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Further Analyses Related to Application of Statistical Catch-at-age Analysis to Southern Hemisphere Minke Whales

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ABSTRACT
The statistical catch-at-age approach developed by Punt and Polacheck (2005, 2006, 2007) is updated to allow selectivity for the JARPA indices of relative abundance to differ from uniform and to include ageing bias as well as ageing imprecision. The approach is applied to catch, catch-at-length, and age-length keys as well as indices of relative and absolute abundance for minke whales in Antarctic Areas III-E, IV, V and VI-W. The results again confirm the result from earlier studies that the recruitment of Southern Hemisphere minke whales in Areas III-W, IV, V and VI-W increased until about the early- to mid-1960s and declined thereafter. Sensitivity tests show that the estimator is more stable and the results more biologically realistic when parameters are shared between the W and E stocks and that the results are insensitive to leaving the JARPA indices of abundance out of the analysis. The results from an initial analysis of the impact of allowing for (time-invariant) ageing bias depend on whether the parameters which determine growth, natural mortality, resilience and changes over time in carrying capacity are shared between the W and E stocks. Estimates of natural mortality and the ability of the model to yield biologically realistic estimates are sensitive to level of random aging error assumed. A preliminary application of the MCMC algorithm to characterize uncertainty was unsuccessful, perhaps because of the complexity of the model. An initial evaluation of the estimation approach using simulation suggests that trends in abundance and natural mortality are generally captured even if some key assumptions are violated, but that estimates of some model outputs can be biased if assumptions are violated. The results also suggest that asymptotic variance estimates are too low. Future simulation evaluation needs to explore a broader range of operating model scenarios and estimation procedures. The results presented remain preliminary because of a number of currently unresolved questions about the model input and structure, including abundance estimates, and ageing error.

KEYWORDS: CATCH-AT-AGE, MINKE WHALE, SOUTHERN HEMISPSHERE

INTRODUCTION

The IWC Scientific Committee has been conducting a multi-year IDCR/SOWER line transect survey for minke whales in the Antarctic, and is aiming to understand the reason or reasons for the apparent large declines in abundance indicated by estimates produced from these surveys. One hypothesis that has been suggested is that the declines are due to “a decrease in carrying capacity due to increase in competition from other predators (e.g. other whales)” (IWC, 2005). It has been suggested that population modelling could provide an approach for addressing the plausibility of this and other population dynamic-related hypotheses for the decline. The ADAPT-VPA approach of Butterworth *et al.* (1996, 1999, 2002) was identified as one approach that would be useful for assessing the plausibility of this hypothesis. However, it was also considered useful to develop alternative modelling approaches.

Punt and Polacheck (2005, 2006) developed a statistical catch-at-age model for Southern Hemisphere minke whales that allows for errors in catch-at-age data, more than a single stock, time-varying growth, multiple areas, environmental covariates, fleet-specific vulnerabilities, and changes over time in vulnerability (see Appendix A for the latest version of this model[1]). Punt and Polacheck (2005, 2006, 2007) applied variants of this model to data for the Southern Hemisphere minke whales and found that the scenario of a resource that increased after 1930 and declined recently is fairly robust to changes to the specifications of the assessment. However, some of the scenarios identified by Punt and Polacheck (2005), particularly those in which allowance was made for dome-shaped vulnerability and when vulnerability is assumed to be age-based, suggest a different conclusion regarding historical trends.

This paper explores alternative model configurations for the statistical catch-at-age analyses, based on discussions at, and suggestions from, the 2007 annual meeting of the IWC Scientific Committee. Specifically, configurations are explored in which some of the parameters (i.e. those related to carrying capacity, resilience, growth, and natural mortality) are assumed to be the same for the W (Areas III-E, IV and V-W) and E (Areas V-E and IV-W) stocks IWC (2007) provides the rationale for the selection of this option for the stocks. The analyses of this paper are based on the assumption that vulnerability is length-specific, that vulnerability for the commercial fisheries is dome-shaped and time-varying, while vulnerability for JARPA is a logistic function of length. These choices for vulnerability are based on the comparison of a variety of alternative vulnerability patterns in Punt and Polacheck (2007) which suggested that these choices are perhaps the most compatible with the existing data and model structure. In particular, age-based vulnerability often leads to fitting problems. As discussed in Punt and Polacheck (2007), the reasons for this needed to be investigated further, particularly since some of the results with age-based vulnerability suggested different historical trends. However, time and resources did not allow us to explore this issue further in the current paper.

This paper also explores alternative choices for the relationship between true and estimated age (i.e. ageing error). The bulk of the analyses of this paper as well as those of Punt and Polacheck (2005, 2006, 2007) are based on the assumption that age-estimates are unbiased but imprecise (generally, CV=0.1). However, concerns about the relationship between true and estimated ages have arisen because comparisons of length-at-age data from the commercial and JARPA catches suggest apparent inconsistency (Punt and Polacheck 2005, Polacheck and Punt 2006). The development of appropriate aging error models which could account for variances and biases in the aging were identified as a high priority for the catch-at-age modelling work in 2006 and 2007 (IWC 2007, 2008). As such, sensitivity is explored in this paper to an alternative ageing error model, in which ages are assumed biased as well as being imprecise as an initial attempt

[1] The model is identical to that in Punt and Polacheck (2007), except that the vulnerability pattern for JARPA is used when calculating the model estimates for the JARPA indices of abundance and allowance is made for bias in age-estimates.

to address this question. This ageing error model is based on model # 1 in Polacheck and Punt (2008). This option was selected to provide one indication of the possible consequences of aging error on the model results given available information. However, as noted in Polacheck and Punt (2008), the currently available information does not allow determination of the most appropriate error model or the range of possible biases and imprecision that may exist in the age data.

The measures of precision reported in previous studies have been based on inverting the Hessian matrix at the minimum of the objective function and applying the delta method to compute standard errors for derived parameters. This is not ideal for several reasons, including that the objective function includes several penalty terms (effectively priors) and it is unclear how quadratic the objective function is at its minimum given the large number of parameters and highly non-linear structure of the model. We therefore explore the application of Markov Chain Monte Carlo algorithm to sample parameter vectors from a posterior distribution.

Finally, Butterworth *et al*. (1999) explored the estimation performance of an earlier version of the ADAPT-VPA estimation procedure, but since then no simulation evaluations have been conducted. This paper conducts a preliminary evaluation of estimation performance to assess the impact of violations of some of the assumptions related to vulnerability and ageing error.

MATERIALS AND METHODS

Data utilized

The data used in this paper consist of catch, abundance estimates, length frequency and age-composition data. The data include the catches and sighting survey information through the 2004/05 season.

Catches and length-frequency data

Table 1 lists the catches by sex, fleet (Japan and Soviet Union) and Area (III-E, IV, V-W, V-E, and VI-W). The catches prior to 1971/72 are not allocated to fleet because these catches were taken by several nations. There is no information on the length-frequency of these catches so the vulnerability patterns for the years prior to 1971/72 are assumed to be equal to that for Japan in 1971/72, and the pre-1971/72 catches for Area V are split equally between Areas V-W and V-E. The results are unlikely to be sensitive to these assumptions given the small magnitude of the catches concerned.

Age-composition data

Age-composition data are only available for the Japanese catches. Table 2 lists the number of animals aged and the number of animals for which length data are available.

Indices of abundance

Table 3 lists the estimates of absolute abundance (from the IDCR programme; supplied by T. Branch, University of Washington) and the indices of abundance based on the JARPA programme (supplied by T. Hakamada, Institute of Cetacean Research).

Parameter estimation for the reference case analysis

The primary aim of the reference case analysis is to contrast alternative assumptions and so this analysis does not necessarily reflect the "best" set of assumptions or choices for data. Comparison of the results of the reference case with sensitivity analyses provides one indication of the robustness of the modelling results. However, if there are substantial interactions among the various factors, conclusions about robustness may be sensitive to the choice of the reference case.

Table 4 lists the estimable parameters of the reference case model of this paper. The values for the other parameters of the model are pre-specified as follows:

- The age-reading error CV is set to 10%, and the age-estimates are assumed to be unbiased (i.e. $\beta_a = a$ and α=0.1 in Equation App.29).
- There is no survey bias for the IDCR/SOWER estimates (i.e. χ=1 for the IDCR estimates), and no additional variance for either IDCR/SOWER or JARPA (i.e. τ^2 =0 in Equation App.21).
- The minus- and plus-group ages when fitting to the age-composition data, $a_{\min,y}$ and $a_{\max,y}$, are set to 1 and 45yr respectively.
- The minus- and plus-group lengths, $l_{\min,y}$ and $l_{\max,y}$ for females are set to 22ft and 32ft for the period of commercial whaling, and 17ft and 32ft for JAPRA while $l_{\min,y}$ and $l_{\max,y}$ for males are set to 22ft and 31ft for the period of commercial whaling and 17ft and 31ft for JAPRA. These choices were made to avoid fitting the model to length-classes with few data.
- Carrying capacity changed in 1930, 1960 and 1980 (years y_1, y_2 and y_3 in Equation App.7).
- Natural mortality changes (in a piecewise linear fashion) at ages 3, 10, 30 and 35 (ages a_1, a_2, a_3 and a_4 in Equation App.3).
- The proportion of animals that have reached the age-at-first-parturition is defined by a logistic curve where 50% of animals reach first parturition at 8.5 years and 95% by 11.5 years. The first age at which an animal may reach first parturition is set equal to 3 years. These specifications were made for consistency with the analyses conducted by Butterworth and Punt (1999).
- An age-specific availability factor is estimated for age 1 only (exploratory analyses, not shown here, indicate that little improvement in fit occurs if availability is estimated for additional ages).
- The extent of variation in births, σ_R, is set to 0.2.
- The standard deviation of the logarithms of measuring the catch, σ_C, is set to 0.05.
- The parameter that determines the extent of variability in the vulnerability deviations, σ_S, is set to 10.
- The parameter that determines the extent of variability in the proportion of each stock in each area, σ_P, is set to 0.2.

