The Effects of Ageing Error on Stock Assessment for Weakfish *Cynoscion regalis*

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Abstract

Inherent uncertainties in the stock assessment for weakfish have precluded accurate and consistent advice concerning the management of commercial and recreational fisheries. Error within ageing techniques, used to assess relative age frequencies within commercial and recreational harvest, has been cited as a potential source for uncertainty during assessments of the weakfish fishery. The implications for age-reading error on weakfish stock assessment were explored using measurement-error growth models (i.e. Chapter 1), ageing error matrices within a statistical catch-at-age framework (i.e. Chapter 2), and Monte Carlo simulations to gauge robustness of ignoring this type of uncertainty during fisheries stock assessment (i.e. Chapter 3). Measurement-error growth models typically resulted in weakfish that grew to reach larger sizes, but at slower rates, with median length-at-age being overestimated by traditional von Bertalanffy growth curves, at least for the observed age range. Measurement-error growth models allow for incorporation of ageing uncertainty during nonlinear growth curve estimation, as well as the ability to estimate the ageing error variance. Age-reading error was further considered during statistical catch-at-age analysis of the weakfish fishery, mainly through permutations of true catch-at-age via ageing error matrices constructed from estimates of the ageing error variance, thus reflecting changes in relative age compositions as a consequence of ageing uncertainty. As a result, absolute levels of key population parameters were influenced, but general trends in those parameters tended to be similar, with strong congruency across models as to weakfish stock dynamics in most recent years. Finally, Monte Carlo simulations showed that implications for age-reading error on weakfish stock assessment are varied, depending upon the direction and

magnitude of the ageing uncertainty. However, relative trends of parameter estimates over time tended to be similar, resulting in proper allocation of weakfish stock status, regardless of the type of ageing error considered. Furthermore, assuming negligible ageing uncertainty within fishery-independent surveys appears reasonable, as simulations incorporating ageing error within indices of relative abundance showed similar patterns to situations that only considered observation noise.

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Dedication

To my mother and father, as well as Jessica and Jacob Hatch. I would also like to dedicate this Thesis to Chad and Jane Crumm, as well as Richard and Emily Hatch. Thank you for everything.

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Preface

> *"the most valuable information obtained from sampled catch, at least for temperate waters, is age."*
>
> *-Hilborn and Walters (1992)*

The recursive collapse of commercial fisheries is ubiquitous in freshwater and marine environments (Pauly et al. 2002); with causes being attributed to overcapitalization, scientific uncertainty, and intricate ecosystem structure (Ludwig et al. 1993). Historically, optimum fishing levels were determined by trial and error (Ludwig et al. 1993), with ecosystem effects of overexploitation being confounded by functional redundancy in complex aquatic food webs (Myers et al. 2007). The sustained decline of marine fish stocks has since prompted novel approaches to fisheries management including marine protected areas (MPAs), catch shares (i.e. Individual Transferable Quotas), conservative biological targets, and ecosystem-based incentives (Weeks and Berkeley 2000; Pauly et al. 2002; Latour et al. 2003; Costello et al. 2008). Concurrently, the impact of uncertainty in fisheries stock assessment has led to the development of biologically risk-averse practices that account for scientific ambiguity regarding fish stock status and/or alternative management approaches (Jiao et al. 2005; Shertzer et al. 2008).

In the U.S., fishery status is largely determined by harvest control rules, which compare indicator reference points with target reference points established by managers (Jiao et al. 2009). Harvest control rules can incorporate multiple biological reference points elicited from risk analysis and/or fisheries stock assessment (Jiao et al. 2010). Jiao et al. (2005) suggests choosing an appropriate level of risk tolerance and evaluating alternative management strategies through risk analysis, instead of setting reference points based on inappropriate assumptions (e.g. $F_{0.1}$ or F_{MSY}). For example, Patterson (1992) found that the exploitation rate of $F_{0.1}$ may be too high for most fish populations (Hilborn 2002). By using risk analysis, uncertainty surrounding the status of a fish stock can be explicitly incorporated into scientific advice concerning the management of commercial and/or recreational fisheries (Jiao et al. 2010).

