The sensitivity to assumed ageing error of the stock assessment used to recommend lake whitefish yield for 2008 from management unit WFH01 of Lake Huron.

# QFC Technical Report 2011-01 

June 22, 2012

Matthew J. Catalano and James R. Bence<br>Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, 138 Giltner Hall, East Lansing, Michigan 48824; email: mcatalan@msu.edu; phone: 517-355-0126


#### Abstract

Age-structured fish stock assessment models are fitted to catch-age data and therefore ageing errors could influence management advice based on these methods. Lake whitefish (Coregonus clupeaformis) populations within much of the U.S. waters of Lake Huron are assessed annually using age-structured assessments, which are used to recommend appropriate yields. We calculated values of ageing error for Lake Huron lake whitefish consistent with paired scale and otolith ages under the assumption that production aging was based on scales and otolith ages represented true age. We evaluated the potential effect of these errors on the stock assessment that was used to recommend appropriate lake whitefish yield for management unit WFH01 of Lake Huron in 2008. Given substantial uncertainty regarding the appropriateness of our ageing error model for describing actual aging error, we also explored how sensitive assessments were when results were adjusted for different levels of ageing error and bias. Our analysis of scale and otolith ages suggested ageing bias associated with scale-


based ages (treating otolith-based ages as true) declined from an upward bias of +1.4 yrs at age 4 to +0.7 yrs for ages $10+$, while ageing noise was constant across ages with a standard deviation of 1.01 yrs. Incorporating these ageing errors into the stock assessment resulted in an 11 to $16 \%$ decline in the recommended yield relative to a model that did not account for ageing errors. Using different levels of noise and bias to adjust stock assessment showed that results were sensitive to the magnitude of these errors and that the effects of adjusting for ageing error could even change in direction dependent on the magnitude of error. We suspect that these specific results depend in part on abundance at age present in the last modeled year, so the specific results should not be generalized to other years and stocks. An examination of how well the assessment models fit, depending on the error structure that was assumed, show that models with constant ageing error across ages and no bias fit better than either the status quo model without aging error or the adjustment based on our analysis of scale-otolith ages. This suggests an intriguing possibility that bias in aging error might be estimable during fit of the model and that treating otolith ages as known may be suggesting more bias than is really the case. While the results of this pilot study are not definitive, they clearly show that what is assumed about aging error can have important effects. We recommend that the influence of aging error on assessment results be explored further using simulations.

## Introduction

Age-structured stock assessment models, such as statistical catch-at-age analysis (SCAA), rely on accurate age composition data to estimate fish abundance, harvest rates, and life history parameters. Errors in age assignment (ageing error) may result in biased age composition data and stock estimates, which could lead to errors in management targets such as total allowable catch (TAC; Reeves, 2003). The form and magnitude of ageing error may have implications for the performance of age structured assessments used to set TACs or otherwise recommend fishery management actions. Ageing error takes on two forms: bias and noise. Bias is systematic error in age assignment whereby fish of true age $a$ are assigned ages that consistently deviate from the true age in either a positive (over-ageing) or negative direction (under-ageing). Noise is random uncertainty in assigned age given true age.

Lake whitefish (Coregonus clupeaformis) populations in much of the U. S. waters of the Laurentian Great Lakes are managed by TACs or other fishery management actions such as effort limitations to achieve recommended yields that do not exceed levels that would create a high risk of spawning stock biomass falling below levels needed for adequate reproduction (Ebener et al., 2005). These TACs or recommended yields (for brevity TACs and recommended yield are jointly referred to as TAC for the rest of this report) are determined from biomass, mortality, and gear selectivity estimates obtained from the most recent SCAA model. The form and magnitude of ageing error, and their effects on stock assessment-based TACs and other parameters used for management advice are not well understood for these populations. There is concern that the use of scales as the primary ageing structure could result in substantial amounts of ageing error. Moreover, lake whitefish growth has declined since the early 1990s and the amount of ageing error is thought to be inversely related to fish growth rates. To address these
issues, we investigated (1) the magnitude of ageing bias and noise for lake whitefish in Lake Huron, and (2) the effect of ageing error on age-structured stock assessments and resulting TACs, using the stock assessment from management unit WFH01 of Lake Huron used to recommend a yield for 2008 as an example.

## Methods

## Approach

Our approach was to first obtain estimates of ageing error bias and noise for lake whitefish from Lake Huron that were consistent with paired scale-otolith ages, an assumption that production ages used scales, and that otolith ages are true ages. We did this by fitting ageing error models that predict scale age (assigned age) as a function of the otolith age (assumed true age) for a sample of fish that were double-aged with scales and otoliths. Ageing error matrices were computed from these estimates and for several additional hypothetical ageing error scenarios. Ageing error matrices were used within the SCAA stock assessment model for WFH01, which had been used to recommend yield for 2008, to adjust the predicted catches-atage for ageing error. The effects of adjusting for ageing error on the assessments and resulting TACs was evaluated by comparing the results of the stock assessments that adjusted for ageing error, with the results of the original assessment, which used a model that did not adjust for ageing error.