- The parameter that determines the extent of variability in growth rate, σ_k, is set to 0.1.

The reference case choices for σ_R, σ_C, σ_S, σ_P, and σ_k were made to force the model to replicate the catches closely, not to allow large deviations in births compared to those expected from the number of mature females, and to allow for large changes in vulnerability from one year to the next and in the proportion of the population in each area, if this suggested by the data. The values for the overdispersion parameters O_3 and O_4 (0.65 and 0.8) were selected as outlined by Punt and Polacheck (2006).

It should be noted that a lack of agreement exists within the IWC Scientific Committee on whether the abundance estimates from JARPA provide meaningful estimates of either absolute or relative abundance and whether the issues and concerns with the estimates are analytically resolvable (IWC 2008). The decision to include the abundance estimates within the reference case is not meant to reflect any judgement on the JARPA estimates. Our intention had been to provide a full set of sensitivity results with and without the JARPA estimates included. However, time and resources precluded this.

Sensitivity analyses

Sensitivity is explored to assuming that the values that determine growth, changes over time in carrying capacity, resilience, and natural mortality are the same for the two stocks. This was anticipated to improve the precision of the resultant estimates and to improve the stability (and between-stock consistency) of the statistical catch-at-age analysis. Sensitivity is also explored to excluding the JARPA indices of abundance from the objective function owing to uncertainty regarding whether these indices are linearly proportional to abundance (see above, IWC 2008). However, the JARPA age data are nevertheless included in the sensitivity analysis in which the index data are ignored. A further set of sensitivity tests explore the implication of negative bias (by 50%) in the estimates of abundance from IDCR/SOWER.

The sensitivity of the results of the reference case analysis to the assumption that age-estimates are unbiased with a CV of 0.1 is examined by assuming that ageing bias and the standard deviation of ageing error follow the form used by Richard *et al*. (1992) and Punt *et al*. (in press):

$$b_a = \begin{cases} b_L + (b_H - b_L)\dfrac{1-e^{-\lambda(a-L)}}{1-e^{-\lambda(H-L)}} & \text{if } \lambda \neq 0 \\ b_L + (b_H - b_L)\dfrac{a-L}{H-L} & \text{if } \lambda = 0 \end{cases} \tag{1}$$

where, for ageing bias, b_L is the expected age of an animal of true age *L*, b_H is the expected age of an animal of true age *H*, and λ determines the extent of non-linearity between age and the expected age. The ages *L* and *H* are set to 1 and 40 respectively. The standard deviation of age-reading for ages 41 and older are set to the standard deviation for age 40 to avoid extrapolating beyond the range of the data.

The values for the parameters of Equation 1 for ageing bias and ageing imprecision are based on fitting it to the results of the 1983 ageing experiment (Polacheck and Punt, 2008). Results are shown show different levels of constant aging error CV under the assumption that the age-estimates are biased.

Quantification of precision using MCMC

The priors for all parameters were assumed to be uniform within wide bounds for this exercise and new parameter vectors were generated based on samples from a multivariate normal distribution based on the current parameter vector and with a variance-covariance matrix set equal to the inverse of the Hessian matrix multiplied by a scalar (to achieve a "reasonable" acceptance rate).

Preliminary simulation evaluation of estimation ability

The operating model for the preliminary simulation evaluation is the reference case model. The pseudo data sets are generated based on the assumed effective samples sizes and survey coefficients of variation. Given limited computing resources, it was only possible to generate 10 data sets. However, this should be sufficient to assess grossly biased estimation (and hence provide a basis for the next steps). The estimators applied to these data sets are:

(a) the reference case estimator;
(b) a variant of the reference case analysis in which the vulnerability pattern for JARPA is assumed to be uniform while the vulnerability patterns for the commercial fisheries are assumed to be time-dependent logistic functions of length;
(c) a variant of the reference case analysis in which ageing error is ignored; and
(d) a variant of the reference case analysis in which growth, changes over time in carrying capacity and resilience are assumed to be the same for the two stocks.

Summary statistics

The summary statistics and plots for which results are reported (Table 5) represent a set of common output statistics to facilitate comparisons among alternative analyses of these data. The set of output statistics was developed by the authors in 2007 in conjunction with Butterworth and Mori, and then reviewed by the Intersessional Working Group on VPA Analysis.

RESULTS AND DISCUSSION

Should some of the parameters be shared between the W and E stocks?

Figures 1 and 2 show the time-trajectories of 1+ population size (Fig. 1) and other model outputs (Fig. 2, Table 5) for the reference case analysis. Table 6 lists the values for the summary statistics for this analysis. As expected from previous analyses, the reference case analysis indicates that the Southern Hemisphere minke whales increased from 1930 until the late 1960s and have subsequently declined. As in previous analyses (e.g. Punt and Polacheck, 2005, 2006, 2007), the model continues to predict large changes in carrying capacity and somatic growth rates. There are no obvious known sources or causes to associate with these changes (particularly the large decline in estimated carrying capacity between 1960 and 1980). This is a question that warrants further consideration. The IDCR/SOWER indices of absolute abundance (Fig. 2b) and the JARPA indices of relative abundance (Fig. 2a) are mimicked well by the model. The number of calves-per-mature females for the years prior to about 1970 from the reference case analysis is unrealistic for the E stock as these ratios exceed 1. One key reason for this is the high rate of natural mortality for animals aged 0-3 years (Table 6b).

Table 7 compares the fit of the reference case analysis and those of sensitivity tests in which some parameters are shared between the W and E stocks. It is not possible to use standard model selection methods to select among analyses in which growth is the same and which it differs for the W and E stocks, primarily because changing the number of growth parameters changes the number of penalty terms (see Equation App.33). Nevertheless, the contributions of only the data components to the objective function for the two formulations of the model are within a few likelihood points while the simpler model has 98 fewer parameters, which suggests that assuming that the growth, natural mortality, changes over time in carrying capacity, and resilience are the same for the W and E stocks is appropriate. Compared to the reference case analysis, the analysis in which parameters are shared leads to lower rates of natural mortality for all ages, but also to more realistic calves-per-mature female ratios. The lower rates of natural mortality for the "All shared" analysis also leads (as expected), to lower levels of recruitment (Fig. 1) and hence total (1+) population size, at least for the years prior to 1980. However, the estimates of total (1+) population size for the years for which estimates of abundance from IDCR/SOWER are available are not surprisingly also similar. One consequence of the lower rate of natural mortality for the "All shared" analysis is that MSYR (1+) is lower for the W stock (Table 6a). The asymptotic standard errors for natural mortality are, as expected, lower for the analysis in which parameters are shared among stocks, although the uncertainty in the estimates of natural mortality are estimated to be low (CV ~ 5-20% depending on age, lowest for the ages which make up the bulk of the catch and highest for the older and, particularly, the younger ages) irrespective of whether parameters are shared or not.

Further consideration of the sharing of parameters between the W and E stocks provides some insight into the source of the high rates of natural mortality for ages 0-3 in the reference case analysis (Table 6). For example, the change in the value of the objective function (9.1) for 3 additional parameters when only the natural mortality rate parameters are shared between stocks (Table 7), would indicate significant differences in natural mortality rates between the two stocks using standard model selection methods. The change in the number of parameters is not confounded by the change in the number of penalty terms in this case. In contrast, if only the growth parameters are shared between the two stocks, the estimates of natural mortality for ages 0-3 for the two stocks are essentially the same (a difference of only 0.007 yr^{-1}). The large changes in the estimates of natural mortality rates therefore appear to result from seemingly small changes to the growth parameters and the expected length-at-age. For this case, the difference in the objective function was 96.4 for 92 additional parameters (Table 7). Interestingly, the estimates of natural mortality rate for ages 0-3 are lower than the estimates for either of the two stocks in the reference case when growth parameters are shared with or without natural mortality being shared. These results suggest that it is the length-at-age data that are the source of the differences in natural mortality rates and that the results, particularly for the E stock, are highly sensitive to the estimated growth curves.

Impact of allowing for increased ageing error

The results are sensitive to how ageing error is treated. For example, increasing the coefficient of variation (of random age-reading error) from 10% to 30% leads to markedly higher natural mortality rates for animals of ages 0-3 and hence much higher recruitments (Figure 3). Recruitment and natural mortality increased substantially when aging error was increased to 20% and when growth and natural mortality rate parameters were shared between stocks (results not shown). The number of calves-per-mature females in the years prior to 1970 becomes unrealistically high for both stocks in the scenarios with higher random age reading error.

The results for stock W are qualitatively unchanged while there are marked changes in the results for stock E if both systematic ageing error and random age-reading error are included based on Model 1 from Polacheck and Punt (2008). The E stock recruitments and overall stock sizes are estimated to have been essentially flat from 1930 to 1960 (Figure 3) when allowance is made for ageing bias. The trajectories of total (1+) abundance for recent years are, however, insensitive to the treatment of ageing error. The changes in results when allowance is made for ageing bias (and greater age-reading error) are due to changes to the estimates of natural mortality (lower for both the youngest and oldest age-classes for stock W and markedly higher for the youngest ages and lower for the oldest ages for stock E). The fit of the model which allows for random and systematic ageing errors to the data is better than the reference case model by almost 100 likelihood points (Table 7).

Figure 4 contrasts the results for the variants of the reference and “with ageing bias” cases in which the parameters which determine natural mortality, changes over time in carrying capacity, resilience, and growth are assumed to be the same for stocks W and E. The differences among cases in Fig. 4 are much smaller than in Fig. 3 although differences do remain, particularly in recruitment, owing primarily to the estimate of natural mortality for animals ages 0-3 being higher when allowance is made for ageing bias and as well as age-reading error.

Other sensitivity tests

The results are not very sensitive to excluding the JARPA estimates of abundance from the objective function (Fig. 5; Table 6). Somewhat surprisingly, there is not a marked increase in the asymptotic standard errors when these data, but not the associated length- and age-composition data, are excluded from the objective function (Table 6). The total number of animals in the population is about twice the reference case values when it is assumed that the IDCR/SOWER estimates are negative biased by 50% (Fig. 5), but the estimates of other quantities are not markedly different from their reference case values for this sensitivity test.

