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Ageing Error Effect Size for the Southern Hemisphere minke whales

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ABSTRACT
Simulations are used to assess the implications of different levels of ageing bias on the performance of the statistical catch-at-age method of Punt and Polacheck (2008). Simulations based on deterministic data suggest that a 20% under-estimate of age which changes over time to zero will lead to estimated time-trajectories of carrying capacity which match those from actual applications of the statistical catch-at-age analysis method when carrying capacity is time-invariant. Allowing for observation error makes the results more variable.
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KEYWORDS: CATCH-AT-AGE, MINKE WHALE, SOUTHERN HEMISPSHERE

INTRODUCTION

Polacheck and Punt (2008) applied some preliminary models to the age estimates for 360 Southern Hemisphere minke whale earplugs by nine independent readers obtained during the 1983 IWC minke whale ageing workshop (IWC 1984). They found that systematic inconsistency (i.e. ageing bias) exists for at least some of the readers, that the extent of bias depends on the true age, and that there is also likely to be a substantial amount of "random" (non-systematic) error in the age estimates, even for experienced readers. Ageing error is known to impact of the outcomes from methods of stock assessment that rely on catch-at-age data, such as Virtual Population Analysis and statistical catch-at-age analysis (e.g. Reeves, 2003). For example, random ageing error can result in "smearing" of cohorts while ageing bias can result in spurious estimated trends in abundance.

The statistical catch-at-age analysis method of Punt and Polacheck (2008) can take account of ageing error (if it can be quantified). Punt and Polacheck showed results when ageing error is assumed to be random (with a CV of 20-30%) and when it is assumed to biased (based on applying the method of Punt *et al*. (2008) to some of the data from the 1983 aging workshop). They found that the trends in recruitment and total (1+) population size (particularly for the P stock) were sensitive to assumptions regarding ageing error. Punt and Polacheck (2008) also conducted a simulation evaluation of the implications on estimation ability of ignoring ageing error when it is present, but the results were preliminary because only low levels of random ageing error, and no ageing bias, was considered in the simulations.

This paper explores the issue of the impact of ageing error further by extending the simulation study of Punt and Polacheck (2008) to attempt to detect the "effect size" at which spurious trends in abundance would occur, in particular that abundance would be estimated to be increasing when this is not actually the case.

METHODS

The "effect size", κ, is defined here as the extent of relative bias in estimates of age, i.e. the value of κ such that the expected age (ignoring the effects of truncation at zero age) of an animal of true age *a* is κ*a*. Given an assumed level of random variation in age-reading error about the expected age, the distribution of estimated ages for an animal of true age *b* is given by:

$$P_{a,b} = e^{-(a-\kappa b)^2/(2\sigma^2)} \Big/ \sum_{a'>0} e^{-(a'-\kappa b)^2/(2\sigma^2)} \qquad (1)$$

where σ is a measure of ageing error (set to 0.1 for the simulations of this paper).

The impact of different values for κ on the estimation performance of the statistical catch-at-age method of Appendix A is evaluated by (a) constructing an operating model that is identical to the population dynamics model underlying the statistical catch-at-age method, (b) parameterising it so that the "true" trajectory of total (1+) abundance is virtually constant, (c) using this model to generate data sets which mimic those available for Southern Hemisphere minke whales (i.e. same years with estimates of abundance, same survey CVs, and same effective sample sizes for age-at-length and length-frequency data), and (d) applying the statistical catch-at-age analysis method under the assumption that κ=1 to these data.

For simplicity, the operating model assumes that age-specific natural mortality is the same for the I and P stocks, as is the value for the resilience parameter. Growth is, however, different between the I and P stocks and, consistent with the results of applying the statistical catch-at-age method to the data for Southern Hemisphere minke whales, growth varies inter-annually. To avoid confounding of results due to differences between the operating model and the estimation model, the estimation model also assumes that resilience and natural mortality-at-age are the same for the two stocks. Furthermore, the deviations about the mean growth curve, about the mean proportions within each area, about the stock-recruitment relationship, and about the mean selection patterns are all assumed to be zero in the operating model (to avoid the results being impacted by the penalties imposed on these quantities in the statistical catch-at-age analysis). These deviations are, however, estimated in the estimation model.

The value of κ changes over time from a reference value in 1970 to 1 in 1986 (Fig. 1a), reflecting the assumption that ageing error has changed over time and current ageing procedures are unbiased. Fig. 1b illustrates the implications of values for κ of 1, 0.75 and 0.5 on the expected age composition for females in Area IV for 1972.

Two sets of analyses are conducted. The first aims to evaluate the implications of different values for κ over a broad range. For simplicity these trials are deterministic. The second set of analyses allows for observation error, but only considers a single value for κ (the lowest value of which leads to obviously spurious trends in abundance).

RESULTS AND DISCUSSION

Deterministic analysis

Figure 2 shows the estimates of natural mortality, total (1+) abundance, and changes over time in carrying capacity based on fits of the statistical catch-at-age analysis method when the plus-group in the operating model is 54 or 80 and ageing is unbiased. The

estimates based on the operating model are somewhat biased even through the data are deterministic. This occurs because of the interaction between the selection pattern (which is dome-shaped for some fleets) and the plus-group age.