## Ageing Error Estimates

We estimated ageing error bias and noise for Lake Huron lake whitefish using data from individual fish that were aged using both scales and otoliths under the assumption that otolith age
represented the true age. Lake whitefish were collected with gill and trap nets in May to October 2000 and 2006 from commercial fisheries and fishery-independent surveys. These fish ranged from otolith age 2 up to age 20. The lake whitefish assessment for management unit WFH01 considered seven age classes: $4-10+$; the last age class served as a plus group representing all fish age-10 or greater. Thus, for this analysis, we aggregated all otolith age 10 and greater fish into an age-10+ group for the ageing error analysis. Sample sizes for young fish were sparse, so we included age 2 and 3 fish in the analysis despite their exclusion from the stock assessment because these age classes could easily be excluded from the ageing error matrices before their inclusion in the stock assessment models (see SCAA Models and TAC, below).

Ageing error was based on models that related scale age (b) as a function of otolith age (a) under varying assumptions regarding the functional form of the relationship and following the general approach of Richards et al. (1992). The expected value of scale age given otolith age ( $\mathrm{E}\{b \mid a\}$ ) was modeled as either a linear or power function of otolith age, with intercept $\beta 0$ and slope $\beta 1$ for the former case, and coefficient $\beta 0$ and exponent $\beta 1$ for the latter. The distribution of scale age given otolith age was modeled as either a normal or gamma distribution with mean $\mathrm{E}\{b \mid a\}$ and variance $\sigma_{a}^{2}$. The standard deviation of scale age $\sigma_{a}$ was modeled as either a linear or power function of otolith age, with intercept $\beta 0_{\sigma}$ and slope $\beta 1_{\sigma}$ for the former case, and coefficient $\beta 0_{\sigma}$ and exponent $\beta 1_{\sigma}$ for the latter. Each four-parameter model was fit using maximum likelihood assuming that the observed scale age frequencies for a given otolith age were multinomially distributed with probability vector $p_{a}$. The probability vector was computed for a given otolith age $a$ by integrating over scale ages from $b-0.5$ to $b+0.5$ for each integer value of $b$ using the appropriate cumulative distribution function (normal or gamma) with expected value $\mathrm{E}\{b \mid a\}$ and variance $\sigma^{2}{ }_{a}$. The probability for the plus group (age-10+) was
computed by integrating over scale ages from $b=9.5$ to $\infty$. Given a working assumption that production ages are based on scales and otolith ages were correct, these probability vectors provided distributions of observed ages given true age. We fit eight models representing all possible combinations of functional forms and distributional assumptions and used Akaike's information criterion (AIC) to select the best-fitting model. We also explored reduced-parameter models to test whether ageing bias (i.e., $\mathrm{E}\{b \mid a\}-a$ ) and standard deviation varied over otolith ages (i.e., bias $\mathrm{H}_{0}: \beta 1=1.0 ; \sigma_{a} \mathrm{H}_{0}: \beta 1_{\sigma}=0$ ).

Ageing error matrices were computed for the best-fitting model for the scale-otolith data and for the hypothetical ageing error scenarios. We used a range of hypothetical scenarios both because there is substantial uncertainty about our assumption that otolith ages represent true ages, and to explore the general sensitivity of the assessment to aging error. The ageing error matrix is a matrix of probabilities that an individual fish of otolith age $a$ (rows) is assigned a scale age $b$ (columns). The ageing error matrix for the best-fitting model was constructed by assembling the maximum likelihood estimates of the multinomial probability vectors for each otolith age $\left(p_{a}\right)$ as the rows of the matrix. Ageing error matrices for hypothetical scenarios were constructed by specifying the appropriate parameters of the ageing error model and carrying out the probability calculations as previously described.

## SCAA Models and TAC

The basis for our analyses was a SCAA model that was used to recommend the 2008 lake whitefish yield (TAC) for management unit WFH01 by fitting to data collected through 2006. Briefly, the model estimated annual age-4 recruitments, annual fishing effort deviations for gill and trap net fisheries, time-varying gear selectivity parameters for both fisheries, and stock-
recruitment parameters. The model was fit to observed age composition, commercial catch, and effort data for both fisheries. The model considered seven age classes: 4-10+, with the last class serving as a plus group representing all fish age-10 or greater. Natural mortality, fecundity, maturity and weight-at-age were estimated external to the model and input as known quantities. Gear selectivity was modeled with a double logistic function and was allowed to trend over time according to quadratic function. The TACs were estimated by projecting the estimated whitefish population forward through the next fishing season, accounting for fishing and expected natural mortality and projecting the associated harvest and yield. The fishing mortality rates in these projections were adjusted to match an upper bound on total annual mortality $(A)$ of 0.65 .

