high values of σ_A and z , the negative bias of all estimators was sufficiently strong to be a substantial contributor to the RMSE (Figs. 4 and 6). Bias of the WLR estimator tended to be a unimodal function of z and was also strongly negative for the lowest value of mortality, $z = 0.1$, especially for $n = 200$. Correspondingly, the RMSE of the WLR estimator was always considerably greater than that of any other estimator for $z = 0.1$ and $n = 200$. Its relative performance generally improved for higher values of z and higher sample size.

The \hat{z}_{CRc} and \hat{z}_{ML} estimators had similar performance under all four measures, especially for $n = 600$. Although \hat{z}_{CRc} is approximately bias-corrected under steady-state conditions, it displayed slightly greater bias than \hat{z}_{ML} .

The actual coverage of nominal 95% confidence intervals obtained from the \hat{z}_{MM} estimator was unanimously superior (or similar) to that of any other estimator. Moreover, the superior coverage was often achieved with a narrower confidence interval. Nonetheless, coverage was somewhat less than the nominal level, being around 70%–90% for low to moderate σ_A . At the high extreme of ageing error, $\sigma_A = 0.2$, coverage reduced dramatically and was as low as 50% for higher values of z .

Discussion

This work has helped to understand the relative properties and performance of the three estimators \hat{z}_{CRc} , \hat{z}_{ML} , and \hat{z}_{WLR} that are derived from steady-state population assumptions. More importantly, it provides a strong case for recommending that these three estimators should no longer be used for catch-curve analysis because they are generally inferior to the proposed GLMM estimator \hat{z}_{MM} that is obtained from a random-intercept Poisson log-linear model.

The similar performance of the CR and Poisson log-linear (i.e., maximum likelihood, \hat{z}_{ML}) estimators can be explained by their joint derivation from the same underlying statistical model. Indeed, from eqs. 6 and 7 it can be seen that the difference in these two estimators is inversely proportional to $n_{a_0}^+$. Thus, the only scenario in which they did not have near-identical performance was for the lower sample size $n = 200$ with higher z . The higher values of z result in greater mortality of prerecruits and thus a greater reduction in $n_{a_0}^+$ relative to n .

An increase in ageing error was seen to induce increasing negative bias in all of the estimators. This can be explained by examining the formulation of the ageing error in eq. 10, from which it follows that the distribution of measured age is symmetrically

Fig. 2. Baseline simulation with standard error of log-recruitment $\sigma_R = 0.67$ and ageing error coefficient of variation $\sigma_A = 0.076$. Data shown include percent bias (row 1), percent root-mean-square error (row 2), percent half-width of the nominal 95% confidence interval (row 3), and the actual coverage of the nominal 95% confidence interval (row 4) for the Chapman–Robson bias-corrected \hat{z}_{CR} (+ symbol), weighted linear regression \hat{z}_{WLR} (triangles), maximum likelihood \hat{z}_{ML} (× symbol), and random-intercept Poisson log-linear mixed model \hat{z}_{MM} (diamonds) estimators of z . Sample sizes are $n = 200$ (column 1) and $n = 600$ (column 2).