Decreasing κ from 1 to 0.6 leads to ever-greater extents of bias in the estimates of the trends in abundance (Fig. 3). The estimation model spuriously estimates that carrying capacity increased from 1930 to 1960 and declined thereafter for $\kappa < 1$ (except when κ=0.6 when carrying capacity is estimated to have increased and then stabilized at a new higher level)

Stochastic analyses

The time-trajectories of abundance for the W stock indicate spurious increases in abundance between 1930 and 1950-70 when allowance is made for observation error. However, such spurious trends are not evident for the I stock and the pattern of results for the W stock in Fig. 4 does not match that in Fig. 3. Analyses (not shown) indicate that the reason for the difference lies in the survey estimates of abundance and the JARPA indices of relative abundance – when these are treated as being deterministic, the results of the stochastic simulations match those in Fig. 3.

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APPENDIX A: THE STATISTICAL CATCH-AT-AGE ANALYSIS METHOD

The population dynamics model

Under the assumption that harvesting occurs instantaneously at the start of the year, the number of animals of sex *g* and age *a* at the start of year *y*, $N^g_{y,a}$, is given by:

$$N^g_{y,a} = \begin{cases} 0.5\,B_y & \text{if } a = 0 \\ (N^g_{y-1,a-1} - C^g_{y-1,a-1})\,e^{-M^g_{a-1}} & \text{if } 1 \le a \le x-1 \\ (N^g_{y-1,x-1} - C^g_{y-1,x-1})\,e^{-M^g_{x-1}} + (N^g_{y-1,x} - C^g_{y-1,x})\,e^{-M^g_x} & \text{if } a = x \end{cases} \quad \text{(App.1)}$$

where B_y is the number of births at the start of year *y* (the sex-ratio at birth is assumed to be 50:50),

$C^g_{y,a}$ is the catch of animals of sex *g* and age *a* during year *y*, calculated as the sum of the catch over all fleets, i.e.:

$$C^g_{y,a} = \sum_f C^{g,f}_{y,a} \quad \text{(App.2)}$$

$C^{g,f}_{y,a}$ is the catch of animals of sex *g* and age *a* by fleet *f* during year *y* (the analyses treat the fleets in each area in which a stock is assumed to be found as separate fleets, and assume that there are three fleets in each of these areas: Japan before 1987/88, Japan from 1987/88, and Soviet Union),

M^g_a is the instantaneous rate of natural mortality on animals of sex *g* and age *a* (assumed to be time-invariant), and

x is the plus-group (set equal to 54 for the analyses of this paper).

The relationship between natural mortality and age is taken to be piecewise linear:

$$M^g_a = \begin{cases} M_0 & \text{if } a \le a_1 \\ M_0 + (M_1 - M_0)\dfrac{(a-a_1)}{(a_2-a_1)} & \text{if } a_1 < a < a_2 \\ M_1 & \text{if } a_2 \le a \le a_3 \\ M_1 + (M_x - M_1)\dfrac{(a-a_3)}{(a_4-a_3)} & \text{if } a_3 < a < a_4 \\ M_x & \text{if } a \ge a_4 \end{cases} \quad \text{(App.3)}$$

where M_0 is the rate of natural mortality for animals aged a_1 and younger,

M_1 is the rate of natural mortality for animals aged between a_2 and a_3, and

M_x is the rate of natural mortality for animals aged a_4 and older.

Births

The number of births during year *y* depends on the number of females that have reached the age-at-first-parturition at the start of year *y* and the extent of density-dependence in pregnancy rate and infant survival[1], i.e.:

$$B_y = B_y^{\mathrm{F}}\ f_0\, e^{A(1-B_y^{1+}/K_y^{1+})}\ e^{\varepsilon_y - \sigma_R^2/2} \qquad \text{(App.4)}$$

where B_y^{F} is the number of females that have reached the age-at-first-parturition at the start of year *y*, i.e.:

$$B_y^{\mathrm{F}} = \sum_{a=1}^{x} \beta_{y,a}\, N_{y,a}^{g} \qquad \text{(App.5)}$$

B_y^{1+} is the number of animals aged 1 and older at the start of year *y*:

$$B_y^{1+} = \sum_{g} \sum_{a=1}^{x} N_{y,a}^{g} \qquad \text{(App.6)}$$

K_y^{1+} is the carrying capacity (expressed in terms of the size of the 1^+ component of the population) at the start of year *y*,

$\beta_{y,a}$ is the proportion during year *y* of animals of age *a* that have reached the age-at-first-parturition,

f_0 is the pregnancy rate / infant survival rate in absence of harvesting,

A is the resilience parameter (assumed to be independent of stock),

ε_y is the logarithm of the ratio of the expected to actual number of births for year *y*, and

σ_R is the standard deviation of ε_y.

Allowance is made for the possibility that carrying capacity has changed in a piecewise linear manner over the period considered in the analyses:

$$K_y^{1+} = \begin{cases} K_{1930}^{1+} & \text{if } y \le y_1 \\ K_{1930}^{1+}[1 + (\tilde{K}_I^{1+} - 1)\dfrac{(y - y_1)}{(y_2 - y_1)}] & \text{if } y_1 < y < y_2 \\ K_{1930}^{1+}[\tilde{K}_I^{1+} + (\tilde{K}_{2002}^{1+} - \tilde{K}_I^{1+})\dfrac{(y - y_2)}{(y_3 - y_2)}] & \text{if } y_2 \le y < y_3 \\ K_{1930}^{1+}\ \tilde{K}_{2002}^{1+} & \text{if } y \ge y_3 \end{cases} \qquad \text{(App.7)}$$

[1] As calves are not harvested, this formulation for density-dependence conceptually encompasses density-dependent effects in the survival rate of calves.

where K_{1930}^{1+} is the carrying capacity from 1930 to year y_1,

K_I^{1+} is ratio of the carrying capacity in year y_2 to that in year y_1, and

K_{2002}^{1+} is ratio of the carrying capacity from year y_3 to that in year y_1.