Estimation of precision

The MCMC analyses of this paper are based on the sensitivity test in which natural mortality, growth, changes over time in carrying capacity, and resilience are assumed to be same between stocks to reduce the number of estimable parameters. Even so, 1,000,000 cycles of the MCMC algorithm took almost two weeks to run on fast desktop compute. Figure 6 shows traces for the objective function, for natural mortality, and for population size in 1930 (initial carrying capacity) and in 2002. The results in Figure 6 suggest that 1,000,000 cycles is insufficient for the parameter vectors to be IID samples from a Bayesian posterior distribution and that many more cycles would be needed for there to be a reasonable chance of finding results which satisfy normal MCMC convergence diagnostics.

Ignoring that Figure 6 suggests that convergence to the posterior distribution has not been achieved successfully, Figure 7 compares the asymptotic 90% confidence intervals for natural mortality-at-age and total (1+) numbers over time with the posterior distributions for these quantities. The asymptotic 90% confidence intervals tend to be wider than the Bayesian 90% credibility intervals, but, more importantly, there is a marked difference between the median time-trajectories of 1+ population size and the maximum likelihood estimates. Furthermore, the 90% probability intervals and the asymptotic 90% confidence intervals do not overlap.

Simulation evaluation

Given the limited number of simulations for each variant of the estimator, the results are summarized by plots which show the true values for natural mortality-at-age, the time-trajectory of total (1+) population size, and the time-trajectories of carrying capacity, and the estimates from the ten replicates (Figures 8a-d).

The estimates are close to the true values when the variant of the estimator which was used to generate the data sets is applied to the pseudo data sets (Figure 8a). In contrast, there are some noteworthy biases when selectivity is assumed to be logistic for the commercial fleets and uniform for JARPA when this is not the case (Figure 8b). Specifically, natural mortality is underestimated for stock W for all ages and for the young ages for stock E, carrying capacity is overestimated for stock W, while the size of the total (1+) population size before 1975 is underestimated for both stocks. The estimates are not markedly impacted by ignoring ageing error (note that ageing error is only 10% for these simulations) (Figure 8c). Sharing parameters between stocks performed fairly well although, as expected, it was impossible to estimate the difference in changes in carrying capacity between stocks (Figure 8d). As was the case for the estimator which made incorrect assumptions regarding selectivity, the estimator which shared resilience, growth and changes in carrying capacity between stocks underestimated natural mortality for the W stock for all ages and natural mortality for the young ages for the E stock (Figure. 8d).

General discussion and future work

The results reported in this paper again confirm the result from earlier studies that the recruitment of Southern Hemisphere minke whales in Areas III-W, IV, V and VI-W increased until about the early- to mid-1960s and declined thereafter. This result is generally robust to assumptions about whether parameters are shared among stocks, whether the JARPA indices of relative abundance are included in the analysis or not, and ageing error (if bounds are placed on between stock differences in parameters). As noted in the introduction, different conclusions regarding historical trends in population sizes were found in scenarios in which vulnerability had been assumed to be domed-shaped and age-based, although model fitting problems and biologically unrealistic parameters were often associated with these scenarios. As noted in Punt and Polacheck (2007), further investigation and discussion is required regarding the model fitting problems when vulnerability is assumed to be-age specific and whether the hypothesis that vulnerability is age-specific needs to be considered in the set of plausible hypotheses on which the final population modelling results are to be based.

The analyses of the paper have explored sensitivity to ageing bias as well as to random age-reading error. Estimates of natural mortality appear to be relatively sensitive to the amount of random aging error. Allowing for greater amounts of random ageing error as well as bias can result in the model producing unrealistic estimates of the number of calves per female. Inclusion of systematic age reading error also had marked effects on the pre-1970 estimates of recruitment and stock size for stock E, particularly when some of the biological parameters are not shared between stocks. The amount of systematic ageing error investigated was based on comparison of a limited sample of independent multiple age readings by different readers (Punt and Polacheck, 2008). What is not clear is if the range investigated provides a reasonable bound on the possible extent of systematic age reading error (see discussion in Polacheck and Punt, 2008) and whether the results for the W-stock would remain consistent with those for the reference case analysis if a larger range were considered. The sensitivity to uncertainties in the amount of aging error further emphasizes the need to better understand and characterize the nature of the relationship between the ear plug-based age estimates and true age.

It should be noted that all of the analyses are predicated on the assumption that any age-reading error is stationary, i.e. there has been no change in, for example, ageing bias over time. There is no direct evidence for such changes. However, changing aging biases would seem to be one plausible explanation for the marked differences in the age-at-length data that are seen with commencement of the JARPA catches and the rather unusual changes in growth required to fit the length-at-age data assuming that the age-estimates are unbiased. Future studies to examine age-reading error should consider this possibility explicitly, as it has the greatest potential to impact the qualitative (rather than just quantitative) outcomes from catch-at-age-based modelling approaches.

Sharing of at least the estimates of the growth parameters between stocks W and E appears to be needed for the model to provide realistic estimates of the number of calves per females prior to 1970 for the E stock (i.e. not “too high” natural mortality rates for ages 0-3). Whether this is a reasonable biological assumption is a question for discussion by the Scientific Committee. What remains unclear is why the age-length data for the E stock are insufficient to provide reliable estimates of the length-at-age relationship. It may be that the later commencement of regular commercial catches from the E stock compared to the W stock means that the available data are insufficient to provide reliable estimates of the stock’s dynamics for the earlier years.

The initial application of the MCMC algorithm led to pathological traces, and posterior distributions for time-trajectories of total (1+) population size that are markedly different from the maximum likelihood estimates (and the data). This indicates a serious problem with simple application of the MCMC algorithm for this (very) complicated model. These problems could be related to the parameters which determine the vulnerability patterns because it is known that these are often the source of problems when using MCMC to sample parameter vectors from posterior distributions for age-structured stock assessment models, particularly when some of the parameters are close to bounds, as is the case here (AEP, pers. obs). Future work should focus on the single stock case (stock W) and explore a sequence of models of increasing complexity to identify when pathological behaviour arises.

The results of the simulation analyses indicate that estimates of some of the quantities of interest are biased when incorrect assumptions are made regarding, for example, selectivity. However, in most cases, the estimator was capable of correctly identifying trends in 1+ abundance and (to a lesser extent) natural mortality. However, the ability to correctly estimate the exact magnitude of changes in carrying capacity can be poor as is the ability to estimate natural mortality for the youngest animals. The use of an estimator that has the same structure as the model used to generate the data mimics a bootstrap procedure. It is therefore noteworthy that the between-simulation variation in Figure 8a is larger than would be expected from the asymptotic standard errors in Figure 7, which suggests that the asymptotic standard errors may underestimate the true extent of parameter uncertainty (conditioned on a given model structure). Such under-estimation of standard errors is perhaps not unexpected because the estimation method is based on the errors-in-variable (EV) approach in contrast to the classical likelihood approach which requires integration over the state space parameters. The EV approach is known to yield inaccurate variance and confidence region estimates in some fishery population modelling situations (de Valpine and Hilborn, 2005). However, the behaviour of the EV approach with complex catch-at-age models such as that developed for minke whales is unknown. Thus, additional work to understand the statistical properties of the estimates from these catch-at-age models is needed if the results are to be used for probabilistic inferences. Also, further work to evaluate the performance of the estimators should consider other operating models (e.g. that in which the parameters are shared among stocks, ageing bias) and different estimators (e.g. that proposed by Mori *et al.*, 2007).

The population modelling work that has been completed strongly indicates that models of the type presented in this paper are likely to be able to provide a "reasonable" and "adequate" fit to whatever the likely set of input values (e.g. abundance, age readings) are deemed appropriate for use in the population modelling analyses. However, less clear, is how to resolve whether the parameter estimates, themselves, are providing plausible meaningful estimates. For example, as discussed above, the model results predict large changes in carrying capacity and somatic growth. There are no obvious known sources or causes to associate with these changes (particularly the large decline in estimated carrying capacity between 1960 and 1980). Similarly, it is not clear whether the predicted vulnerability patterns, their changes over time and the differences among fleets can be considered consistent with current perception of the biology and harvesting operations for minke whales (Punt and Polacheck 2007). If vulnerability patterns change over time (particularly for the youngest animals) for reasons other than operational effects, this would also have implications for the interpretation of the IDCR/SOWER abundance estimates and how they are used in the model. Interpretations of implications of the results of the population modelling work will remain an open question without discussion/resolution of these matters.

A primary motivation for the extensive population modelling work that has been done over the past several years was to provide a basis for evaluating the plausibility of the hypotheses that declines in the IDCR/SOWER abundance estimates are due to "a decrease in carrying capacity due to an increase in competition from other predators (e.g. other whales)". The model outcomes in this and all previous work predict large declines in estimated carrying capacity between 1960 and 1980, while declines in carrying capacity since 1980 are not required . The sensitivity analyses that have been conducted suggest that this result is robust to a large range of uncertainty in the model structure and input data. The model provides poor fits to the input data without allowance for declines during the 1960-1980 period. The estimated decline in carrying capacity can be viewed as a surrogate for possibility of other factors (e.g. a disease epidemic) effecting recruitment and natural mortality. Nevertheless, it seems unlikely that increased competition from other whales is a source given current understanding of the abundance trends of large whales in the Antarctic. A full examination of this issue would require integrating such trends in the model, along with plausible mechanisms, which is currently infeasible. Nevertheless, the Scientific Committee needs to consider what conclusions can be drawn from the current work or are likely from future work relative to the hypotheses that motivated it in the context of the motivation for undertaking the population modelling work and the priority for future work. In other words, what do the modelling results obtained to date suggest about the hypotheses that declines in the IDCR/SOWER abundance estimates are the result of a decrease in carrying capacity due to increases in other large whale abundances.