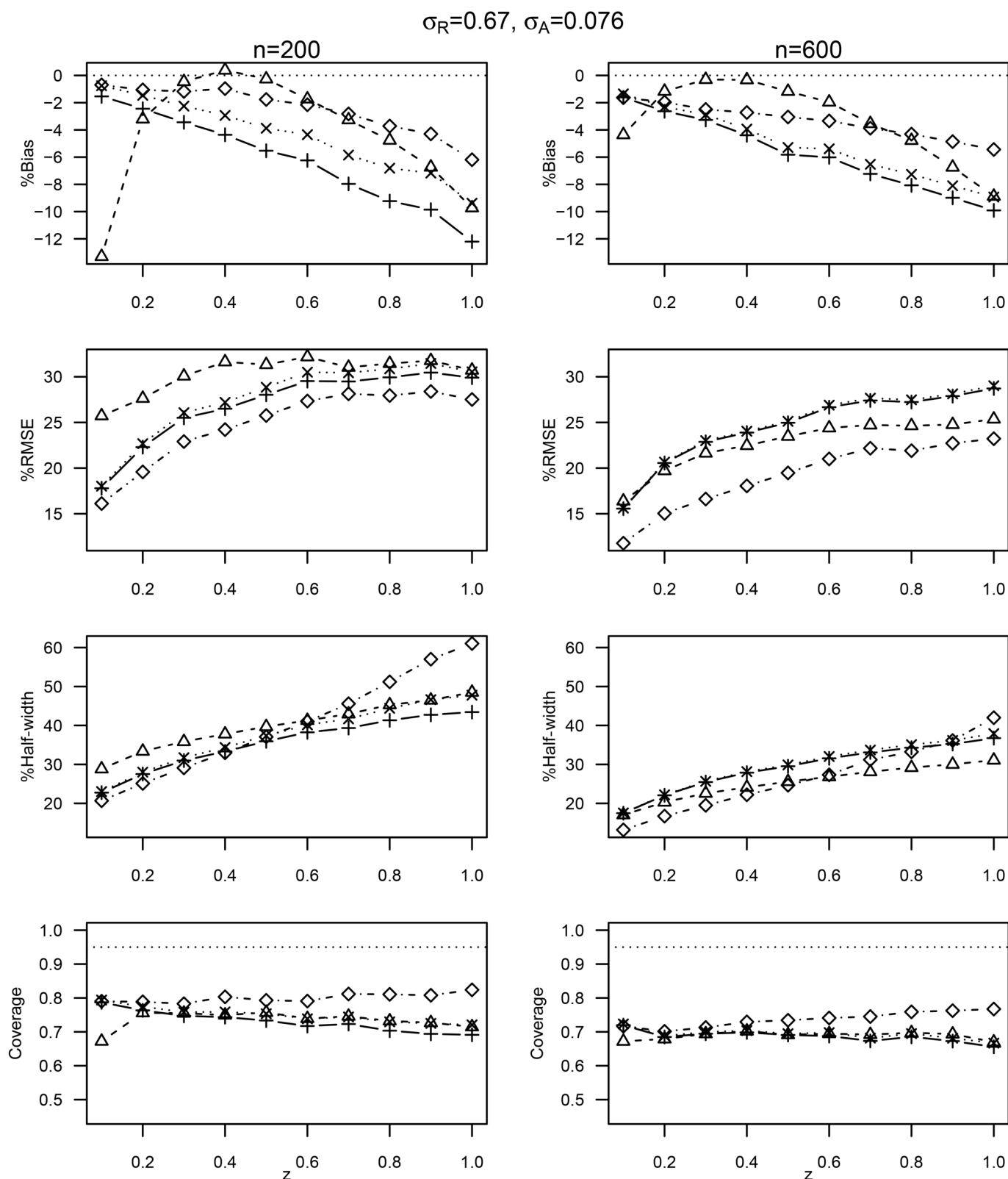