Catches

The model-estimate of the catch of animals of sex *g* and age *a* by fleet *f* during year *y* depends on the number of animals of sex *g* and age *a*, the exploitation rate by fleet *f* on animals of sex *s* during year *y*, and the relative vulnerability (the combined effects of harvest selectivity and availability) of animals of sex *g* and age *a* during year *y* to fleet *f*. $C_{y,a}^{g,f}$ is computed using the formula:

$$C_{y,a}^{g,f} = \sum_l C_{y,a,l}^{g,f} \qquad \text{(App.8)}$$

where $C_{y,a,l}^{g,f}$ is the catch during year *y* by fleet *f* of animals of sex *g* and age *a* that are in length-class *l*:

$$C_{y,a,l}^{g,f} = \begin{cases} \tilde{S}_a \, S_{y,l}^{g,f} \, X_{y,a,l}^{g} \, N_{y,a}^{g} \, F_y^{g,f} & \text{if vulnerability is length-specific} \\ \tilde{S}_a \, S_{y,a}^{g,f} \, X_{y,a,l}^{g} \, N_{y,a}^{g} \, F_y^{g,f} & \text{if vulnerability is age-specific} \end{cases} \qquad \text{(App.9)}$$

$S_{y,l}^{g,f}$ is the vulnerability of animals of sex *g* and length *l* to fleet *f* during year *y*,

$S_{y,a}^{g,f}$ is the vulnerability of animals of sex *g* and age *a* to fleet *f* during year *y*,

$\tilde{S}_a$ is a factor to reduce the availability of animals of certain (younger) ages to the fishery,

$F_y^{g,f}$ is the exploitation rate due to fleet *f* on fully-selected (i.e. $S_{y,l}^{g,f} \to 1$; $S_{y,a}^{g,f} \to 1$) animals of sex *g* during year *y*, and

$X_{y,a,l}^{g}$ is the proportion of animals of sex *g* and age *a* that are in length-class *l* during year *y*.

Vulnerability

Vulnerability is either assumed to be a function of length, fleet and sex, or a function of age, fleet and sex. Recall that separate fleets are defined for each area in which each stock is assumed to be found. Thus, separate vulnerability curves are estimated for each area and operational type. Note, however, that for the JARPA catches it is assumed that the vulnerability function is the same in all areas for each stock. This is because there are insufficient data to support the estimation of area-specific vulnerability curves for JARPA. The model has options which allow vulnerability to be uniform (Equations App.10a and App.11a), logistic (Equations App.10b and App.11b), or domed-shaped (Equations 10c and 11b), and can vary over time:

$$S_{y,l}^{g,f} = 1 \qquad \text{(App.10a)}$$

$$S_{y,l}^{g,f} = (1+e^{-\ell n19(L_l - L_{50,y}^{g,f})/L_{\text{diff}}^{g,f}})^{-1} \qquad \text{(App.10b)}$$

$$S_{y,l}^{g,f} = \begin{cases} \exp(-(L_l - L_{50,y}^{g,f})^2 / L_{\text{left}}^{g,f}) & \text{if } L_l \le L_{50,y}^{g,f} \\ \exp(-(L_l - L_{50,y}^{g,f})^2 / L_{\text{right}}^{g,f}) & \text{otherwise} \end{cases} \qquad \text{(App.10c)}$$

$$S_{y,a}^{g,f} = 1 \qquad \text{(App.11a)}$$

$$S_{y,a}^{g,f} = (1+e^{-\ell n19(a - a_{50,y}^{g,f})/a_{\text{diff}}^{g,f}})^{-1} \qquad \text{(App.11b)}$$

$$S_{y,a}^{g,f} = \begin{cases} \exp(-(a - a_{50,y}^{g,f})^2 / a_{\text{left}}^{g,f}) & \text{if } a \le a_{50,y}^{g,f} \\ \exp(-(a - a_{50,y}^{g,f})^2 / a_{\text{right}}^{g,f}) & \text{otherwise} \end{cases} \qquad \text{(App.11c)}$$

where $L_{50,y}^{g,f}$ is the length-at-50%-vulnerability (logistic vulnerability) / length-at-full-vulnerability (dome-shaped vulnerability) for fleet *f* fishing during year *y* for animals of sex *g*:

$$L_{50,y}^{g,f} = L_{50,y-1}^{g,f} + \delta_y^{g,f} \qquad \text{(App.12a)}$$

$a_{50,y}^{g,f}$ is the age-at-50%-vulnerability (logistic vulnerability) / age-at-full-vulnerability (dome-shaped vulnerability) for fleet *f* fishing during year *y* for animals of sex *g*:

$$a_{50,y}^{g,f} = a_{50,y-1}^{g,f} + \delta_y^{g,f} \qquad \text{(App.12b)}$$

$\delta_y^{g,f}$ is the "vulnerability deviation" during year *y* for fleet *f* fishing for animals of sex *g*,

$L_{\text{diff}}^{g,f}$ is the width of the length-specific vulnerability ogive for fleet *f* fishing for animals of sex *g*,

$a_{\text{diff}}^{g,f}$ is the width of the age-specific vulnerability ogive for fleet *f* fishing for animals of sex *g*,

$L_{\text{left}}^{g,f}$ and $L_{\text{right}}^{g,f}$ are the parameters that determine the extent of dome-shapedness for the length-specific vulnerability ogive for fleet *f* fishing for animals of sex *g*,

$a_{\text{left}}^{g,f}$ and $a_{\text{right}}^{g,f}$ are the parameters that determine the extent of dome-shapedness for the age-specific vulnerability ogive for fleet *f* fishing for animals of sex *g*, and

L_l is the length (in ft) corresponding to the mid-point of length-class *l*.