Uncertainties in fisheries stock assessment can be allocated into five categories based on respective origin and include measurement error, process error, model error, estimation error, and implementation error (Rosenberg and Retrespo 1994). Of particular concern is the influence of measurement error on fisheries stock assessment performance (i.e. accuracy and precision). Measurement error or uncertainty occurs when data used to fit a stock assessment model are measured with error (e.g. age), which can be further compounded by observation uncertainty in the misreporting of landed catch. Chen (2003) and Chen et al. (2003) indicated that the quality and quantity of data used to fit a model can negatively affect the stock assessment process, leading to biased estimates of vital and/or auxiliary parameters. This could potentially lead to flawed scientific advice and mismanagement of a fishery, resulting in overexploitation of a fish stock or loss of harvest opportunities by fishers (Chen 2003; Jiao et al. 2010).

The application of mathematical models to the assessment of fish populations requires parameters to be estimated from observed data. In age-structured analyses, parameters are approximated by some form of age-dependent estimation procedure (e.g. virtual population analysis). The typical input required by these methods is a catch-at-age matrix, which includes catch by age for each year of the fishery to be covered by the assessment (Panfili et al. 2002). Compilation of catch-at-age data is rather intensive and requires the assignment of age to total catch based on sampled age proportions (i.e. age-length key). Furthermore, age-length keys are used to construct age-structured indices of catch-per-unit-effort (CPUE), stock weights-at-age and maturity at age (Reeves 2003; Bertignac and Pontual 2007). If estimates of age are biased, then subsequent biological reference points will be skewed (Shepherd 1982), consequently influencing management decisions. Our ability to assess and correct for age-reading error becomes pertinent, as harvest control roles that do not incorporate uncertainty may lead to the overexploitation of fish stocks (Jiao et al. 2010).

Campana (2001) delineates ageing error into two respective sources, including process and/or interpretation error. Process error is the inability of an ageing structure to accurately record growth sequence information (Campana 2001). In other words, it is the inability of ageing structures to form interpretable patterns of growth that correspond to the true age of the fish (Maceina et al. 2007). Process error tends to be biased, leading to consistent over- or under-estimation of age by readers. On the other hand, interpretation error is the subjective assignment of age to individual fish based on presumed annular or daily increments (Campana 2001). Interpretation error can be either random or biased, depending upon the complexity of the ageing structure or the inability of the reader to accurately discern annual or daily growth rings. In general, process error is assumed to be negligible in the production ageing process undertaken for fisheries stock assessment. This is because age validation is a key consideration in the development of any successful ageing program (Campana 2001). Regrettably, use of a validated technique does not guarantee accurate or reliable age estimates, as subjectivity is always inherent in the ageing of fishes (Buckmeier 2002).

Systematic errors (i.e. bias) in the fish ageing process primarily arise from within and among reader variability (Kimura and Lyons 1991; Buckmeier 2002). This variation can be attributed to the utilization of different preparation methods by ageing laboratories (Morison et al. 2005) or to the unreliability of readers to precisely or accurately estimate age (Kimura and Lyons 1991; Buckmeier 2002). Assessing the consistency of readers has gained much attention in the scientific literature, with various indices of precision being proposed to ensure consistent age interpretation (Beamish and Fournier 1981; Chang 1982; Campana et al. 1995; Campana 2001). Furthermore, quality control programs have been enacted to detect and correct for reader drift in the production ageing process (Morison et al. 1998), although the ability to fully attenuate age-reading error is impractical and investigating potential effects in a fisheries management context are vital.

The most recent assessment of the weakfish stock used an age-structured model (ADAPT-VPA) approved by the Stock Assessment Review Committee (SARC) to explore historical trends in abundance and fishing pressure. Initial results demonstrated a severe retrospective bias in estimates of fishing mortality (F) and spawning stock biomass (SSB), possibly due to insufficient data. The Weakfish Technical Committee (WTC) concluded that the model was overestimating SSB and underestimating F in recent years, citing high uncertainty in parameter estimates and instability of results (ASMFC 2009). The WTC recognized two potential causes for the unreliable stock assessment: 1) poor biological sampling of commercial and recreational catch and discard and 2) unrealistic assumptions of the age-structured model (i.e. catch-at-age matrix is error-free) (NEFSC 2009). This thesis, over three chapters, addresses the concern of ageing error within catch-at-age data and explores the influence of ageing uncertainty during fisheries stock assessment for weakfish by: 1) incorporating and quantifying ageing error during nonlinear growth curve analysis, 2) exploring the use of ageing error matrices within a statistical catch-at-age framework and 3) simulating the potential effects of ageing error during fisheries stock assessment.