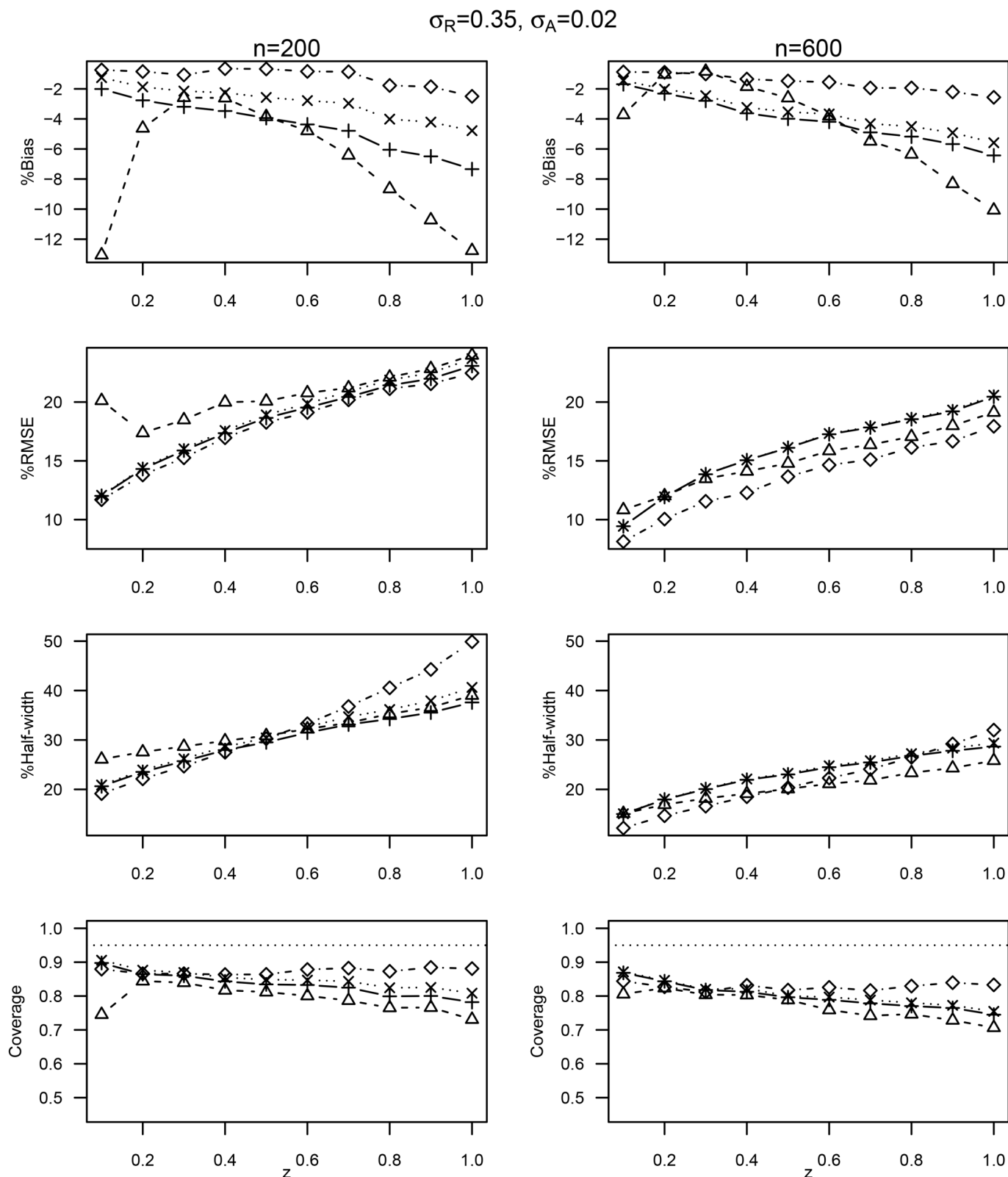