Time-dependence in vulnerability is modelled by allowing the length- (or age-)at-50%-/full-vulnerability to change from one year to the next, i.e. the shape of the vulnerability ogive is the same each year, but the point at which vulnerability first equals 1 changes.

Time-dependence in vulnerability was modelled in this way to avoid the over-parameterization that might occur if allowance was also made for time-dependence in the parameters that determine the shape of the vulnerability ogive. Note that vulnerability is assumed to be time invariant for the JARPA catches.

Growth

The proportion of animals of sex g in age-class a that are in length-class l during y, $X^{g}_{y,a,l}$, is given by:

$$X^{g}_{y,a,l} = \int_{L_l-\Delta L}^{L_l+\Delta L} \frac{1}{\sqrt{2\pi}\sigma^{g}_{\gamma}} e^{-\frac{(L-\tilde{L}^{g}_{y,a})^2}{2(\sigma^{g}_{\gamma})^2}} dL \qquad \text{(App.13)}$$

where ΔL is half of the width of each length-class (0.5 ft),

σ^{g}_{γ} is the extent of variability about the growth curve for sex g,

$\tilde{L}^{g}_{y,a}$ is the expected length of an animal of sex g and age a during year y, assuming that length-at-age is governed by a von Bertalanffy growth curve and that the growth rate parameter k^{g}_{y} varies for every year from 1963/64 until 2004/05, i.e.:

$$L^{g}_{y,a} = \begin{cases} L^{g}_{\infty}(1-e^{-k^{g}_{y}t^{g}_{0}}) & \text{if } a=0 \\ L^{g}_{\infty} - (L^{g}_{\infty} - L^{g}_{y-a,a-1})(1-e^{-k^{g}_{y-1}}) & \text{otherwise} \end{cases} \qquad \text{(App.14)}$$

L^{g}_{∞} is the asymptotic length for animals of sex g,

k^{g}_{y} is the value of the Brody growth coefficient for animals of sex g during year y:

$$k^{g}_{y} = k^{g}_{y-1} e^{\upsilon_y} \qquad \text{(App.15)}$$

t^{g}_{0} is the theoretical age at which length is zero for animals of sex g, and

υ_y is the extent to which the growth rate changes from year y-1 to year y.

Initial conditions

The initial conditions (y_1=1930) correspond to a population at its unexploited equilibrium level, i.e.:

$$N^{g}_{y_1,a} = \begin{cases} 0.5\,B_0 & \text{if } a=0 \\ N^{g}_{y_1,a-1}\, e^{-M^{g}_{a-1}} & \text{if } 1 \le a \le x-1 \\ N^{g}_{y_1,x-1}\, e^{-M^{g}_{x-1}} / (1-e^{-M^{g}_{x}}) & \text{if } a=x \end{cases} \qquad \text{(App.16)}$$

where B_0 is the expected number of calves in the absence of exploitation.

The value of the parameter f_0 is chosen so that the population remains in balance in the absence of exploitation, i.e.:

$$f_0 = \left[\sum_{a=1}^{x-1} \beta_{y_1,a}\, e^{-\sum_{a'=0}^{a-1} M_{a'}^{\mathrm{f}}} + \beta_{y_1,x} e^{-\sum_{a'=0}^{x-1} M_{a'}^{\mathrm{f}}} / (1 - e^{-M_x^{\mathrm{f}}}) \right]^{-1} \qquad \text{(App.17)}$$

The objective function

The objective function contains contributions from the data and from penalties on some of the parameters, i.e.:

$$L = \sum_i O_i\, \ell\mathrm{n} L_i + \sum_j P_j \qquad \text{(App.18)}$$

where $\ell\mathrm{n}L_i$ is the contribution of the ith data source to the objective function,

P_j is the contribution of the jth penalty term to the objective function, and

O_i is a factor to account for overdispersion.

The data included in the analyses are the annual catches (by fleet and sex), the estimates of abundance (IDCR and JARPA), the catch length-frequency data and the age-length keys, while there are penalties on the magnitudes of the deviations from the expected number of births (Equation App.4), on the inter-annual deviations in the growth rate (Equation App.15), on the inter-annual variation in the proportion of the population in each area (see Equation App.23), and on the inter-annual deviations in vulnerability (Equation App.12). Each of these contributions is discussed in turn below. The equations listed below assume that data for each data-type are available for every year, and for all Areas and fleets. This is not the case in reality and the equations are modified appropriately in the absence of data for specific years, areas and fleets.

Catches

The contribution of the catches to the objective function is based on the assumption that any errors when measuring the catch are log-normally distributed[2], i.e.:

$$\ell\mathrm{n}L_1 = \sum_y \sum_g \sum_f \left\{ \ell\mathrm{n}\sigma_C + \tfrac{1}{2\sigma_C^2} \sum_y (\ell\mathrm{n}\tilde{C}_y^{g,f} - \ell\mathrm{n}C_y^{g,f})^2 \right\} + Const \qquad \text{(App.19)}$$

where $\tilde{C}_y^{g,f}$ is the actual catch by fleet *f* of animals of sex *g* during year *y* (see Table 1), and

σ_C quantifies the extent of variation in catches.

[2] Note that very high weight is assigned to this component of the objective function so the model effectively replicates the actual catches exactly.