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Chapter 1: Bayesian errors-in-variables approach to incorporate ageing uncertainty during nonlinear growth curve estimation for weakfish *Cynoscion regalis*

Abstract

Inferring growth for aquatic species is dependent upon accurate descriptions of age-length relationships, which may be degraded by measurement error in age estimates. Ageing error arises from biased and/or imprecise age determinations as a consequence of misinterpretation by readers or inability of ageing structures to accurately reflect true age. A Bayesian errors-in-variables (EIV) approach (i.e. measurement-error modeling) can account for ageing uncertainty during nonlinear growth curve estimation by allowing observed ages to be parametrically modeled as random deviates. Information on the latent age composition then comes from the specified prior distribution, which represents the true age structure of the sampled fish population. In this study, weakfish growth was modeled by means of traditional and measurement-error von Bertalanffy growth curves using otolith- and/or scale-estimated ages. Age determinations were assumed to be log-normally distributed, thereby incorporating multiplicative error with respect to ageing uncertainty. The prior distribution for true age was assumed to be uniformly distributed between ±4 of the observed age for each individual. Measurement-error growth models resulted in weakfish that grew to reach larger sizes, but at slower rates, with median length-at-age being overestimated by traditional growth curves for the observed age range. In addition, measurement-error models produced slightly narrower credible intervals for parameters of the von Bertalanffy growth function, which may be an artifact of the specified prior distributions. Subjectivity is always apparent in the ageing of fishes and it is recommended that measurement-error growth models be used in conjunction with otolith-

estimated ages to accurately capture the age-length relationship that is subsequently used in fisheries stock assessment and management for weakfish.

1. Introduction

Effects of measurement error in solving nonlinear models have been well documented (Carroll et al. 2006), causing bias in parameter estimates (Solow 1998; Jiao et al. 2006; Biggs et al. 2009; Heery and Berkson 2009), confounding relationships among covariates (Walters and Ludwig 1981; Gustafson 2003), and exaggerating model selection uncertainty (Punt et al. 2008; Biggs et al. 2009). Of particular concern is the role observation error plays in nonlinear growth curve estimation, as age-length relationships play a key role in eliciting biological reference points from age-structured stock assessment models. While several methods have been constructed to account for gear selectivity and variable length-at-age in fitting nonlinear growth curves (Sainsbury 1980; Pilling et al. 2002; Taylor et al. 2005; He and Bence 2007; Alós et al. 2010; Jiao et al. 2010), relatively few approaches have been developed to incorporate ageing error when inferring growth for aquatic species (Kimura 2000; Cope and Punt 2007; Schwarz and Runge 2009).

Ageing error is largely determined through multiple age reads of the same individual, with relative bias and imprecision being evaluated graphically through age-bias plots and/or various age-discrimination statistics (Chang 1982; Campana et al. 1995; Campana 2001). If age validation data are available, then known biases can be corrected for during the model fitting process by calibrating observed ages to reflect true age estimates (Schwarz and Runge 2009). Unfortunately, the majority of age-length data sets used in fisheries stock assessment comprise a single age and length measurement per individual with true age being unknown (Cope and Punt 2007; Punt et al. 2008). A single age read per individual complicates the parameter estimation procedure, as traditional methods for correcting age misclassification require an estimate of the ageing error variance, necessitating multiple age reads per individual and/or that observed ages are randomly distributed around the latent variable of true age (Cook and Stefanski 1994; Cope and Punt 2007; Punt et al. 2008). As a consequence, most growth investigations assume ageing error is negligible or relatively non-influential, with respect to process noise, in describing the age-length relationship (Pondella et al. 2001; Harris et al. 2007). Ignoring ageing error may be an unreasonable approach, as conventional methods tend to underestimate the uncertainty in parameter values, with respect to error in both the dependent and independent variables, leading to overconfidence in the description of growth and subsequent management decisions derived from growth curve analyses (Clark 1991).