Fig. 3. As for Fig. 2, but with $\sigma_R = 0.35$, $\sigma_A = 0.02$.

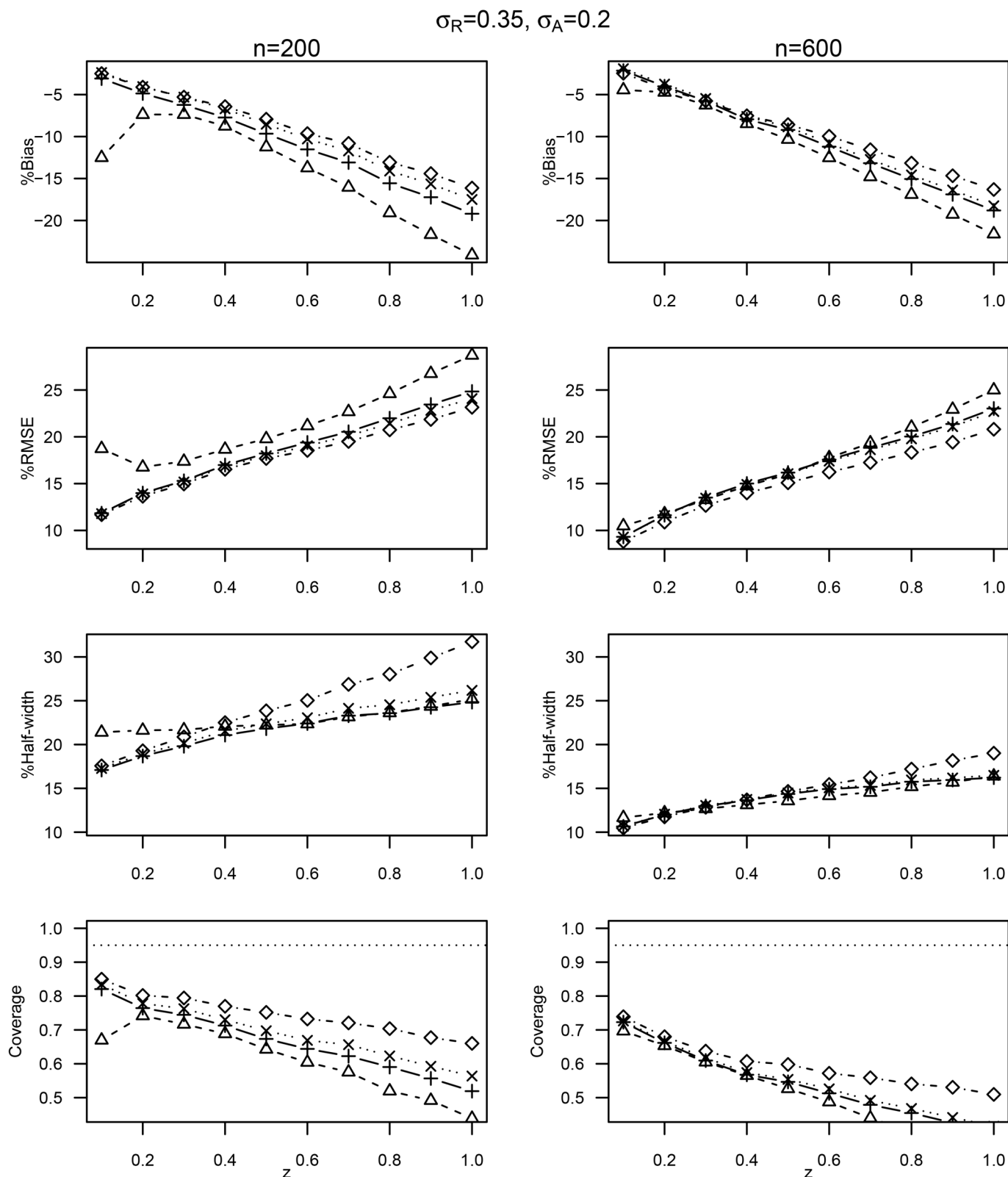


distributed around true age. The fitted model will be more influenced by overestimation of true age than by underestimation of true age by virtue of the fact that younger animals are more prevalent in the population than older animals. Thus, the greater influence

due to overestimation of true age will result in a tendency for z to be underestimated when ageing error is high.