Estimates of abundance
The estimates of abundance are assumed to be indices of 1^+ abundance, i.e.:

$$\ell \mathrm{n} L_2 = \sum_A \sum_y \left\{ \ell \mathrm{n} \tilde{\sigma}_y^A + \tfrac{1}{2(\tilde{\sigma}_y^A)^2} (\ell \mathrm{n} V_y^A - \ell \mathrm{n}(\chi^A B_y^{\mathrm{Surv},A}))^2 \right\} + Const \qquad \text{(App.20)}$$

where V_y^A is the estimate of abundance for Area *A* and year *y*,

χ^A is the bias factor for Area *A*,

$\tilde{\sigma}_y^A$ is the measurement error standard deviation, determined from the observation error standard deviation and the extent of additional variance, i.e.:

$$(\tilde{\sigma}_y^A)^2 = \tau^2 + (\phi_y^A)^2 \qquad \text{(App.21)}$$

τ^2 is the extent of additional variance,

ϕ_y^A is the coefficient of variation of V_y^A,

$B_y^{\mathrm{Surv},A}$ is the model-estimate of the total (1+) abundance in Area *A* at the start of year *y*, i.e.:

$$B_y^{\mathrm{Surv},A} = \sum_a \sum_l P_y^A X_{y,a,l}^g S_{y,l}^{g,f*} N_{y,a}^g \qquad \text{(App.22)}$$

P_y^A is the proportion of the population that is in the region *A* during year *y*:

$$P_y^A = \overline{P^A} e^{\varphi_y^A} / \sum_{A'} e^{\varphi_y^{A'}} \qquad \text{(App.23)}$$

f^* is the fleet to which the abundance estimates pertain (set to the post-1987 Japanese fleet for the JARPA indices; set to uniform selectivity for the IDCR indices),

$\overline{P^A}$ is the expected proportion of the population that is in the Ath region, and

φ_y^A is the deviation from the expected proportion in Area *A* for year *y*.

Length-frequency data
The contribution of the length-frequency data to the objective function is based on the assumption that the catch by sex is taken multinomially from the vulnerable population, i.e.:

$$\ell \mathrm{n} L_3 = -\sum_y \sum_f \sum_g M_y^{g,f} \sum_{l=l_{\min,y}}^{l_{\max,y}} \rho_{y,l}^{g,f} \ell \mathrm{n}(\hat{\rho}_{y,l}^{g,f} / \rho_{y,l}^{g,f}) + Const \qquad \text{(App.24)}$$

where $M_y^{g,f}$ is the effective sample size for the length-frequency data for animals of sex *g* taken by fleet *f* during year *y* (set equal to the number of animals of sex *g* taken by fleet *f* during year *y* for which information on length is available),

$\rho_{y,l}^{g,f}$ is the observed fraction of the catch of animals of sex *g* taken by fleet *f* during year *y* that is in length-class *l*,

$\hat{\rho}_{y,l}^{g,f}$ is the model-estimate of the fraction of the catch of animals of sex *g* taken by fleet *f* during year *y* that is in length-class *l*:

$$\hat{\rho}_{y,l}^{g,f} = \frac{\sum_a C_{y,a,l}^{g,f}}{\sum_{a'}\sum_{l'} C_{y,a',l'}^{g,f}} \qquad \text{(App.25)}$$

Lengths $l_{\min,y}$ and $l_{\max,y}$ define the plus and minus groups for the length-frequency data for year *y* (data and model-predictions for animals with length less than $l_{\min,y}$ are pooled in the $l_{\min,y}$ length-class while data and model-predictions for animals with length greater than $l_{\max,y}$ are pooled in the $l_{\max,y}$ length-class).

Age-length keys

The age-length keys are included in the objective function under the assumption that sampling for age is multinomial conditioned on length, i.e.

$$\ell \mathrm{n} L_4 = \sum_y \sum_f \sum_g \sum_{l=l_{\min,y}}^{l_{\max,y}} \tilde{M}_{y,l}^{g,f} \sum_{a=a_{\min,y}}^{a_{\max,y}} \theta_{y,a,l}^{g,f} \ell \mathrm{n}\left(\hat{\theta}_{y,a,l}^{g,f} / \theta_{y,a,l}^{g,f}\right) + Const \qquad \text{(App.26)}$$

where $\tilde{M}_{y,l}^{g,f}$ is the effective sample size for the age breakup of the animals of sex *g* in length-class *l* taken by fleet *f* during year *y* (set equal to the number of animals of sex *g* in length-class *l* taken by fleet *f* during year *y* for which information on length and age is available),

$\theta_{y,a,l}^{g,f}$ is the observed fraction of the catch of animals in length-class *l* of sex *g* taken by fleet *f* during year *y* that were aged to be age *a*,

$\hat{\theta}_{y,a,l}^{g,f}$ is the model-estimate of the fraction of the catch of animals in length-class *l* of sex *g* taken by fleet *f* during year *y* that were aged to be age *a*, i.e.:

$$\hat{\theta}_{y,a,l}^{g,f} = \frac{\tilde{C}_{y,a,l}^{g,f}}{\sum_{a'} C_{y,a',l}^{g,f}} \qquad \text{(App.27)}$$

$\tilde{C}_{y,a,l}^{g,f}$ is the model-estimate of the number of animals of sex *g* caught by fleet *f* during year *y* that would have been aged to be age *a*:

$$\tilde{C}^{g,f}_{y,a,l} = \sum_{a'} Y^{g}_{a,a'} C^{g,f}_{y,a',l} \qquad \text{(App.28)}$$

$Y^{g}_{a,a'}$ is the fraction of animals of sex *g* and age *a'* that are aged to be age *a* (the age-reading error matrix), i.e. assuming that the coefficient of variation of the age-reading error is independent of age:

$$Y^{g}_{a,a'} = \int_{a-0.5}^{a+0.5} \frac{1}{\sqrt{2\pi}\sigma''_{a'}} e^{-\frac{(\lambda-\beta_a)^2}{2(\sigma''_{a'})^2}} d\lambda \qquad \text{(App.29)}$$

β_a is the expected age based on age-readings for an animal of true age *a*,

σ''_a is the standard error of the age-estimate for an animal of true age *a* (generally $\sigma''_a = \alpha a$) , and

α is the coefficient of variation of the age-reading error.