We fit eleven different SCAA models, each representing a different assumption about the magnitude of ageing error bias and noise. Ageing error was incorporated into the stock assessments by multiplying the model-predicted catch-at-age by an ageing error matrix representing one of the 11 ageing error scenarios using the general approach of Fournier and Archibald (1982). The ageing error matrices were computed as previously described in Ageing Error Estimates, above). Ageing error matrices were treated as known without error.

The baseline SCAA model assumed no ageing error (ageing error matrix $=$ identity) and was identical to the stock assessment that was used to recommend the 2008 TAC. Model 2 adjusted for ageing error by assuming estimates of ageing error, calculated as described in Ageing Error Estimates (above), represented the magnitude of ageing error that was present throughout the time series. Model 3 assumed ageing error bias and standard deviation before 1992 was $50 \%$ of the current estimates. This scenario attempted to address the concern that lake whitefish growth rates have declined since the early 1990s and the magnitude of ageing error is inversely related to growth rate. The reduction percentage of $50 \%$ was arbitrarily chosen, but
was an attempt to characterize this hypothetical case in the absence of data from the early time period.

In addition to refitting the SCAA model using levels of aging error consistent with the analysis of scale-otolith ages, the SCAA model was fit with a range of hypothetical levels of bias and standard deviation for noise to explore how incorporating these levels of error influenced estimates. Models 4-7 represented increasing ageing noise and were characterized by error standard deviations of $0.25,0.5,1.0$, and 2.0 years, but with no ageing bias. Ageing error matrices for these models were computed such that ageing error was unbiased, constant across ages, and had a standard deviation of the appropriate value. This was accomplished by assuming a linear relationship between assigned age and true age with an intercept of 0 yrs, slope of 1.0, and a normal distribution for assigned age given true age with a standard deviation set at the appropriate value. Models $8-11$ represented increasing ageing bias in the presence of a modest amount of ageing noise (sigma $=0.25 \mathrm{yr}$ ) from a bias of $0.25,0.5,1.5$, and 2.5 years. We added this noise so that fractional amounts of bias (e.g. 0.5 yrs ) were meaningful. Ageing error matrices for these models were computed such that the ageing error had the appropriate amount of bias, was constant over ages, and had a standard deviation of 0.25 yrs. This was accomplished by assuming a linear relationship between assigned age and true age with an intercept representing the appropriate amount of bias, slope of 1.0, and age-invariant normally-distributed assigned age given true age with $\sigma=0.25$ yrs.

## Results

Ageing Error Estimates

A total of 202 lake whitefish were aged by scales and otoliths for use in the ageing error analysis. Sample sizes for lake whitefish less than age 10 were small $(n=49)$ relative to the number of fish in the age-10+ group $(n=153)$. Across all ages, scale ages for lake whitefish younger than otolith age 10 were positively biased whereas scale ages for fish greater than age 10 were negatively biased (Figure 1). Ageing error models, which were fit to aggregated data with an age 10+ plus group, suggested that aging error bias, but not noise, depended on fish age. The best-fitting model estimated the expected scale age as a linear function of otolith age and assumed a normal distribution for scale age given otolith age with a constant standard deviation (Table 1). From the best-fitting model, expected bias (i.e., $\mathrm{E}\{b \mid a\}-a$ ) declined with age from +1.4 yrs at age 4 (i.e., otolith age) to 0.7 yrs at age 10 . Noise was constant across ages with a standard deviation of 1.01 yrs . To illustrate the magnitude of ageing error based on these estimates, consider that the scale age for an otolith age-6 lake whitefish would have a $95 \%$ prediction interval of $5-9$ yrs. Model-predicted frequencies of scale-aged fish for a given otolith age matched the observed data reasonably well but model fit for young age classes (i.e., < 8 yrs ) was difficult to ascertain because of small sample sizes (Figure 2).