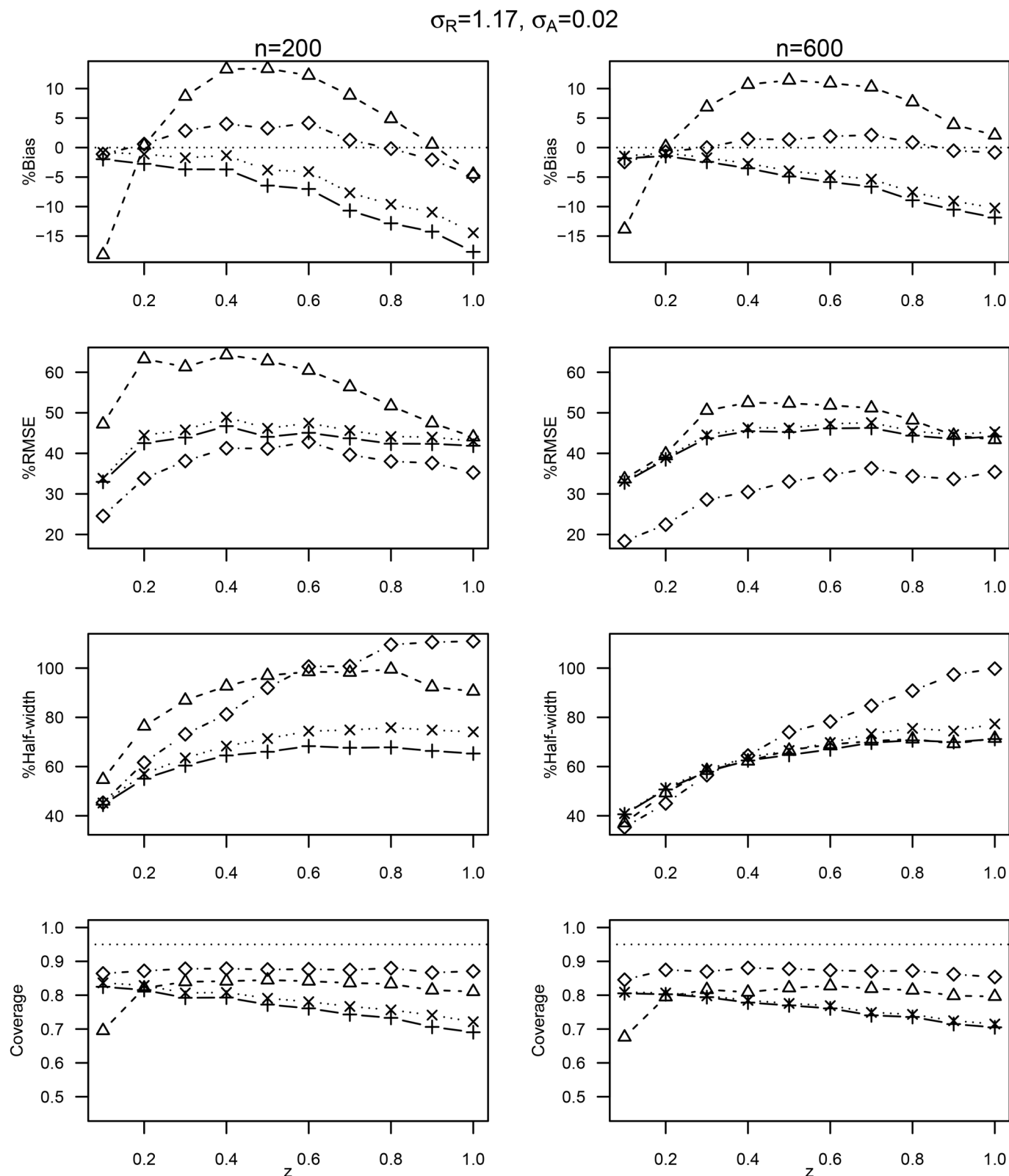
The simulation study of Smith et al. (2012) compared \hat{z}_{CRc} with \hat{z}_{WLR} for $0.2 \leq z \leq 1.0$ and $\sigma_R = 0.3$ and 0.6 . Notwithstanding that

Fig. 4. As for Fig. 2, but with $\sigma_R = 0.35$, $\sigma_A = 0.20$.



their study did not consider ageing error or variability in annual survival, they found that \hat{z}_{WLR} generally had slightly lower RMSE, but recommended \hat{z}_{CRC} owing to ad hocery in the weighting used in \hat{z}_{WLR} . The weighting is indeed quite arbitrary, and

numerous alternative specifications (such as $\hat{\mu}_d^2$) could be considered. The relative performance of such modified weightings may be satisfactory under a limited range of scenarios but will not generally be so. The weighting used by \hat{z}_{WLR} was seen to