Ages $a_{\min,y}$ and $a_{\max,y}$ define the plus and minus groups for the ageing data for year *y*, i.e. data and model-predictions for animals with age greater than $a_{\max,y}$ are pooled at age $a_{\max,y}$ [3] and those with age less than $a_{\min,y}$ are pooled at age $a_{\min,y}$.

Penalties

The penalty on the deviations from the expected number of births is based on the assumption that these deviations are log-normally distributed, i.e.:

$$P_1 = \tfrac{1}{2\sigma_R^2} \sum_{y} (\varepsilon_y)^2 \qquad \text{(App.30)}$$

The penalty on the changes over time in the vulnerability deviations is based on the assumption that these deviations are normally distributed, i.e.:

$$P_2 = \tfrac{1}{2\sigma_S^2} \sum_{g} \sum_{y} \sum_{f} (\delta_y^{g,f})^2 \qquad \text{(App.31)}$$

where σ_S is the extent of inter-annual variation in the age-at-50%-vulnerability.

The penalty on the annual deviations in the proportion of each stock in each area is based on the assumption that these deviations are normally distributed, i.e.:

$$P_3 = \tfrac{1}{2\sigma_P^2} \sum_{y} \sum_{A} (\varphi_y^A)^2 \qquad \text{(App.32)}$$

where σ_P is the extent of variation in the distribution of the stock.

[3] Note that the evaluation of the impact of age-reading error is determined before the application of the plus-group.

The penalty on the inter-annual changes in the von Bertalanffy growth rate parameter is based on the assumption that these deviations are normally distributed, i.e.:

$$P_4 = \frac{1}{2\sigma_k^2} \sum_y \upsilon_y^2 \qquad \text{(App.33)}$$

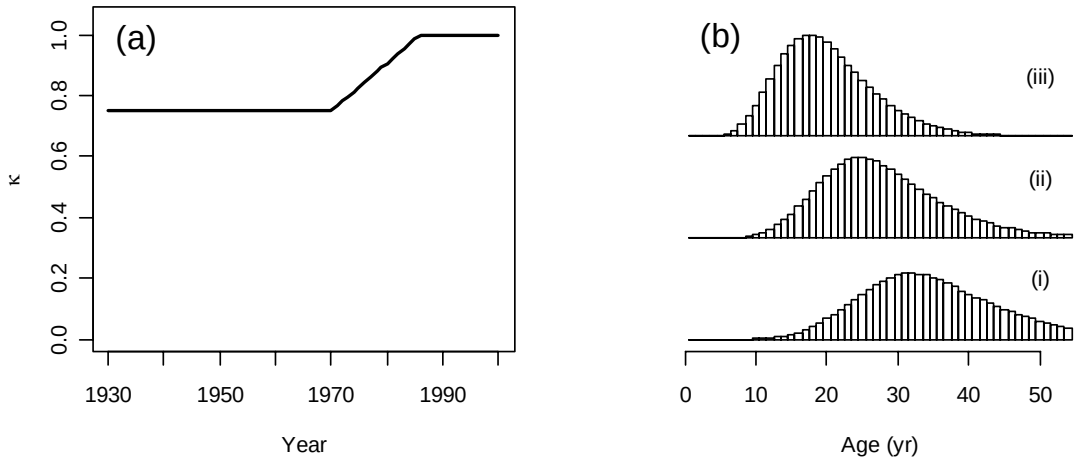

Fig. 1. Time-trajectory for the parameter that determines the extent of ageing bias (a), and three true age compositions for females in Area IV for 1972 (b). Results are shown in (b) for (i) κ=1, (ii) κ=0.75, and (iii) κ=0.5.