## SCAA Models and TAC

Adjusting for ageing error within the lake whitefish stock assessment model affected parameter estimates and TACs in complex and unpredictable ways. Adjusting for ageing noise had relatively modest effects on estimated recruitment, biomass, and gear selectivity, whereas adjusting for ageing bias had greater effects on these quantities (Figures 3, 4, 6, and 7). Adjusting for ageing noise increased the relative magnitude of recruitment peaks, thereby making recruitment appear more variable from year to year (Figure 3b) compared to the baseline
stock assessment (Model 1). Adjusting for ageing bias caused a general decline in the magnitude of estimated recruitment along with shifting estimated recruitment peaks to later years, but did not affect the relative magnitude of the peaks (Figure 3c). Incorporating observed levels of uncertainty (Model 2), which included moderate bias and noise, resulted in a general decrease in the magnitude of recruitment across years but also a large estimated recruitment peak in 2003 that was not produced by any of the other models (Figure 3a). Assuming less ageing error before 1992 (Model 3) resulted in similar recruitment estimates as Model 2 (Figure 3a).

Biomass estimates were generally lower when adjusting for ageing error, and these effects were more severe for bias than noise (Figure 4). For example, adjusting for a bias of +2.5 years resulted in biomass estimates that were less than $50 \%$ of baseline estimates in some years (Figure 4c). Incorporating observed levels of ageing error (Model 2) resulted in substantially lower biomass estimates early in the time series but recent estimates were close to the baseline model (Figure 4a). Assuming less ageing error before 1992 (Model 3) produced biomass estimates that were more similar to the baseline model early in the time series, but recent estimates were similar to Model 2 and the baseline (Figure 4a). Gill and trap net estimated selectivity generally shifted toward younger age classes when adjusting for ageing error (Figures 5 and 6). This effect was most pronounced for ageing bias than for noise and for gill net (Figure 5) than for trap net selectivity (Figure 6).

Total annual mortality estimates were generally higher than the baseline model when adjusting for bias and noise (Figure 7). However, mortality estimates were close to the baseline estimates for all but the most severe cases of ageing error. The models of observed ageing errors (Models 2 and 3) produced total annual mortality estimates that were similar to baseline estimates in recent years.

Adjusting for ageing errors resulted in an increase in the TAC for moderate amounts of ageing error, but as ageing error increased, a dome shaped pattern was revealed whereby TAC declined below the baseline TAC at very high levels of bias and noise (Figure 8). Adjusting for observed amounts of ageing error (Model 2) resulted in a modest decrease in the estimated TAC suggesting that the baseline TAC may have been overly optimistic by approximately $16 \%$. If ageing error was less prior to 1992 (Model 3) then the baseline TAC was overly optimistic by $11 \%$.

There were substantial differences among the stock assessment models that made different adjustments for ageing error in how well they matched observed data. Model 6, which assumed no ageing bias and moderate ageing noise ( $\sigma=1.0 \mathrm{yrs}$ ), fit the observed data better than the other models we tested (Table 2). None of the top- 5 best-fitting models assumed ageing bias of more than +0.25 yrs. The worst-fitting models were those that adjusted for large amounts of ageing bias. The observed ageing error models (Models 2 and 3) were in the bottom half in terms of model fit suggesting that these scenarios were less plausible than the low-moderate noise/low bias scenarios, based on the observed age composition, catch, and effort data. These findings disagreed with our estimates of ageing error from the otoliths vs. scales analysis.

## Discussion

Our study suggests that if ageing error levels are close to those estimated based on the scale-otolith analysis then adjusting for aging error in the stock assessment could have a modest influence on estimated stock sizes and exploitation rates for the 2006 assessment and resulting 2008 TAC for management unit WFH01. Specifically, the 2008 TAC may have been too high because it did not properly account for ageing error. We must take care in drawing general
conclusions from these results about the effects of aging error on lake whitefish assessments in the Great Lakes for several reasons.

First, our analysis considered a single assessment year (and TAC) for a single management unit. Conclusions regarding other assessment years and management units would be invalid because they are outside the scope of this analysis. It is clear that the effect of adjusting for ageing error should depend in principle on the actual age composition of the stock. Thus, for example, although accounting for observed ageing error in our analysis resulted in a decrease in the 2008 TAC, we have no reason to believe that similar levels of ageing error applied to an earlier assessment for WFH01 would produce the same result, or would produce similar results for other stocks.

Second, our analysis accounted for effects of ageing error on the age composition data only and did not consider effects on other age-based inputs such as maturity and weight-at-age estimates. Under positive ageing bias (over-ageing) weights-at-age that ignore ageing error would be underestimated. Therefore, adjusting for ageing error would result in an increase in the mean weight of an age class, which would adjust biomass estimates upwards. An increase in estimated biomass could result in a higher TAC, which could counteract the decreased TAC attributable to the ageing error adjustment to the age composition. Maturity-at-age (i.e., proportion mature) would be underestimated if ageing error was ignored, which could affect spawning stock biomass estimates.