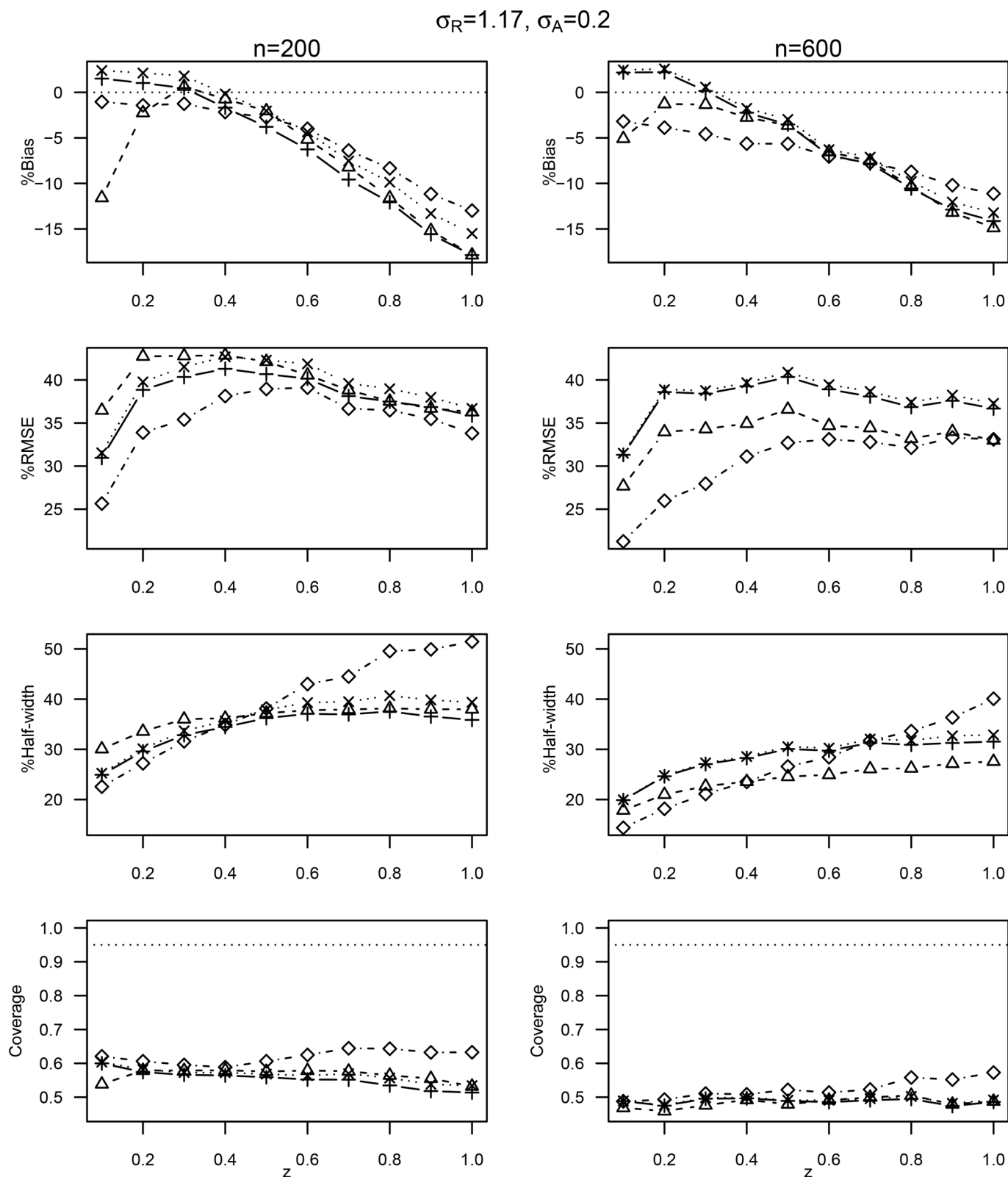
Fig. 5. As for Fig. 2, but with $\sigma_R = 1.17$, $\sigma_A = 0.02$.

correspond reasonably closely to the variance of $\log(y_a)$ under the GLMM for lower values of σ_R and moderate to high values of $\hat{\mu}_a$. This may explain why \hat{z}_{WLR} and \hat{z}_{MM} had similar performance under scenarios with low σ_R for the higher sample size $n = 600$. In contrast, for the median value $\sigma_R = 0.67$ and upper

extreme $\sigma_R = 1.17$, \hat{z}_{WLR} was vastly inferior to \hat{z}_{MM} , especially for $n = 200$.

The \hat{z}_{MM} estimator attains its superior performance by virtue of being based on a statistical model (eq. 9) that includes independently distributed random variability in the expected frequencies