Finally, we would stress that the results in this paper, of course, remain preliminary, not only because of the lack of information to quantify ageing error, but also because the Scientific Committee has yet to finalize the estimates of abundance, their interpretation in terms of trends, their relationship to absolute population size, and how they should be treated within the catch-at-age modelling framework. In order for this work to meaningfully progress beyond a preliminary nature, it is imperative that a resolution is reached with respect to the inputs or set of inputs that should be used.

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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[2], 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:

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

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

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

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

K^{1+}_{2002} 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*. $C^{g,f}_{y,a}$ is computed using the formula:

$$C^{g,f}_{y,a} = \sum_{l} C^{g,f}_{y,a,l} \tag{App.8}$$

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

$$C^{g,f}_{y,a,l} = \begin{cases} \tilde{S}_a\, S^{g,f}_{y,l}\, X^{g}_{y,a,l}\, N^{g}_{y,a}\, F^{g,f}_{y} & \text{if vulnerability is length-specific} \\ \tilde{S}_a\, S^{g,f}_{y,a}\, X^{g}_{y,a,l}\, N^{g}_{y,a}\, F^{g,f}_{y} & \text{if vulnerability is age-specific} \end{cases} \tag{App.9}$$

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

$S^{g,f}_{y,a}$ 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,

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

$X^{g}_{y,a,l}$ 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:

$$S^{g,f}_{y,l} = 1 \tag{App.10a}$$

$$S_{y,l}^{g,f} = (1 + e^{-\ell n 19 (L_l - L_{50,y}^{g,f}) / L_{\text{diff}}^{g,f}})^{-1} \tag{App.10b}$$

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

$$S_{y,a}^{g,f} = 1 \tag{App.11a}$$

$$S_{y,a}^{g,f} = (1 + e^{-\ell n 19 (a - a_{50,y}^{g,f}) / a_{\text{diff}}^{g,f}})^{-1} \tag{App.11b}$$

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

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*:

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

$a_{50,y}^{g,f}$ 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*:

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

$\delta_y^{g,f}$ 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.:

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

The objective function

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

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

where $\ell n L_i$ is the contribution of the i[th] data source to the objective function,
P_j is the contribution of the j[th] 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[3], i.e.:

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

where $\tilde{C}^{g,f}_y$ 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.

[3] 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 A^{th} 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:

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

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.

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

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.:

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

$\tilde{C}_{y,a,l}^{g,f}$ 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 $a_{\max,y}$ [4] 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.:

$$P_1 = \frac{1}{2\sigma_R^2} \sum_y (\varepsilon_y)^2 \qquad \text{(App.30)}$$

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

$$P_2 = \frac{1}{2\sigma_S^2} \sum_g \sum_y \sum_f (\delta^{g,f}_y)^2 \qquad \text{(App.31)}$$

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.:

$$P_3 = \frac{1}{2\sigma_P^2} \sum_y \sum_A (\varphi^A_y)^2 \qquad \text{(App.32)}$$

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

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[4] 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.:

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

Table 1
Catches by sex and Area

Table 1(a) – pre-1971/72 catches

Year	Area III*		Area IV		Area V*		Area VI*	
	Female	Male	Female	Male	Female	Male	Female	Male
1953/54	1	0	0	0	0	0	0	1
1954/55	0	0	0	0	0	0	0	0
1955/56	8	4	3	2	1	1	2	2
1956/57	5	2	0	1	0	0	6	3
1957/58	127	54	49	21	17	5	50	31
1958/59	28	10	20	9	7	3	5	3
1959/60	51	21	35	15	28	9	2	1
1960/61	55	24	8	4	15	4	12	7
1961/62	0	1	0	0	0	0	0	0
1962/63	8	3	1	1	0	1	0	0
1963/64	3	1	51	43	2	0	0	0
1964/65	1	2	0	1	0	0	0	0
1965/66	4	5	0	0	0	1	1	0
1966/67	10	5	1	1	0	1	1	2
1967/68	27	73	327	273	1	0	1	0
1968/69	43	72	27	23	2	1	0	1
1969/70	84	102	7	4	2	1	0	0
1970/71	0	0	16	10	1	1	0	0

* - split equally between the eastern and western half-Areas.

Table 1(b) – catches 1970/71 – 1986/87

Year	Area III-E				Area IV				Area V-W				Area V-E				Area VI-W			
	Japan		Soviet Union		Japan		Soviet Union		Japan		Soviet Union		Japan		Soviet Union		Japan		Soviet Union	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
1971/72	184	170	0	0	1728	929	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1972/73	0	0	351	298	975	1116	1172	1294	0	0	0	0	0	0	0	0	0	0	0	0
1973/74	818	260	86	50	1282	761	1526	1000	0	0	0	0	0	0	0	0	3	10	0	0
1974/75	751	519	0	0	410	430	913	477	310	190	165	69	0	0	0	0	0	0	0	0
1975/76	604	417	757	376	237	198	215	231	160	260	154	57	0	0	0	0	0	0	0	0
1976/77	940	445	1176	313	432	518	251	399	495	515	375	82	0	0	0	0	0	0	0	0
1977/78	614	398	656	133	353	128	359	123	316	298	189	27	22	32	0	0	83	156	74	110
1978/79	958	642	542	175	573	386	285	126	104	69	168	73	0	0	0	0	0	0	5	5
1979/80	395	308	641	132	482	1048	202	129	113	383	687	161	0	0	0	0	0	0	0	0
1980/81	292	327	343	275	664	529	841	352	330	105	132	114	156	34	335	42	99	100	10	48
1981/82	71	188	485	380	1043	582	0	0	779	369	0	0	11	18	0	0	67	218	0	0
1982/83	0	0	638	464	490	530	741	207	1480	416	0	0	0	0	0	0	170	137	319	150
1983/84	0	0	105	158	518	589	631	357	945	436	0	0	56	8	0	0	349	126	0	0
1984/85	0	0	377	142	364	137	659	328	573	337	0	0	0	0	0	0	92	277	0	0
1985/86	0	0	0	0	292	222	664	229	670	343	0	0	0	0	0	0	97	300	0	0
1986/87	0	0	41	21	321	193	628	322	851	162	0	0	0	0	0	0	285	129	0	0

Table 1(c) – catches by Japan post 1986/87

Year	Area III-E		Area IV		Area V-W		Area V-E		Area VI-W	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
1987/88	0	0	119	153	0	0	0	0	0	0
1988/89	0	0	0	0	0	0	151	85	0	0
1989/90	0	0	142	184	0	0	0	0	0	0
1990/91	0	0	0	0	77	110	68	54	14	0
1991/92	0	0	123	165	0	0	0	0	0	0
1992/93	0	0	0	0	87	118	53	45	20	4
1993/94	0	0	130	200	0	0	0	0	0	0
1994/95	0	0	0	0	27	113	103	87	0	0
1995/96	41	68	126	204	0	1	0	0	0	0
1996/97	0	0	0	0	72	55	80	77	82	74
1997/98	36	75	123	204	0	0	0	0	0	0
1998/99	0	0	0	0	88	95	34	111	20	41
1999/00	46	63	160	170	0	0	0	0	0	0
2000/01	0	0	0	0	45	95	73	87	64	76
2001/02	56	54	183	147	0	0	0	0	0	0
2002/03	0	0	0	0	46	54	116	114	43	67
2003/04	48	62	192	138	0	0	0	0	0	0
2004/05	0	0	0	0	47	35	137	75	79	67

Table 2
Summary of the age-composition data (number of animals aged and number of animals measured from the catch by Japan)

Year	Area III-E				Area IV			
	Age-composition		Length-frequency (Japan)		Age-composition		Length-frequency (Japan)	
	F	M	F	M	F	M	F	M
1971/72	12	6	184	170	487	235	1728	929
1972/73	0	0	0	0	413	418	975	1116
1973/74	250	85	818	260	436	272	1282	761
1974/75	468	285	751	519	235	257	410	430
1975/76	169	100	604	417	114	71	237	198
1976/77	352	146	940	445	156	168	432	518
1977/78	254	148	614	398	194	67	353	128
1978/79	643	439	958	642	428	274	573	386
1979/80	283	211	395	308	355	781	482	1048
1980/81	252	250	292	327	544	417	664	529
1981/82	62	149	71	188	864	491	1043	582
1982/83	0	0	0	0	392	398	490	530
1983/84	0	0	0	0	380	385	518	589
1984/85	0	0	0	0	303	110	364	137
1985/86	0	0	0	0	247	188	292	222
1986/87	0	0	0	0	293	177	321	193
1987/88	0	0	0	0	99	135	119	153
1988/89	0	0	0	0	0	0	0	0
1989/90	0	0	0	0	118	155	142	184
1990/91	0	0	0	0	0	0	0	0
1991/92	0	0	0	0	102	143	123	165
1992/93	0	0	0	0	0	0	0	0
1993/94	0	0	0	0	102	173	130	200
1994/95	0	0	0	0	0	0	0	0
1995/96	36	54	41	68	98	176	126	204
1996/97	0	0	0	0	0	0	0	0
1997/98	36	63	36	75	91	168	123	204
1998/99	0	0	0	0	0	0	0	0
1999/00	34	48	46	63	145	147	160	170
2000/01	0	0	0	0	0	0	0	0
2001/02	45	49	56	54	157	131	183	147
2002/03	0	0	0	0	0	0	0	0
2003/04	35	53	48	62	169	111	192	138
2005/05	0	0	0	0	0	0	0	0

(Table 2 Continued)