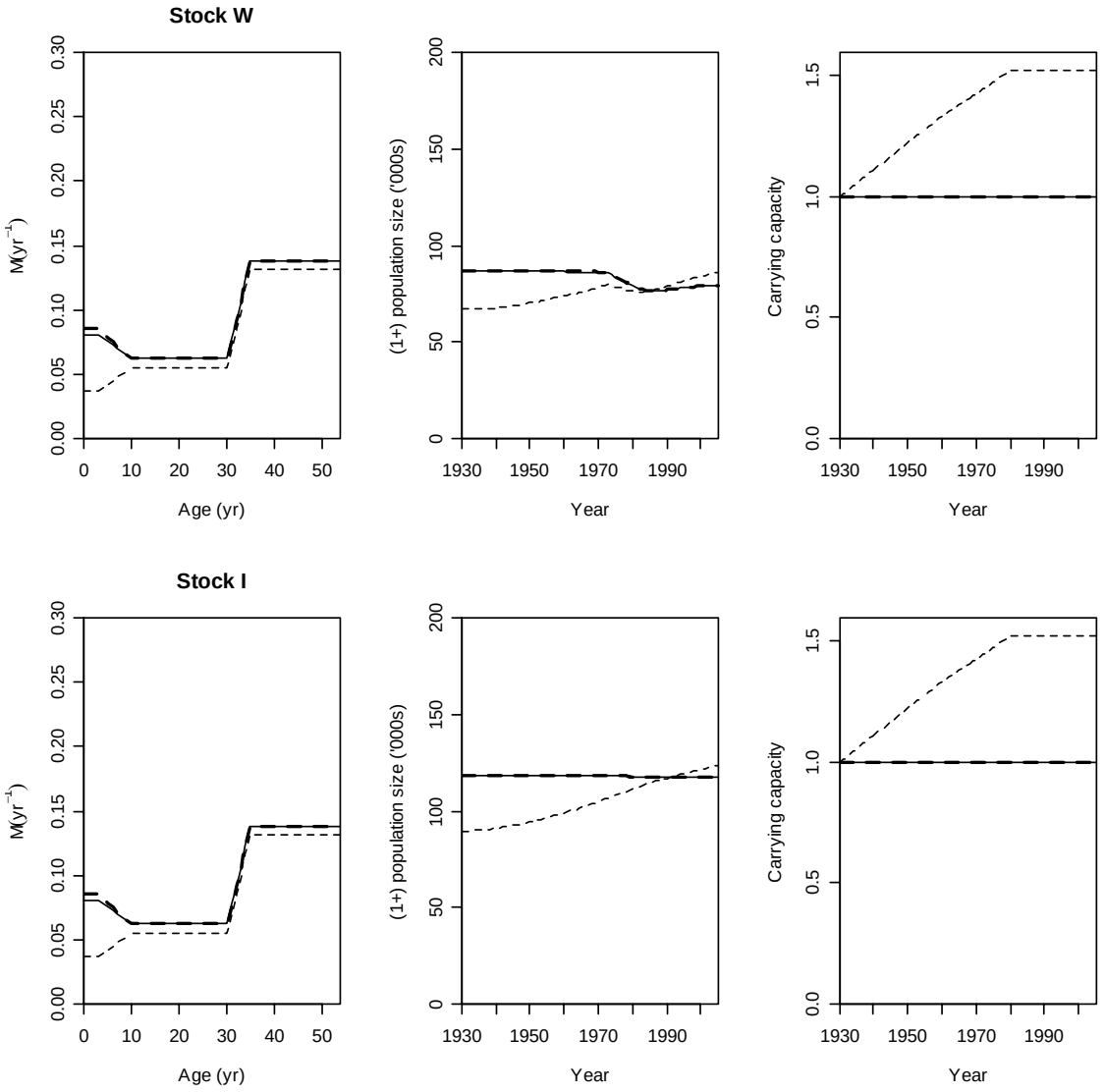

Fig. 2. Results from fitting the statistical catch-at-age estimator to data sets generated from an operating model in which the true plus group age in 54 (solid line) and in which it is 80 (dashed lines). The bold dash-dot line indicates the true (operating model) values. The operating model on which this plot is based assumed that κ=1 (no ageing bias).