It is generally accepted that ageing error can introduce bias into stock assessments and management advice. Some modern stock assessments account for ageing error by using ageing error matrices to adjust predicted catches-at-age as we did in our analysis (e.g., Courtney et al., 1999; Dorn et al., 2003; Bence et al., 2011). However, surprisingly few studies have attempted
to make general inferences concerning the effects of aging error on stock assessments. One possible explanation for this is that ageing error effects are stock- and time-specific. Reeves (2003) is one of the few peer-reviewed studies to use a simulation approach to assess the expected effects of ageing error on age-structured stock assessments. Reeves (2003), which used Baltic Sea cod stocks as an example, found that all types of ageing error tended to cause management advice to be overly optimistic. However, the effects of ageing error on spawning stock biomass estimates varied substantially among individual realizations of the simulation. This finding suggests that ageing error effects on a stock assessment for a particular year may deviate from the expectation of an overly-optimistic TAC.

We attempted to assess the influence of changes in the magnitude of ageing error over time by exploring a scenario in which ageing error was lower early in the time series. This approach required selection of an arbitrary reduction in ageing error (i.e. 50\%). Although this reduction is a reasonable starting point, we have no information from which to assess changes in ageing error over time. Length-at-age data for lake whitefish clearly show declining growth since the 1980s but the relationship between ageing error and fish growth rates remains unclear for these populations. Samples of double-aged fish from early in the time series, which to our knowledge do not exist, would be required to fully investigate this phenomena and conduct a more informed assessment of ageing error effects on TACs.

The scale vs. otolith ages analysis rested on the assumption that otolith ages represented the true age. Anecdotal evidence suggests that otolith ages for young lake whitefish may underestimate the true age as has been seen in other species (M. Ebener, personal communication). If this is the case, then our scale vs. otoliths ageing error analysis would overestimate ageing bias for young fish. Unfortunately, further investigation of this potential
problem is difficult without an analysis of otoliths of known-age lake whitefish, which has not been attempted to our knowledge. Regardless of the accuracy of otolith ages, the ageing error analysis would benefit from an increase in the sample size of age- 2 to 8 fish, which would improve precision of ageing error estimates.

We found that assessment fits to the observed data were influenced by the adjustments for ageing error. This suggests that it may be possible to estimate ageing error parameters as part of the assessment process. This is not a new idea (Fournier and Archibald 1982) but has proven difficult to accomplish for some applications. Even if all the ageing error parameters prove difficult to estimate solely internally to the assessment, this result is promising because it may be possible to estimate noise externally based on repeat ageing of structures and estimate bias internally. Estimating bias externally based on aging of multiple structures (e.g., otoliths and scales) is problematic, because it requires assuming one structure provides true ages.

## Future Analyses

One possible next step would be to repeat our analysis using data from other management units to assess the spatial generality of the results. Retrospective analyses conducted on a stock-by-stock basis would reveal the temporal generality of our findings. Together these might suggest whether adjustment for aging error has any general tendency to either increase or decrease TACs or produce other systematic effects. Another route for investigation, which we believe would be more definitive, would be a simulation study, which would provide estimates of the effects of ageing error that would be more general that the results of our analysis on WFH01. With this approach, we would generate data representing various ageing error scenarios and fit assessment models that make adjustments for ageing error to test the
performance of the adjustments at reducing parameter bias due to ageing error. By repeating these simulation-estimation experiments many times, we could begin to understand the expected effects of aging error along with estimates of uncertainty in these responses. We could also use such simulations to explore the extent to which ageing error can be estimated internally to the assessment.

## References

Bence, J., S. Sitar, and M. Ebener. 2011. Stock Assessment Models. Pages 5-16 in: D.C. Caroffino and S.J. Lenart (eds), Statistical catch-at-age models used to describe the status of lean lake trout populations, a report prepared by the 1836 Treaty Waters Modeling Subcommittee for Technical Fisheries Committee, Parties to the 2000 Consent Decree, and the Amici Curiae.

Courtney, D. L., J. Heifetz, M. F. Sigler \& D. M. Clausen, 1999. An age-structured model of northern rockfish, Sebastes polyspinis, recruitment and biomass in the Gulf of Alaska. Alaska Fisheries and Science Center, National Marine Fisheries Service, Juneau, Alaska.

Dorn, M., S. Barbeaux, M. Guttormsen, B. Megrey, A. Hollowed, M. Wilkins \& K. Spalinger, 2003. Assessment of Walleye Pollock in the Gulf of Alaska. Alaska Fisheries and Science Center, National Marine Fisheries Service, Juneau, Alaska.

Ebener, M. P., J. R. Bence, K. R. Newman \& P. J. Schneeberger, 2005. Application of statistical catch-at-age models to assess lake whitefish stocks in the 1836 treaty-ceded waters of the upper Great Lakes. In Mohr, L. C. \& T. F. Nalepa (eds.), Proceedings of a workshop on the dynamics of lake whitefish (Coregonus clupeaformis) and the amphipod Diporeia spp. in the Great Lakes. Great lakes Fishery Commission Technical Report 66.