Fisheries scientists have long recognized that most independent variables necessary for stock assessment are measured with non-negligible uncertainty, although most attention has been spent on estimating the degree of bias in parameter estimates instead of attenuating error through increased model complexity (Hilborn and Walters 1992). Recent advances in computational techniques have led to increased utilization of measurement-error models that allow for uncertainty in both the dependent and independent variables (Clark 2005; Jiao et al. 2006), although it is still necessary to understand the tradeoffs between model articulation and descriptive accuracy (Costanza and Sklar 1985; Clark 2005; Biggs et al. 2009). A Bayesian approach allows for stochasticity at multiple levels within a hierarchically structured framework for nonlinear regression, with presumed understanding of the independent variable's distribution (i.e. true age) coming from the specified prior (Clark 2007). Hence, Bayesian errors-in-variables (i.e. measurement-error) models allow for the fitting of nonlinear growth curves when the ageing error distribution is unknown or inestimable using contemporary methods (i.e. one age read per individual).

Variability in age estimates for individual fish could be a consequence of misinterpretation by readers of ageing structures (e.g. scales and otoliths) or inability of ageing structures to accurately record growth sequence information (Neilson 1992; Campana 2001). While most calcified structures have the potential to provide accurate estimates of age (Campana 2001), subjectivity is always apparent in the production ageing process undertaken for fisheries stock assessment (Kimura and Lyons 1991; Heifetz et al. 1998; Morison et al. 1998; Buckmeier 2002). Two of the most commonly used hard parts in the assignment of age to individual fish include otoliths and scales (Hilborn and Walters 1992), with the general understanding that otoliths provide more accurate and precise age estimates compared to scale-estimated ages (Lowerre-Barbieri et al. 1995; Maceina et al. 2007). However, various sources of error still confound the assignment of age to individual fish for otolith-estimated ages (Neilson 1992; Pepin et al. 2001) and incorporation of measurement error into nonlinear growth curve analysis is still prudent.

Weakfish *Cynoscion regalis* are a marine finfish found along the eastern coast of the United States, ranging from Massachusetts to Florida (Shepherd and Grimes 1983). Historically, weakfish have supported important commercial and recreational fisheries along the Northwest Atlantic (Nye et al. 2008), with recent landings in the commercial sector being relegated to bycatch. While several studies have investigated the age and growth of weakfish at various spatial and temporal scales (Seagraves 1981; Shepherd and Grimes 1983; Hawkins 1988; Villoso 1989; Lowerre-Barbieri et al. 1995), effects of ageing error on describing the age-length relationship are largely unknown (NEFSC 2009). The goal of this study was to evaluate and compare traditional and measurement-error growth models for weakfish *Cynoscion regalis* using otolith- and/or scale-estimated ages incorporating unbiased ageing error. Length-at-age was calculated using the von Bertlanffy growth equation assuming a multiplicative error structure. Growth models considering ageing uncertainty allowed observed ages to follow a log-normal distribution, with the prior for true age being uniformly distributed between ±4 of the determined age for each individual. A Bayesian estimator was used to solve the aforementioned traditional and measurement-error von Bertalanffy growth curves.

2. Materials and methods

2.1 - Data

Age-length data for weakfish *Cynoscion regalis* were obtained from Wenner and Gregory (2000), with age for the same individual being estimated from sagittal otolith and scale readings. The otolith-scale age comparison database comprised 2,318 weakfish caught intermittently from five states (i.e. New York, Delaware, Maryland, Virginia, and North Carolina) for years 1989, 1992, 1995, and 1996 (Table 1). Individuals were pooled across states and years to fit von Bertalanffy and measurement-error von Bertalanffy growth curves using otolith- and/or scale-estimated ages. An age-bias plot (Figure 1) indicated ageing uncertainty for weakfish, with scale readings tending toward younger age estimates compared to otolith-estimated ages. Also, percent agreement between ageing structures declined with age, suggesting error in the ability of readers to consistently discern age for older fish (i.e. multiplicative ageing uncertainty) (Figure 2).