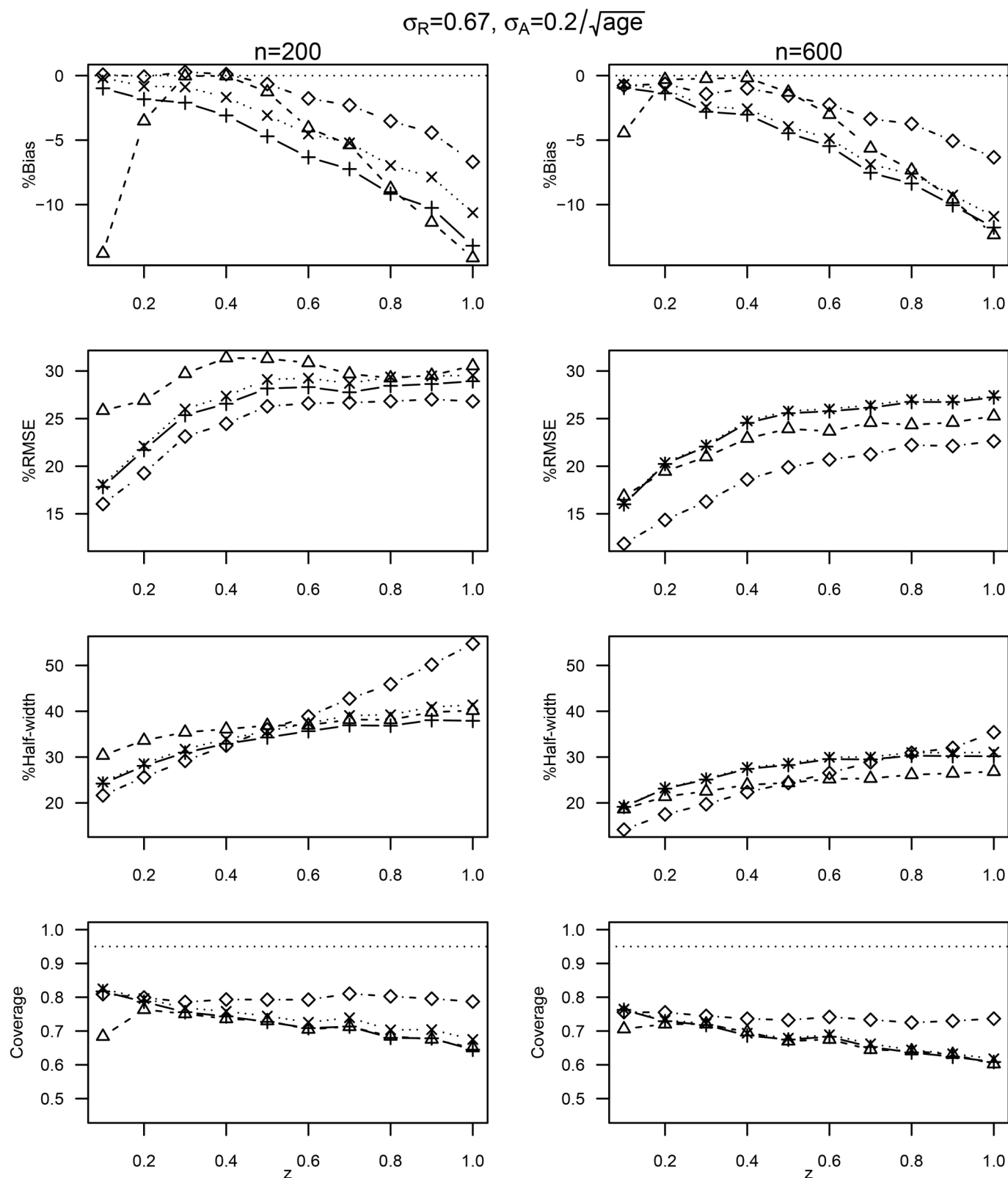
Fig. 6. As for Fig. 2, but with $\sigma_R = 1.17$, $\sigma_A = 0.20$.



at each age. This is equivalent to including independent random variability in recruitment. Hence, it was the simulation scenarios with moderate to high levels of σ_R that showed the greatest performance gains by \hat{z}_{MM} . Indeed, \hat{z}_{MM} performed to even greater advantage than seen here when exploratory simulations were im-

plemented under the specification of Smith et al. (2012), where variability in recruitment was the sole departure from steady-state. In particular, actual coverage of the nominal 95% confidence intervals was then very close to the nominal level. The simulations reported herein included autocorrelated recruitment, annual

Fig. 7. As for Fig. 2, but with $\sigma_R = 0.67$, $\sigma_A = 0.20/\sqrt{\text{age}}$.



variability in survival, and ageing error as additional departures from steady-state population dynamics for a more relevant comparison of the four estimators under consideration. Consequently, \hat{z}_{MM} no longer maintained the nominal coverage of the

95% confidence intervals, but continued to be the strongly preferred estimator.