Fournier, D. \& C. P. Archibald, 1982. A general theory for analyzing catch at age data. Canadian Journal of Fisheries and Aquatic Sciences 39: 1195-1203.

Reeves, S. A., 2003. A simulation study of the implications of age-reading errors for stock assessment and management advice. ICES Journal of Marine Science 60: 314-328.

Richards, L. J., J. T. Schnute, A. R. Kronlund \& R. J. Beamish, 1992. Statistical-models for the analysis of aging error. Canadian Journal of Fisheries and Aquatic Sciences 49: 18011815.

Table 1. Models relating scale age (b) to otolith age (a) that were fit to data from lake whitefish that were aged with scales and otoliths. All models shown here assumed scale ages were normally-distributed given otolith age.

| Functional Form |  | $\beta 0$ | $\beta 1$ | $\beta 0_{\sigma}$ | $\beta 1_{\sigma}$ | $\Delta \mathrm{AIC}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{E}\{b \mid a\}$ | $\sigma_{a}$ |  |  |  |  |  |
| linear | constant; $\mathrm{B} 1{ }_{\mathrm{\sigma}}=0$ | 1.82(0.39) | 0.89(0.05) | 1.01(0.11) |  | 0 |
| linear; $\beta 1=1$ | constant; $\beta 1_{\text {o }}=0$ | 1.04(0.15) |  | 1.16 (0.10) |  | 1.91 |
| linear | linear | 1.84(0.40) | 0.89(0.05) | 1.07(0.31) | -0.01(0.04) | 1.94 |
| linear | power | 1.82(0.40) | 0.89(0.05) | 1.06(0.42) | -0.03(0.20) | 1.98 |
| power | linear | 1.88(0.24) | 0.75(0.06) | 1.27(0.32) | -0.03(0.04) | 5.32 |
| power | power | 1.85(0.24) | 0.76(0.06) | 1.41(0.54) | -0.17(0.20) | 5.34 |

Table 2. Negative log likelihoods of the SCAA models representing different assumption regarding the magnitude and type of ageing error. The parameters of the scale-otolith age model used to compute the ageing error matrix are shown for each model. The ageing error matrix for each model can be found in Appendix A.

|  | Ageing Error Parameters |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- |
| Model | $\beta 0$ | $\beta 1$ | $\beta 0_{\sigma}$ | $\beta 1_{\sigma}$ | $-\ln (L)$ |
| (6) noise: sd=1.00 | 0.00 | 1.00 | 1.00 | 0.00 | $8,109.87$ |
| (5) noise: sd=0.50 | 0.00 | 1.00 | 0.50 | 0.00 | $8,194.53$ |
| (8) bias: +0.25 | 0.25 | 1.00 | 0.25 | 0.00 | $8,197.71$ |
| (4) noise: sd=0.25 | 0.00 | 1.00 | 0.25 | 0.00 | $8,207.42$ |
| (1) no ageing error | 0.00 | 1.00 | 0.00 | 0.00 | $8,207.77$ |
| (9) bias: +0.50 | 0.50 | 1.00 | 0.25 | 0.00 | $8,215.02$ |
| (2) full ageing error | 1.82 | 0.89 | 1.01 | 0.00 | $8,306.88$ |
| (3) 50\% ageing error pre-1992 | 0.91 | 0.95 | 0.50 | 0.00 | $8,427.60$ |
| (7) noise: sd=2.00 | 0.00 | 1.00 | 2.00 | 0.00 | $8,796.10$ |
| (10) bias: +1.50 | 1.50 | 1.00 | 0.25 | 0.00 | $11,289.60$ |
| (11) bias: +2.50 | 2.50 | 1.00 | 0.25 | 0.00 | $18,290.30$ |



Figure 1. Scale age (y axis) vs. otolith age (x axis) for a lake whitefish from Lake Huron aged by both scales and otoliths. The dots are jittered to reveal the number of samples. The fine dashed line depicts the 1:1 line for reference.


Figure 2. Observed (dots) and model-predicted (lines) frequency distribution of scale ages (x axis) for a given otolith age (different panels). Note the two orders of magnitude variation in sample size among panels. Note that the SCAA models that adjusted for ageing error considered only age classes 4 to $10+$.