The weakfish age-length dataset was characterized by a lack of older, larger-sized individuals compared to the most recent investigation of age and growth (Lowerre-Barbieri et al.

1995). Changes in weakfish age- and size-structure are most likely a culmination of several factors, including: residual effects of excessive fishing mortality (NEFSC 2009), gear selectivity, and seasonal variation in spatial distribution as a result of differential migration by size (Lowerre-Barbieri et al. 1995). In order to avoid inflated estimates of asymptotic length (L_∞), and consequent underestimation of the Brody growth coefficient (k), posterior values for L_∞ were bounded by the specified prior distribution.

2.2 - Nonlinear growth models

The von Bertalanffy growth function has a long history in fisheries science and has been used extensively to describe fish growth (i.e. length and weight) as a function of age (Haddon 2001). Despite criticisms (Roff 1980), the von Bertalanffy growth curve has been advocated as an appropriate growth model because of its ability to capture observed trends between length and age for a variety of fish species (Chen et al. 1992). Weakfish growth is currently modeled using a von Bertalanffy growth function that can be written as

$$(1) \qquad L_i = L_\infty \left(1 - e^{\left(-k\left(t'_{i,j} - t_o\right)\right)}\right) \cdot e^{\varepsilon_i}$$

where L_i is the length-at-age for the ith individual, L_∞ is the asymptotic length, k is the Brody growth coefficient, t_o is the hypothetical length at age-0, and $t'_{i,j}$ is the observed age for the ith individual using the jth ageing structure. Error ε_i is assumed to be independent and normally distributed with mean 0 and variance σ_L^2.

Extending the von Bertalanffy growth model to incorporate measurement error is relatively straight forward, and can be written as

(2) $L_i = L_\infty\left(1 - e^{\left(-k(t_i - t_o)\right)}\right) \cdot e^{\varepsilon_i}$

$t'_{i,j} = t_i \cdot e^{\varepsilon_{i,j}}$

where t_i is the true age for the *i*th individual. The logarithm of observed age $\log_e(t'_{i,j})$ is assumed to be independent and normally distributed with mean $\log_e(t_i)$ and variance $\sigma^2_{A,j}$. In order to facilitate the use of a log-normal distribution for observed ages, a small constant (i.e. 10E-05) was added to age-0 individuals during model fitting.

2.3 - Statistical estimator

A Bayesian estimator was used to construct the joint posterior probability distribution for parameters in the von Bertalanffy and measurement-error von Bertalanffy growth curves. The full conditional distribution for the traditional von Bertalanffy growth model follows that

(3) $$p(L_\infty, k, t_o, \sigma^2_L \mid L_i) \propto \prod_{i=1}^{n} \mathcal{L}(L_i \mid L_\infty, k, t_o, \sigma^2_L) \times \pi(\sigma^2_L)\pi(L_\infty)\pi(k)\pi(t_o)$$

While the full conditional distribution for the measurement-error von Bertalanffy growth model follows that

(4) $$p(L_\infty, k, t_o, \sigma^2_L, \sigma^2_A, t_i \mid L_i) \propto \prod_{i=1}^{n} \prod_{j=1}^{n} \mathcal{L}(L_i \mid L_\infty, k, t_o, \sigma^2_L, t_i)\mathcal{L}\left(t'_{i,j} \mid t_i, \sigma^2_{A,j}\right) \times \pi(\sigma^2_L)\pi\left(\sigma^2_{A,j}\right)\pi(L_\infty)\pi(k)\pi(t_o)\pi(t_i)$$

where $p(\cdot)$ denotes the posterior probability, $\mathcal{L}(\cdot)$ denotes the likelihood function, and $\pi(\cdot)$ denotes the prior distribution.