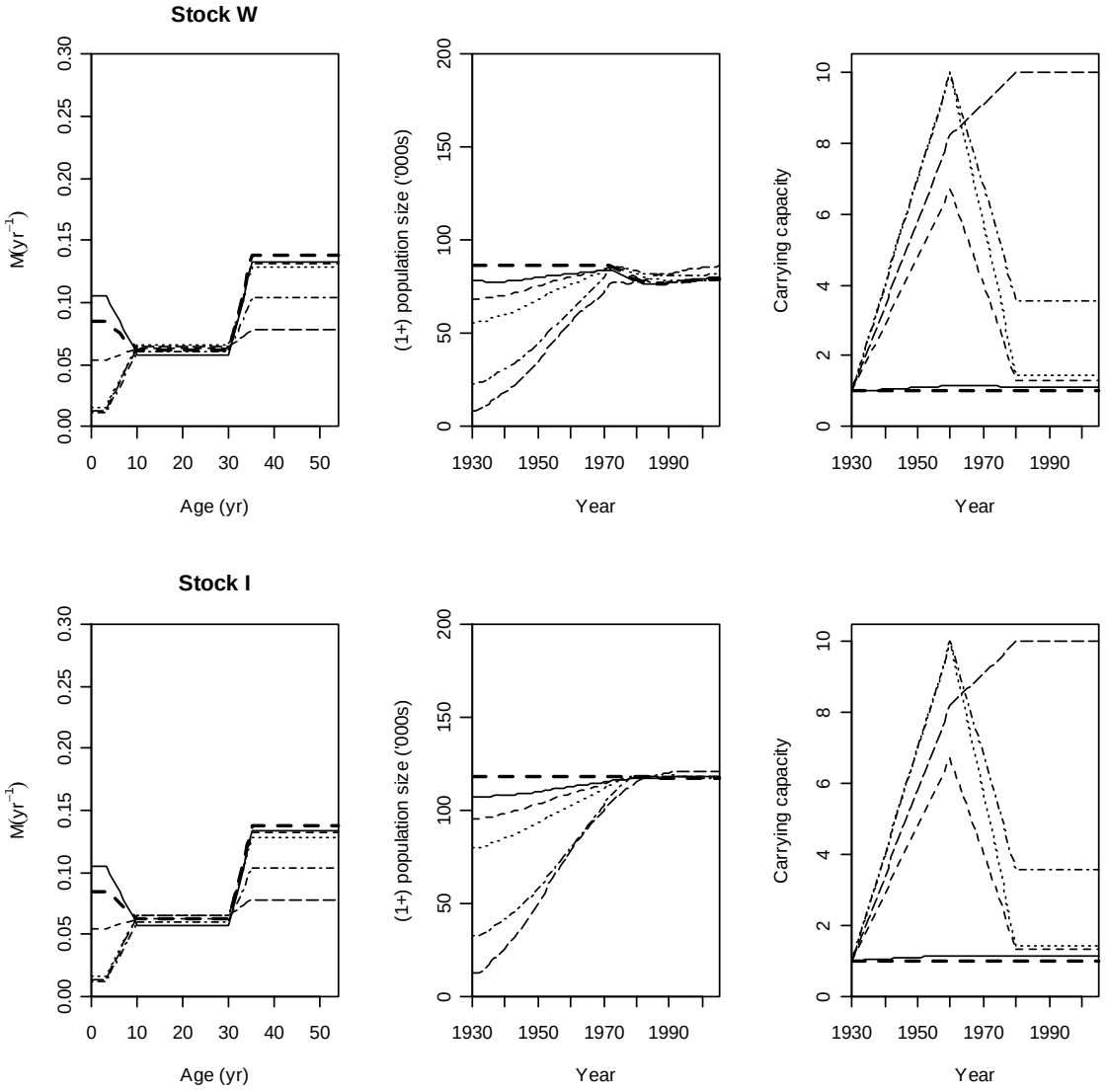

Fig. 3. Results from fitting the statistical catch-at-age estimator to data sets generated from an operating model in which the value of κ is varied from 1 to 0.6. The bold dash-dot line indicates the true (operating model) values.

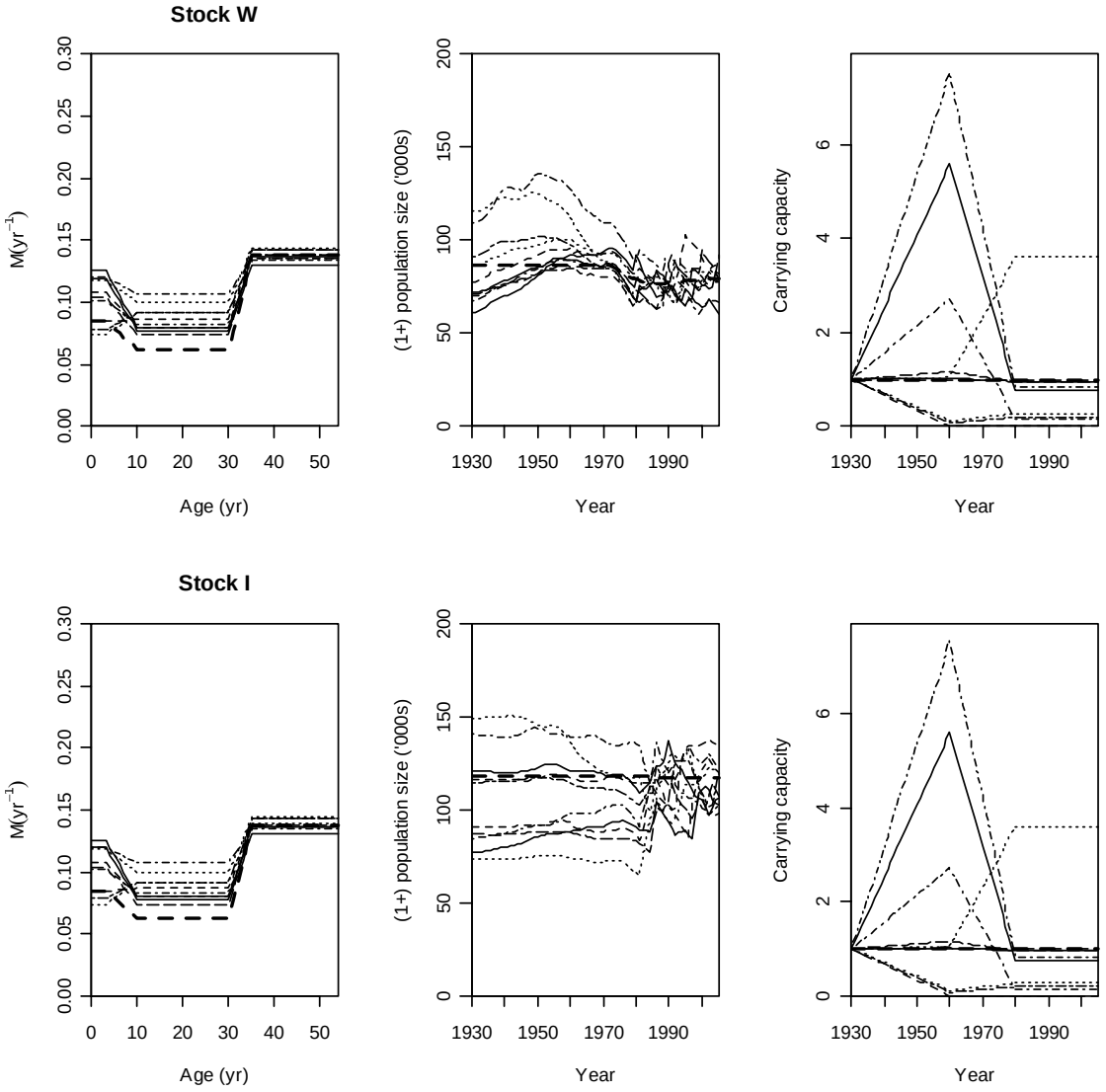

Fig. 4. Results from fitting the statistical catch-at-age estimator to data sets generated from an operating model in κ=0.8 and the data are generated stochastically. The bold dash-dot line indicates the true (operating model) values.