	Area V-W				Area V-E				Area VI-W			
	Age-composition		Length-frequency (Japan)		Age-composition		Length-frequency (Japan)		Age-composition		Length-frequency (Japan)	
Year	F	M	F	M	F	M	F	M	F	M	F	M
1971/72	0	0	0	0	0	0	0	0	0	0	0	0
1972/73	0	0	0	0	0	0	0	0	0	0	0	0
1973/74	0	0	0	0	0	0	0	0	1	4	3	10
1974/75	145	54	310	190	0	0	0	0	0	0	0	0
1975/76	66	132	160	260	0	0	0	0	0	0	0	0
1976/77	263	237	495	515	0	0	0	0	0	0	0	0
1977/78	209	191	316	298	19	24	22	32	23	45	83	156
1978/79	93	54	104	69	0	0	0	0	0	0	0	0
1979/80	81	257	113	383	0	0	0	0	0	0	0	0
1980/81	257	71	330	105	119	28	156	34	68	78	99	100
1981/82	548	256	779	369	10	15	11	18	49	157	67	218
1982/83	1109	303	1480	416	0	0	0	0	130	98	170	137
1983/84	717	316	945	436	48	6	56	8	279	87	349	126
1984/85	485	274	573	337	0	0	0	0	79	240	92	277
1985/86	596	311	670	343	0	0	0	0	77	250	97	300
1986/87	743	143	851	162	0	0	0	0	242	112	285	129

(Table 2 Continued)

	Area V-W				Area V-E				Area VI-W			
	Age-composition		Length-frequency (Japan)		Age-composition		Length-frequency (Japan)		Age-composition		Length-frequency (Japan)	
Year	F	M	F	M	F	M	F	M	F	M	F	M
1987/88	0	0	0	0	0	0	0	0	0	0	0	0
1988/89	0	0	0	0	122	64	151	85	0	0	0	0
1989/90	0	0	0	0	0	0	0	0	0	0	0	0
1990/91	67	101	77	110	65	50	68	54	14	0	14	0
1991/92	0	0	0	0	0	0	0	0	0	0	0	0
1992/93	78	112	87	118	49	42	53	45	17	4	20	4
1993/94	0	0	0	0	0	0	0	0	0	0	0	0
1994/95	25	99	27	113	88	72	103	87	0	0	0	0
1995/96	0	1	0	1	0	0	0	0	0	0	0	0
1996/97	64	51	72	55	69	70	80	77	72	66	82	74
1997/98	0	0	0	0	0	0	0	0	0	0	0	0
1998/99	64	51	72	55	32	90	34	111	12	38	20	41
1999/00	0	0	0	0	0	0	0	0	0	0	0	0
2000/01	34	81	45	95	62	78	73	87	59	62	64	76
2001/02	0	0	0	0	0	0	0	0	0	0	0	0
2002/03	37	48	46	54	100	98	116	114	32	54	43	67
2003/04	0	0	0	0	0	0	0	0	0	0	0	0
2004/05	43	35	47	35	120	65	137	75	67	58	79	67

Table 3
The estimates of abundance

(a) IDCR Estimates

Year	Estimate	Year	Estimate
Area III-E		Area IV	
1979/80	80 551 (0.381)	1978/79	130 333 (0.178)
1987/88	37 428 (0.426)	1988/89	84 815 (0.288)
1994/95	20 465 (0.238)	1998/99	13 409 (0.279)
Area V-W		Area V-E	
1980/81	78 093 (0.470)	1980/81	164 993 (0.328)
1985/86	77 194 (0.249)	1985/86	172 828 (0.147)
1991/92	10 055 (0.282)	1991/92	187 266 (0.210)
2001/02	46 169 (0.174)	2001/02	100 658 (0.170)
Area VI-W			
1983/84	67 161 (0.227)		
1990/91	8 394 (0.294)		
1995/96	33 323 (0.230)		

(b) JARPA indices of relative abundance

Area III-E		Area IV		Area V-W	
Year	Estimate	Year	Estimate	Year	Estimate
1995/96	10 262 (0388)	1989/90	48 167 (0.203)	1990/91	56 381 (0.210)
1997/98	5 618 (0.637)	1991/92	52 467 (0.274)	1992/93	41 922 (0.227)
1999/00	12 940 (0.837)	1993/94	41 398 (0.192)	1994/95	20 113 (0.248)
2001/02	54 717 (0.488)	1995/96	42 363 (0.203)	1996/97	23 719 (0.241)
2003/04	35 241 (0.352)	1997/98	25 922 (0.220)	1998/99	84 405 (0.319)
		1999/00	44 931 (0.151)	2000/01	19 608 (0.321)
		2001/02	48 280 (0.188)	2002/03	100 775 (0.205)
		2003/04	44 564 (0.291)	2004/05	38 790 (0.192)

Area V-E		Area VI-W	
Year	Estimate	Year	Estimate
1990/91	105 409 (0.248)	1996/97	12 533 (0.317)
1992/93	82 137 (0.282)	1998/99	38 355 (0.296)
1994/95	143 596 (0.256)	2000/01	21 873 (0.261)
1996/97	118 335 (0.256)	2002/03	12 358 (0.297)
1998/99	40 755 (0.277)	2004/05	18 700 (0.247)
2000/01	141 389 (0.210)		
2002/03	75 210 (0.201)		
2004/05	53 387 (0.177)		

Table 4
The estimable parameters of the population dynamics model and the objective function.

Parameter	Number of parameters	
	Stock W	**Stock E**
Calves in the absence of exploitation, B_0	1	1
Natural mortality: M_0, M_1/M_0, M_2/M_1	3	3*
Resilience, A	1	1*
Survival deviation, ε_y	76	76
Expected proportion in each Area, $\overline{P^{s,A}}$	2	1
Annual deviations about the expected proportions in each area, φ_y^A	63	31
Exploitation rate by year, sex and fleet, $F_y^{g,f}$	267	108
Changes in carrying capacity, $\tilde{K}_I^{1+}$, $\tilde{K}_{2002}^{1+}$	2	2*
Parameters of the growth curve, L_∞^g, k^g, t_0^g, σ_γ^g	8	8*
Inter-annual deviations in growth rate, υ_y	84	84*
Parameters to vulnerability, $L_{50,y}^{g,f}$, $\delta_y^{g,f}$, $L_{dff}^{g,f}$, $L_{\text{left}}^{g,f}$, $L_{\text{right}}^{g,f}$	152	76
JARPA survey bias, χ	3	2
Total	**662**	**393**

* The values for these parameters are set equal to those for Stock W in the analyses in which parameters are shared among stocks.

Table 5

The summary statistics and plots reported in this paper

(a) Statistics

$b_{rec,1945\text{-}68}$ - slope of the linear regression of the estimates of the logarithms of the numbers of recruits (age 1 animals) on time (1945-68).
$b_{rec,1968\text{-}88}$ - slope of the linear regression of the estimates of the logarithms of the numbers of recruits on time (1968-88).
$b_{rec,1988\text{-}End}$ - slope of the linear regression of the estimates of the logarithms of the numbers of recruits on time (1988-last year).
$N_{tot,1945\text{-}68}$ - slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1945-68).
$N_{tot,1968\text{-}88}$ - slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1968-88).
$N_{tot,1988\text{-}Endr}$ - slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1988-last year).
$N_{\text{End-5,1}}/N_{1968,1}$ – Ratio of the number of recruits in 1999 to that in 1968.
K_{1930} – Carrying capacity in 1930.
K_{2000}/K_{1960} – ratio of K in 2000 to that in 1960.
K_{1960}/K_{1930} – ratio of K in 1960 to that in 1930.
Natural mortality (ages 0-3, 10-30, 35+)
Average proportions in each management area
Survey q for JARPA.
MSYR (1+)

(b) Plots

Total (1+) population size versus year (by stock and by area)
Age 1 animals (recruits) versus time
Carrying capacity versus year (*)
Natural mortality versus age (*)
Number of females beyond the age-at-first parturition (*)
Number of calves as a fraction of the number of females beyond the age-at-first parturition (*)
Selectivity-at-age (*)
Selectivity-at-length (*)
Brody growth coefficient versus year (*)

* Final reference runs only

Table 6

Results of the reference case analysis and the analyses to examine the sensitivity of the results to modifying some of the assumptions of the analysis method. The asymptotic standard errors for the estimates for natural mortality are given in parenthesis.

(a) Stock W

Case	b_{rec}			N_{tot}							Natural mortality (ages)			JARPA q / Mean proportion			MSYR
	1945-68	1968-88	1988-End	1945-68	1968-88	1988-End	$N_{End\text{-}5,1}$/ $N_{1968,1}$	K_{1930}	K_{2000}/ K_{1960} (%)	K_{1960}/ K_{1930} (%)	0-3	10-30	35+	III-E	IV	V-W	
Reference	2.462	-6.161	0.934	3.447	-5.502	-0.899	0.391	101722	23.2	461.9	0.087 (0.015)	0.085 (0.004)	0.172 (0.009)	1.225	1.351	1.919	0.057
All shared	4.310	-4.730	0.453	4.940	-3.492	-0.990	0.426	52151	24.2	1000.0	0.055 (0.011)	0.066 (0.002)	0.162 (0.006)	0.881	0.919	1.473	0.038
M shared	3.024	-5.967	0.857	4.039	-5.117	-0.927	0.390	73474	23.9	624.3	0.091	0.079	0.166	1.190	1.297	1.860	0.055
Growth shared	3.087	-5.743	0.930	4.097	-4.926	-0.877	0.404	70705	24.8	635.9	0.079	0.079	0.165	1.174	1.275	1.847	0.054
M and growth shared	3.113	-5.737	0.921	4.107	-4.909	-0.878	0.404	70199	24.9	638.9	0.079	0.078	0.166	1.175	1.275	1.847	0.054
Ageing error	-0.655	-3.762	1.427	2.355	-4.613	0.070	0.470	105380	36.0	331.4	0.013	0.063	0.079	0.910	1.012	1.520	0.093
Ageing error – shared	1.065	-2.778	0.939	3.640	-2.922	0.048	0.462	53907	43.7	725.4	0.127	0.048	0.060	0.727	0.764	1.392	0.067
30% ageing error CV	4.433	-9.060	0.473	5.069	-6.986	-1.822	0.231	69512	13.6	1000.0	0.255	0.080	0.400	1.664	1.767	2.413	0.054
No JARPA	2.306	-6.200	0.887	3.222	-5.585	-1.042	0.370	115439	22.7	406.4	0.080 (0.014)	0.086 (0.005)	0.175 (0.010)	N/A	N/A	N/A	0.024
50% IDCR Bias	2.183	-5.546	0.865	3.135	-4.837	-1.058	0.430	208073	25.5	394.0	0.082	0.088	0.176	0.623	0.671	0.966	0.058
50% IDCR bias shared	3.013	-4.945	0.827	4.012	-4.060	-0.960	0.459	124604	28.3	605.0	0.075	0.080	0.167	0.595	0.630	0.929	0.056