As shown in equation 4, observed lengths (L_i) are conditionally independent of observed ages ($t'_{i,j}$), with the majority of information about true age (t_i) coming from the prior, as well as feedback from both likelihood functions on the posterior. At least for fish, length can be considered a loose proxy for age, and it is commonly assumed that lengths are weakly informative of ages (e.g. age-length keys). Essentially, measurement-error growth models work to pull observations closer to the median of length-at-age, suggesting the need for an informative prior on true age for species that exhibit an asymptotic length early in life, relative to the maximum age, or have diffuse age-length distributions. Otherwise, issues with identifiability will prevent effective estimation of variance parameters, resulting in non-convergence and/or poor mixing of Markov chains. If an informative prior on true age is unjustifiable, then multiple age determinations will be necessary to estimate ageing-error variance(s) or a reference collection will be required, in which true age for a set of individuals is known, so that validation data can help calibrate the model during estimation.

Prior distributions were constructed around historic estimates of weakfish growth, thereby encompassing biological relevancy (Seagraves 1981; Shepherd and Grimes 1983; Hawkins 1988; Villoso 1989; Lowerre-Barbieri et al. 1995) (Table 2). Age validation data were unavailable and consequently the latent variable of true age was assumed to follow a uniform distribution, with lower and upper bounds being defined by ±4 of the observed age for each individual, as the largest difference between otolith- and scale-estimated age was 3 years (Table 3). Truncation of the joint posterior distribution for L_∞ and k was expected, as specified priors were used to constrain posterior draws to biologically reasonable values. The age-length data for weakfish fail to accurately capture the asymptotic length, leading to unrealistic estimates that are based on extrapolation of the age-length trend (Knight 1968). A summary of prior distributions and parameter estimates can be found in Table 2.

All models were run with three Markov chains for 100,000 simulations per chain using the software packages WinBUGS version 1.4.3 and R version 2.13.1. Convergence of the Markov chains to the stationary distribution was determined by monitoring trace plots and computing Gelman and Rubin diagnostics. The first 50,000 iterations from each chain were discarded to allow for adequate burn-in and a thinning interval of 5 was used to reduce autocorrelation among iterative samples and improve computational efficiency. A total number of 30,000 iterations were used to summarize the posterior distribution for each model.

2.4 - Model selection criteria

Growth is a vital component in discerning the population dynamics of fishes and modeling age-length relationships requires the ability to effectively compare and discriminate among alternative hypotheses that represent biological realism. In this study, model checking and discrimination were conducted using posterior predictive *p*-values and deviance information criterion (DIC), respectively. While DIC has the potential to identify correct model structure for catch-at-age analyses (Wilberg and Bence 2008), its ability to select preferred models in an errors-in-variables context is less clear (Spiegelhalter et al. 2002; Celeux et al. 2006). To circumvent this issue, posterior predictive model checks and model discrimination statistics were used in an effort to corroborate anecdotal beliefs regarding the applicability of measurement-error models during nonlinear growth curve analyses.

2.4.1 - Posterior predictive *p*-values

Posterior predictive *p*-values were used to conduct posterior predictive model checks in evaluating the ability of posited models to replicate data similar to that observed. Generally, a discrepancy statistic is used to assess model goodness-of-fit based on observed data and the posterior predictive distribution, where the posterior predictive distribution is defined as

(5) $$p(y^{rep}|y) = \int p(y^{rep}|\theta)p(\theta|y)d\theta$$

where $p(y^{rep}|\theta)$ is the data distribution for replicated observations y^{rep} and $p(\theta|y)$ is the posterior distribution for the unknown parameter vector θ given the observed data y. The discrepancy measure utilized in this study was the Bayesian residual sum of squares (Gelman et al. 1996), which can be written as

(6) $$\chi^2(y;\theta) = \sum_{i=1}^{n} \frac{[y_i - E(y_i|\theta)]^2}{Var(y_i|\theta)}$$

where $E(\cdot)$ is the expectation, $Var(\cdot)$ is the variance, and y_i is the *i*th observation of the data y or simulated data y^{rep}. The posterior predictive *p*-value, then, is simply the proportion of times $\chi^2(y^{rep}; \theta) \geq \chi^2(y; \theta)$. The closer the posterior predictive *p*-value is to 0.50, the more adequate the model is at replicating data similar to that observed.