Figure 3. Time series of age-0 lake whitefish recruitment estimates from 11 stock assessment models that adjusted for varying types and amounts of ageing error. Each panel contains the estimated time series for the baseline model that did not adjust for ageing error (solid line; model 1). The upper panel shows estimates from two models (models 2 and 3 ) that adjusted for estimated amounts of ageing error from an analysis of lake whitefish that were double-aged with scales and otoliths. The middle and lower panels show results of hypothetical scenarios representing unbiased ageing with varying levels of noise (middle panel) and nearly noiseless errors with varying degrees of bias (lower panel).


Figure 4. Time series of age-0 lake whitefish biomass estimates from 11 stock assessment models that adjusted for varying types and amounts of ageing error. Each panel contains the estimated time series for the baseline model that did not adjust for ageing error (solid line; model 1). The upper panel shows estimates from two models (models 2 and 3 ) that adjusted for estimated amounts of ageing error from an analysis of lake whitefish that were double-aged with scales and otoliths. The middle and lower panels show results of hypothetical scenarios representing unbiased ageing with varying levels of noise (middle panel) and nearly noiseless errors with varying degrees of bias (lower panel).


Figure 5. Age-specific gill net selectivity estimates for lake whitefish in 2006 from 11 stock assessment models that adjusted for varying types and amounts of ageing error. Each panel contains the estimates for the baseline model that did not adjust for ageing error (solid line; model 1). The upper panel shows estimates from two models (models 2 and 3) that adjusted for estimated amounts of ageing error from an analysis of lake whitefish that were double-aged with scales and otoliths. The middle and lower panels show results of hypothetical scenarios representing unbiased ageing with varying levels of noise (middle panel) and nearly noiseless errors with varying degrees of bias (lower panel).


Figure 6. Age-specific trap net selectivity estimates for lake whitefish in 2006 from 11 stock assessment models that adjusted for varying types and amounts of ageing error. Each panel contains the estimates for the baseline model that did not adjust for ageing error (solid line; model 1). The upper panel shows estimates from two models (models 2 and 3) that adjusted for estimated amounts of ageing error from an analysis of lake whitefish that were double-aged with scales and otoliths. The middle and lower panels show results of hypothetical scenarios representing unbiased ageing with varying levels of noise (middle panel) and nearly noiseless errors with varying degrees of bias (lower panel).


Figure 7. Time series of age-0 lake whitefish total annual mortality estimates from 11 stock assessment models that adjusted for varying types and amounts of ageing error. Each panel contains the estimated time series for the baseline model that did not adjust for ageing error (solid line; model 1). The upper panel shows estimates from two models (models 2 and 3) that adjusted for estimated amounts of ageing error from an analysis of lake whitefish that were double-aged with scales and otoliths. The middle and lower panels show results of hypothetical scenarios representing unbiased ageing with varying levels of noise (middle panel) and nearly noiseless errors with varying degrees of bias (lower panel).


Figure 8. 2008 TACs (projected from the 2006 assessment) from 11 stock assessment models that adjusted for varying types and amounts of ageing error.

Appendix A. Ageing error matrices used to adjust for ageing error within the SCAA models.