(Table 6 Continued)

(b) Stock E

Case	b_{rec}			N_{tot}			$N_{End-5,1}$/ $N_{1968,1}$	K_{1930}	K_{2000}/ K_{1960} (%)	K_{1960}/ K_{1930} (%)	Natural mortality (ages)			JARPA q / Mean proportion		MSYR
	1945-68	1968-88	1988-End	1945-68	1968-88	1988-End					0-3	10-30	35+	V-E	VI-W	
Reference	3.394	-5.862	0.147	3.397	-2.360	-1.910	0.297	88142	11.7	1000.0	0.200 (0.030)	0.077 (0.004)	0.167 (0.013)	1.120	1.298	0.023
All shared	3.792	-5.493	1.060	4.244	-1.294	-1.728	0.356	53322	24.2	1000.0	0.055 (0.011)	0.066 (0.002)	0.162 (0.006)	0.903	1.048	0.038
M shared	3.534	-5.456	0.740	3.653	-1.691	-1.822	0.339	74189	15.1	1000.0	0.091	0.079	0.166	1.030	1.200	0.026
Growth shared	3.603	-6.205	0.854	3.824	-1.999	-1.933	0.315	72965	15.2	1000.0	0.085	0.077	0.169	1.036	1.214	0.028
M and growth shared	3.616	-6.214	0.889	3.852	-2.002	-1.935	0.315	72566	15.3	1000.0	0.079	0.078	0.166	1.035	1.213	0.028
Ageing error	-1.402	-7.937	-0.734	-0.368	-4.474	-3.061	0.307	504966	8.5	0.0	0.249	0.079	0.095	1.086	1.338	0.000
Ageing error – shared	1.645	-4.550	1.508	3.807	-1.519	-0.581	0.742	48909	43.7	725.4	0.127	0.048	0.060	0.876	0.952	0.067
30% ageing error CV	2.628	-8.744	-0.966	2.488	-4.640	-2.725	0.201	161547	4.2	1000.0	0.364	0.077	0.385	1.506	1.804	0.017
No JARPA	3.415	-5.764	0.248	3.417	-2.247	-1.865	0.307	86043	12.1	1000.0	0.190 (0.030)	0.076 (0.004)	0.167 (0.013)	N/A	N/A	0.024
50% IDCR Bias	3.400	-5.802	0.173	3.401	-2.270	-1.901	0.301	173301	11.8	1000.0	0.195	0.076	0.167	0.559	0.647	0.023
50% IDCR bias shared	3.605	-6.318	0.906	3.881	-2.058	-1.991	0.309	145376	15.1	1000.0	0.075	0.080	0.167	0.520	0.611	0.029

Table 7
Objective function values and number of estimable parameters for the analyses of this paper

Case	Parameters shared	Objective function	Number of parameters
Reference	None	16654.3	1050
All Shared	All	16505.3	952
M shared	*M*	16663.4	1047
Growth shared	Growth	16750.7	958
M and growth shared	*M* and growth	16750.8	955
Model 1 Ageing error	None	16564.2	1050
Model 1Ageing error – shared	All	16443.3	952
30% ageing error CV	None	16393.3	1050
No JARPA*	None	16663.7	1003
50% IDCR bias	None	16656.4	1050
50% IDCR bias – shared	*M* and growth	16753.7 **	955

* Objective function not comparable with reference case.
** May not have converged fully.

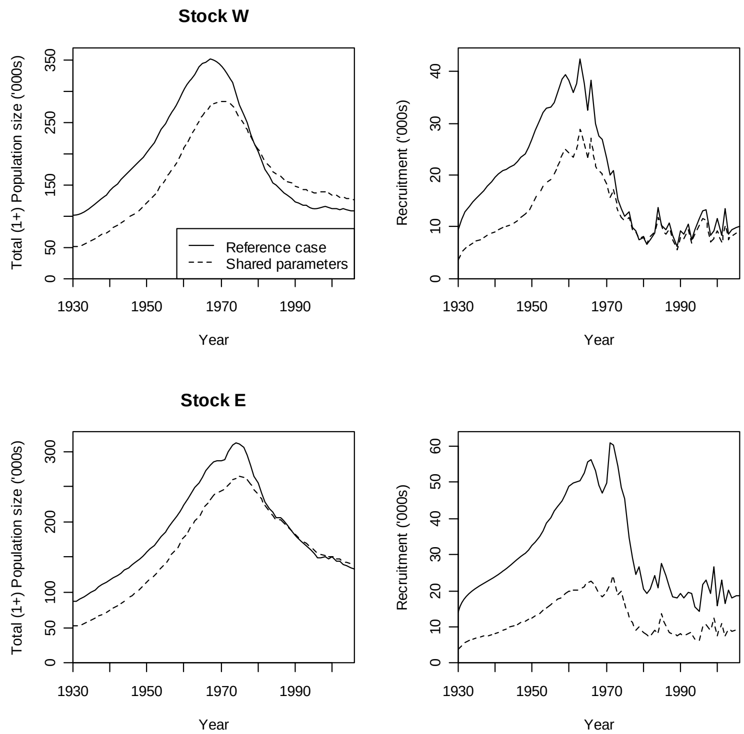


Figure 1: Time-trajectories of total (1+) population size and recruitment for the reference case analysis and the sensitivity test in which natural mortality, growth, resilience and changes over time in carrying capacity are assumed to be the same for the two stocks.

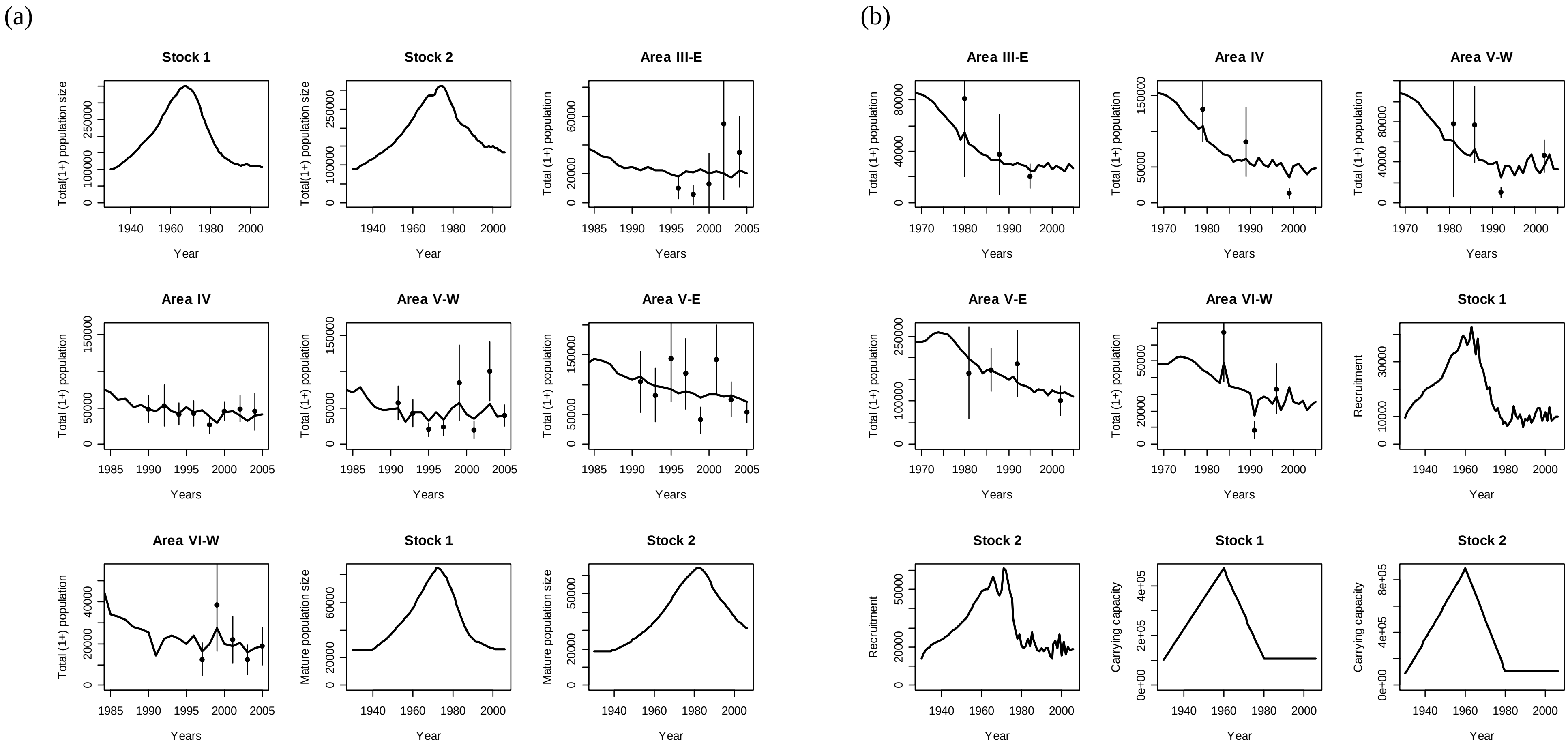
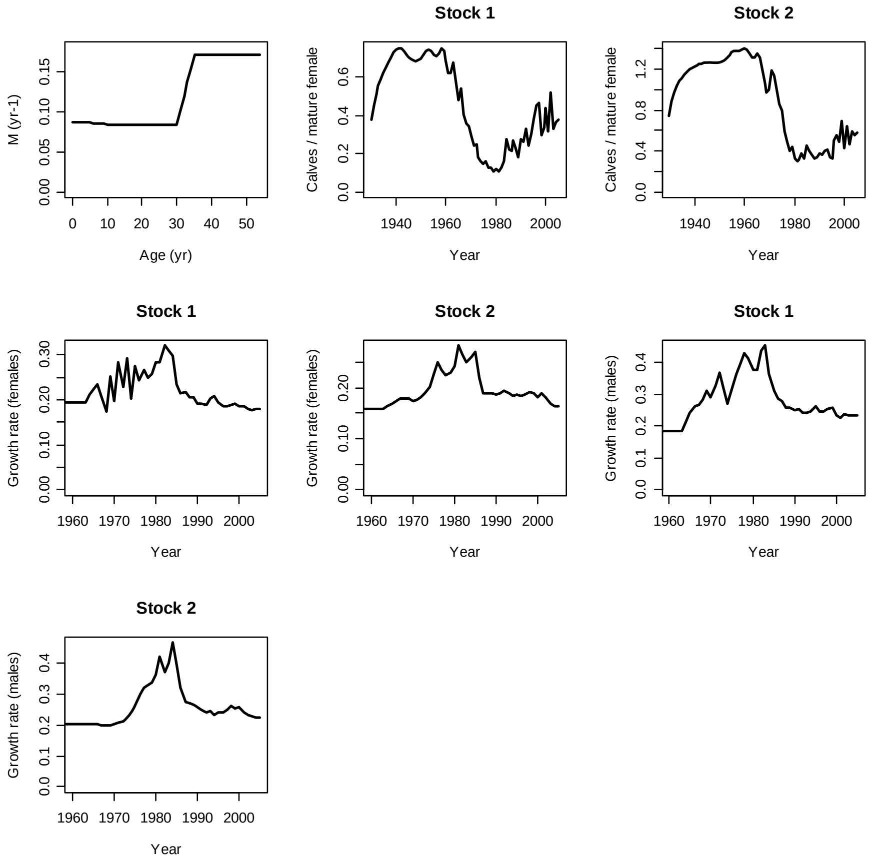