In addition to having the best performance, inference about z using \hat{z}_{MM} was also the easiest to implement. A crucial point to

remember is that the age-frequency data need to be extended to contain older ages than those present in the measured sample. For example, if using the R language, suppose that the age-frequency data are contained in a dataframe called *Dat* having two columns, *Age* and *Freq*. The extension of the dataframe, as implemented in the simulations, is achieved with the following snippet of code:

```
max.age=max(Dat$Age)
extdDat=rbind(Dat,cbind(Age=(max.age+1):(2*max.age),
                        Freq=rep(0,max.age)))
```

The value of \hat{z}_{MM} and its standard error can then be obtained with the following line:

```
glmer(Freq~Age+(1|Age),family=poisson,data=extdDat)
```

where function *glmer* is provided by the *lme4* library, or for those users of the *glmmADMB* package:

```
glmmadmb(Freq~Age,family="poisson",
          random=~1|AgeFac,data=extdDat)
```

where *AgeFa* = *as.factor(Dat\$Age)*.

While it is also the case that \hat{z}_{CR} and \hat{z}_{ML} can be obtained with a single line of code, additional coding is required to obtain their approximate variance due to the overdispersion arising from non-steady-state conditions (Smith et al. 2012). In contrast, the approximate variance of \hat{z}_{MM} is returned directly by the above use of *glmer* or *glmmadmb* and does not require any adjustment since such overdispersion is accommodated through the mixed model formulation. The approximate variance of \hat{z}_{WLR} is obtained directly from the weighted regression, but additional programming is required because the two-step implementation requires the weights to be obtained by a standard linear regression in step one.

Before concluding this work, it is worth considering the situation where the sampled ages are not from a simple random sample taken at one point in time. In particular, one reviewer of this work was interested in the situation where age sampling had a longitudinal component. Since the Poisson log-linear mixed model underlying \hat{z}_{MM} is explicitly quantifying additional annual variability, it would be straightforward to extend it to other sources. So, for longitudinal age samples, it would be possible to explicitly incorporate both cohort and age-within-cohort as random effects.

A further consideration is the situation where the age-frequency sample is overdispersed compared with the assumed Poisson distribution, even after taking into account all nonsampling variability. Moderate overdispersion of this form can be incorporated using *glmmadmb* by specifying the family as negative binomial rather than Poisson. An extreme case of such overdispersion would occur if an age-length key had been applied to provide estimated age frequencies for the entire catch rather than just for those fish that were aged. In this case, the estimated age frequencies for the entire catch should be divided by a scaling factor, so that they sum to the sample size of the fish that were actually aged. This may result in non-integer frequencies, but these are still amenable to Poisson log-linear mixed modeling, notwithstanding that at the time of writing, *glmer* does not yet permit non-integer frequencies, but *glmmadmb* does.

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Appendix A

The random-intercept Poisson log-linear model can be written as follows:

$$\log(\mu) = \eta + \epsilon$$

$$y \sim \text{Poisson}(\mu)$$

where ϵ is distributed $N(0, \sigma^2)$. Since μ is log-normal distributed $\text{LN}(\eta, \sigma^2)$, it follows that $E[y] = E[\mu] = e^{\eta + \sigma^2/2}$. Analogously, since $1/\mu$ is distributed $\text{LN}(-\eta, \sigma^2)$, it is the case that $E[1/\mu] = e^{-\eta + \sigma^2/2}$.

Then, using first-order approximation

$$\begin{aligned} \text{var}(\log y) &= \text{var}(E[\log y|\mu]) + E[\text{var}(\log y|\mu)] \\ &\approx \text{var}(\log(\mu)) + E[1/\mu] \\ &= \sigma^2 + e^{-\eta + \sigma^2/2} \\ &= \sigma^2 + \frac{e^{\sigma^2}}{E[y]} \end{aligned}$$

In reality, the variance of $\log(y)$ is infinite because there is always a nonzero chance y could take the value 0. Nonetheless, the variance approximation will be of practical use provided that $E[y]$ is sufficiently large so that the probability of $y = 0$ is sufficiently small.