| Model | True Age | Assigned Age |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 4 | 5 | 6 | 7 | 8 | 9 | 10+ |
| (1) no ageing error | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | 5 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
|  | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
|  | 7 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
|  | 8 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
|  | 9 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
|  | $10+$ | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| (2) full ageing error | 4 | 0.16 | 0.37 | 0.33 | 0.12 | 0.02 | 0 | 0 |
|  | 5 | 0.04 | 0.18 | 0.37 | 0.3 | 0.1 | 0.01 | 0 |
|  | 6 | 0 | 0.05 | 0.2 | 0.38 | 0.28 | 0.08 | 0.01 |
|  | 7 | 0 | 0.01 | 0.06 | 0.23 | 0.38 | 0.25 | 0.08 |
|  | 8 | 0 | 0 | 0.01 | 0.07 | 0.25 | 0.38 | 0.29 |
|  | 9 | 0 | 0 | 0 | 0.01 | 0.08 | 0.28 | 0.63 |
|  | 10+ | 0 | 0 | 0 | 0 | 0.01 | 0.1 | 0.89 |
| (3) $50 \%$ ageing error pre-1992 | 4 | 0.35 | 0.6 | 0.06 | 0 | 0 | 0 | 0 |
|  | 5 | 0.01 | 0.38 | 0.56 | 0.04 | 0 | 0 | 0 |
|  | 6 | 0 | 0.02 | 0.42 | 0.53 | 0.03 | 0 | 0 |
|  | 7 | 0 | 0 | 0.02 | 0.46 | 0.5 | 0.03 | 0 |
|  | 8 | 0 | 0 | 0 | 0.03 | 0.49 | 0.46 | 0.02 |
|  | 9 | 0 | 0 | 0 | 0 | 0.03 | 0.53 | 0.44 |
|  | $10+$ | 0 | 0 | 0 | 0 | 0 | 0.04 | 0.96 |
| (4) noise: $\mathrm{sd}=0.25$ | 4 | 0.98 | 0.02 | 0 | 0 | 0 | 0 | 0 |
|  | 5 | 0.02 | 0.95 | 0.02 | 0 | 0 | 0 | 0 |
|  | 6 | 0 | 0.02 | 0.95 | 0.02 | 0 | 0 | 0 |
|  | 7 | 0 | 0 | 0.02 | 0.95 | 0.02 | 0 | 0 |
|  | 8 | 0 | 0 | 0 | 0.02 | 0.95 | 0.02 | 0 |
|  | 9 | 0 | 0 | 0 | 0 | 0.02 | 0.95 | 0.02 |
|  | 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| (5) noise: $\mathrm{sd}=0.5$ | 4 | 0.81 | 0.19 | 0 | 0 | 0 | 0 | 0 |
|  | 5 | 0.16 | 0.68 | 0.16 | 0 | 0 | 0 | 0 |
|  | 6 | 0 | 0.16 | 0.68 | 0.16 | 0 | 0 | 0 |
|  | 7 | 0 | 0 | 0.16 | 0.68 | 0.16 | 0 | 0 |
|  | 8 | 0 | 0 | 0 | 0.16 | 0.68 | 0.16 | 0 |
|  | 9 | 0 | 0 | 0 | 0 | 0.16 | 0.68 | 0.16 |
|  | 10+ | 0 | 0 | 0 | 0 | 0 | 0.02 | 0.98 |
| (6) noise: $\mathrm{sd}=1.0$ | 4 | 0.55 | 0.35 | 0.09 | 0.01 | 0 | 0 | 0 |
|  | 5 | 0.26 | 0.41 | 0.26 | 0.06 | 0.01 | 0 | 0 |
|  | 6 | 0.06 | 0.24 | 0.39 | 0.24 | 0.06 | 0.01 | 0 |
|  | 7 | 0.01 | 0.06 | 0.24 | 0.38 | 0.24 | 0.06 | 0.01 |
|  | 8 | 0 | 0.01 | 0.06 | 0.24 | 0.38 | 0.24 | 0.07 |
|  | 9 | 0 | 0 | 0.01 | 0.06 | 0.24 | 0.38 | 0.31 |
|  | 10+ | 0 | 0 | 0 | 0 | 0.01 | 0.05 | 0.94 |

Appendix A. Continued.

| Model | True Age | Assigned Age |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 4 | 5 | 6 | 7 | 8 | 9 | 10+ |
| (7) noise: $\mathrm{sd}=2.0$ | 4 | 0.33 | 0.29 | 0.2 | 0.11 | 0.05 | 0.02 | 0 |
|  | 5 | 0.23 | 0.26 | 0.23 | 0.16 | 0.08 | 0.04 | 0.02 |
|  | 6 | 0.14 | 0.2 | 0.22 | 0.2 | 0.14 | 0.07 | 0.04 |
|  | 7 | 0.07 | 0.13 | 0.18 | 0.21 | 0.18 | 0.13 | 0.11 |
|  | 8 | 0.03 | 0.07 | 0.12 | 0.18 | 0.2 | 0.18 | 0.23 |
|  | 9 | 0.01 | 0.03 | 0.07 | 0.12 | 0.18 | 0.2 | 0.4 |
|  | $10+$ | 0 | 0 | 0.01 | 0.02 | 0.04 | 0.07 | 0.86 |
| (8) bias: +0.25 | 4 | 0.84 | 0.16 | 0 | 0 | 0 | 0 | 0 |
|  | 5 | 0 | 0.84 | 0.16 | 0 | 0 | 0 | 0 |
|  | 6 | 0 | 0 | 0.84 | 0.16 | 0 | 0 | 0 |
|  | 7 | 0 | 0 | 0 | 0.84 | 0.16 | 0 | 0 |
|  | 8 | 0 | 0 | 0 | 0 | 0.84 | 0.16 | 0 |
|  | 9 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0.16 |
|  | $10+$ | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| (9) bias: +0.5 | 4 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 0 |
|  | 5 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0 |
|  | 6 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 |
|  | 7 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 0 |
|  | 8 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0 |
|  | 9 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.5 |
|  | $10+$ | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| $\text { (10) bias: }+1.5$ | 4 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0 |
|  | 5 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 |
|  | 6 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 0 |
|  | 7 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0 |
|  | 8 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.5 |
|  | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
|  | 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| (11) bias: +2.5 | 4 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 |
|  | 5 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 0 |
|  | 6 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0 |
|  | 7 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.5 |
|  | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
|  | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
|  | 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