Figure 2. Detailed model outputs for the reference case analysis.

(Figure 2 Continued)

(c)



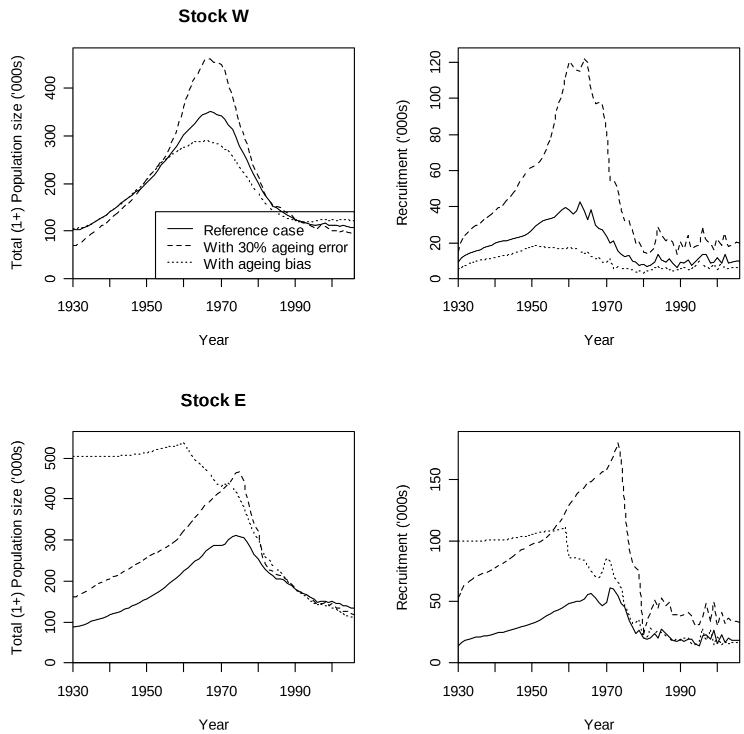


Figure 3. Time-trajectories of total (1+) population size and recruitment for the reference case analysis and the sensitivity tests in which allowance is made for (a) random age-reading error with a CV of 30%, and (b) random age-reading error and ageing bias according to model #1 of Polacheck and Punt (2008).

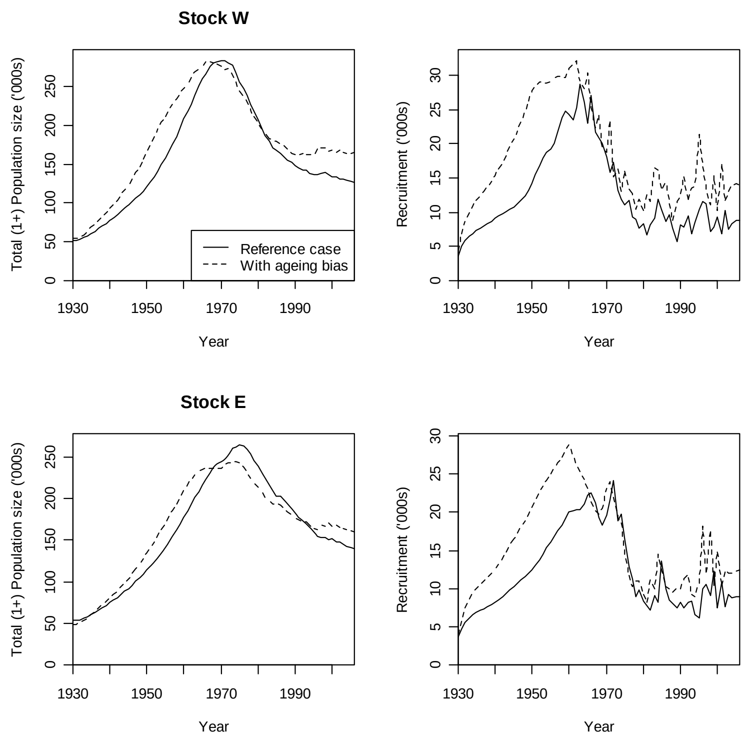


Figure 4. Time-trajectories of total (1+) population size and recruitment for the variants of the reference case analysis and the sensitivity test in which allowance is made for both random age-reading error and ageing bias, in which natural mortality, changes over time in carrying capacity, resilience and growth are assumed to be the same for the two stocks.

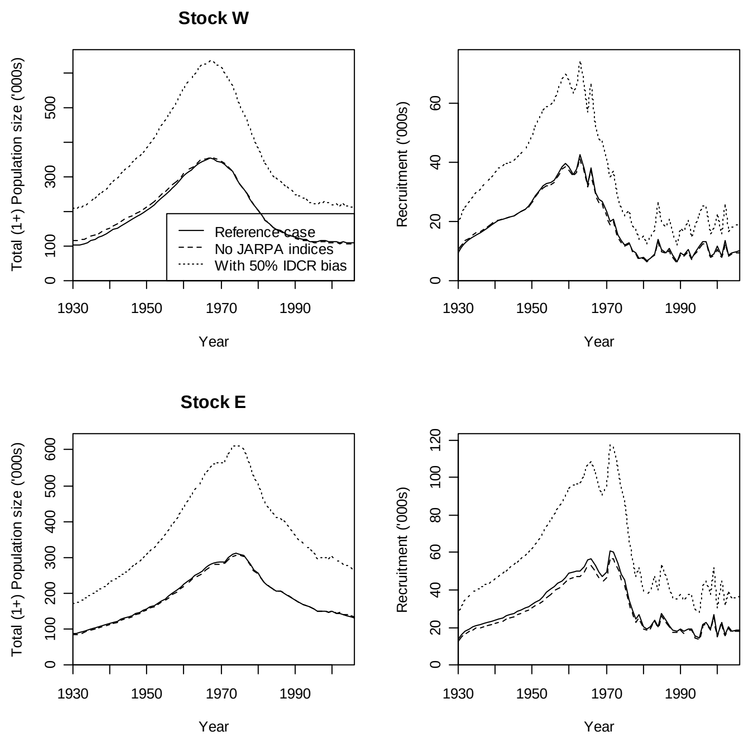


Figure 5. Time-trajectories of total (1+) population size and recruitment for the reference case analysis and the sensitivity tests in which (a) the JARPA indices of abundance are ignored, and (b) the IDCR/SOWER estimates of abundance are assumed to be subject to 50% negative bias.

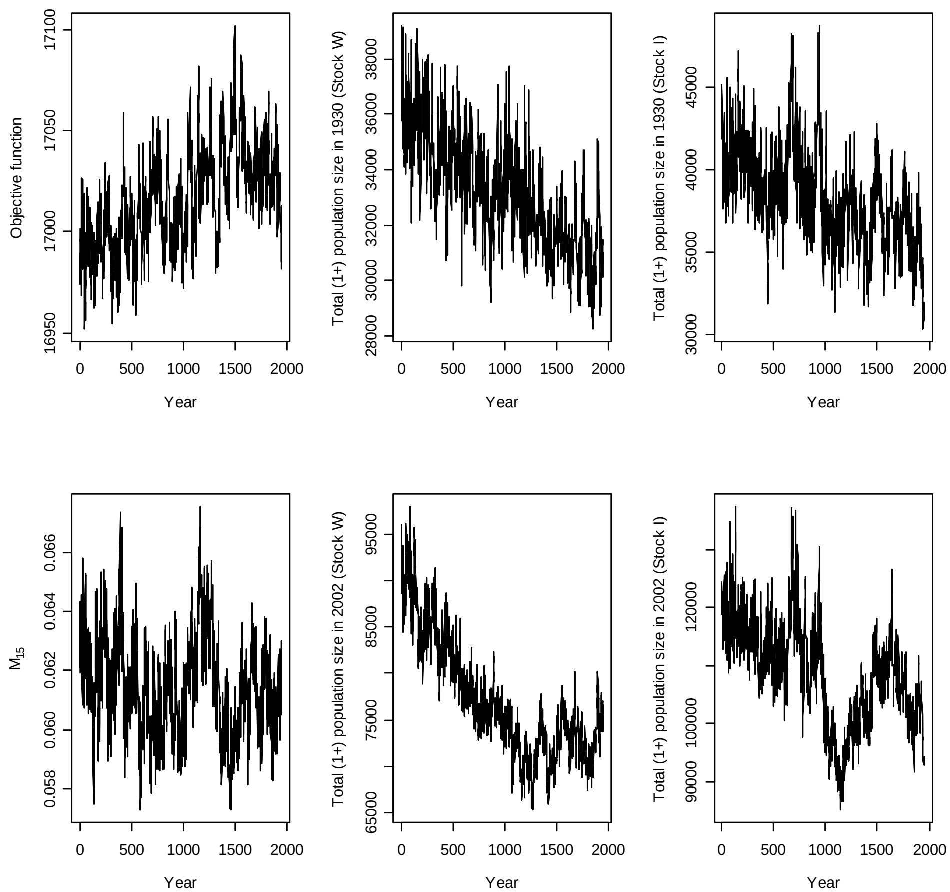


Figure 6. Trace plots for the objective function and five model outputs from the application of the MCMC algorithm to the model variant in which parameters are shared between the two stocks.

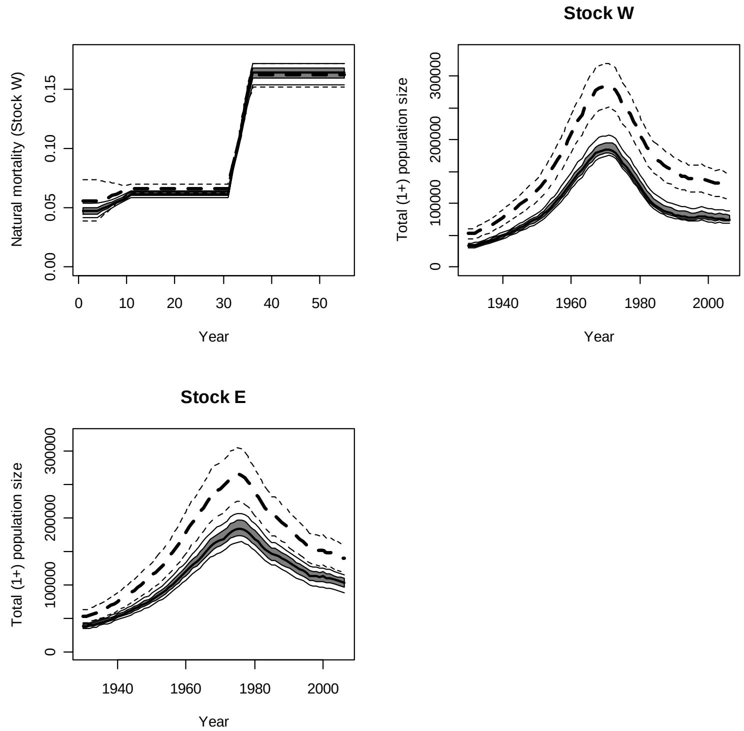


Figure 7. Posterior distributions (posterior median wide solid line; central posterior 50% intervals shaded region; 90% credibility intervals narrow solid lines) for natural mortality-at-age and the time-trajectory of total (1+) population size. The dashed lines indicate the maximum likelihood estimates and the asymptotic 90% confidence intervals for these quantities.

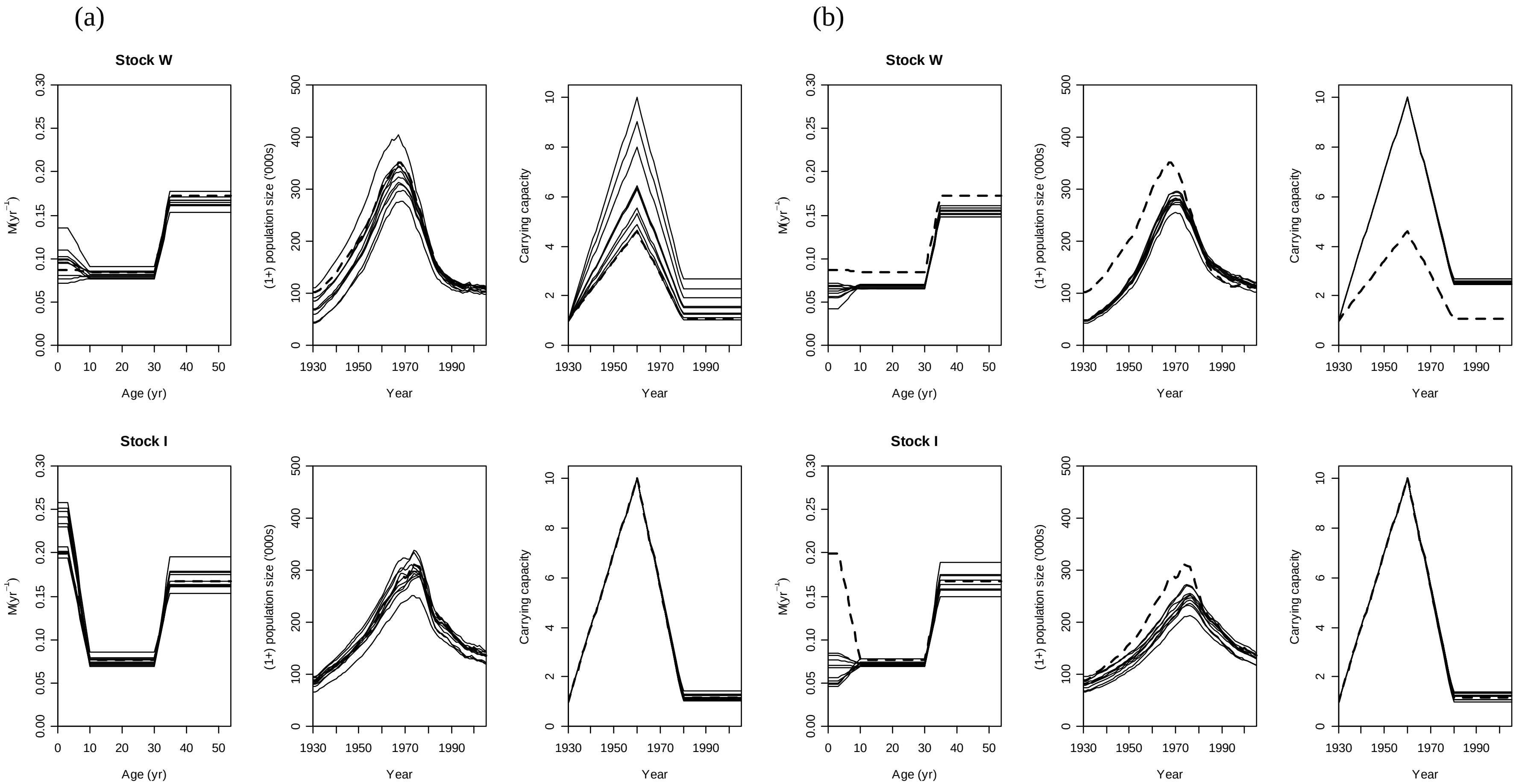
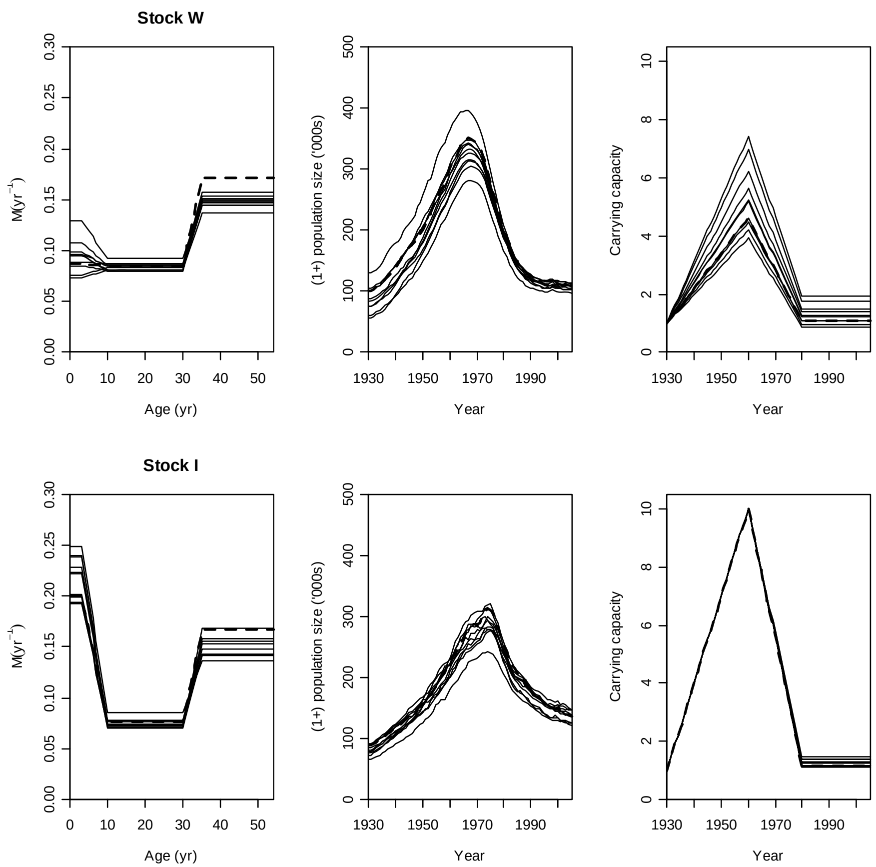


Figure 8. Outcomes of the simulation experiment. The wide dashed lines indicate the true values for natural mortality, total (1+) population size, and changes over time in carrying capacity, while the light solid lines indicate the outcomes from 10 simulated data sets (note that what appears to be a wide solid line in some figures is due to the close proximity of several closely spaced light solid lines reflecting the simulation results with nearly identical results). Results are shown in (a) for the reference case estimator, in (b) for an estimator with simpler assumptions about vulnerability, in (c) for an estimator that ignores ageing error, and in (d) for an estimator with shares resilience, growth, and changes in carrying capacity between stocks.

(Figure 8 continued)

(c)



(d)