2.4.2 - Deviance information criterion

Deviance information criterion was used to compare model goodness-of-fit, as measurement-error models are hierarchically structured and the number of parameters is difficult to enumerate (Spiegelhalter et al. 2002; Ward 2008; Wilberg and Bence 2008). Like other information-theoretic approaches, DIC penalizes overparamaterization and descriptive accuracy in order to select effective models with high explanatory power. DIC can be written as

(7) $$DIC = \overline{D} + p_D$$

$$p_D = \overline{D} + D(\bar{\theta})$$

$$D(\cdot) = -2\log\left(\mathcal{L}(y|\theta)\right)$$

where $D(\cdot)$ is the deviance defined as -2 times the log-likelihood of the data y given the unknown parameter vector θ, $\overline{D}$ is the posterior mean of the deviance, $D(\bar{\theta})$ is the deviance evaluated at the posterior mean of θ, and p_D is the effective number of parameters in the Bayesian model as formulated by Spiegelhalter et al. (2002). While Celeux et al. (2006) recommend alternatives to this definition of DIC for missing-data models, of which errors-in-variables regression is a subset; our approach is to use the most commonly encountered form within fisheries science. Given that the observed outcomes (i.e. length) are conditioned on the missing data (i.e. true age), the default calculation of DIC by WinBUGS is appropriate.

3. Results

3.1 - Model discrimination

According to the DIC statistic, traditional von Bertalanffy growth curves outperformed measurement-error growth models for both otolith- and scale-estimated ages (Table 3). Alternatively, posterior predictive *p*-values for measurement-error growth curves were substantially closer to 0.50 (Table 3 and Figure 3), suggesting improved adequacy of errors-in-variables models to reflect observed trends in the age-length relationship for weakfish.

However, all growth curves considered in this study had posterior predictive p-values < 0.50, possibly suggesting underparameterization in the ability of formulated models to partition the overall variance to its respective sources (i.e. variability in age or length). Nonetheless, predictive approaches to model comparison may be beneficial for errors-in-variables regression, as the utility of information-theoretic-based methods for measurement-error model selection are still circumstantial (Jiao et al. 2009).

3.2 - von Bertalanffy growth curve parameters

Growth models considering ageing error resulted in higher posterior mean values for L_∞ and t_o (Table 2 and Figures 5a and 5c), while producing lower posterior mean values for k and σ_L (Table 2 and Figures 5b and 5c). As a consequence, measurement-error models demonstrated growth patterns where weakfish grew to reach larger sizes, but at slower rates, with traditional von Bertalanffy growth curves overestimating median length-at-age for the observed age range (Figure 4). In addition, 95% prediction intervals were wider for traditional von Bertalanffy growth models, compared to their measurement-error analogs (Figure 4). The growth curve incorporating ageing uncertainty, while simultaneously considering otolith- and scale-estimated ages (M5), produced comparable posterior mean values of 1189.599 for L_∞, 0.063 for k, and -2.526 for t_o. However, using M5 resulted in higher posterior mean values of 0.357 and 0.565 for the ageing-error standard deviation (σ_A), regarding otolith- and scale-estimated ages respectively, and a lower posterior mean value of 0.140 for the standard deviation in predicted lengths (σ_L) (Figure 5). Generally, measurement-error growth models produced slightly narrower credible intervals for parameters of the von Bertalanffy growth function, with less difference between posterior mean values for biologically relevant parameter estimates using different ageing structures or a combination thereof (Table 2 and Figure 5).

4. Discussion

Conceptually, the errors-in-variables approach is trying to correct the misallocation of younger, smaller-sized individuals to older age classes and older, larger-sized individuals to younger age classes, resulting in higher estimates for L_∞ and lower estimates for k. While the biological association between maximum size and growth rate may be plausible for weakfish, it is most likely a consequence of the von Bertalanffy growth equation imposing a negative correlation between L_∞ and k, which is further confounded by diffuse length-at-age distributions (Schwarz and Runge 2009). Similarly, narrower credible intervals for measurement-error models are most likely an artifact of prior constraints on posterior values, so as to coerce biologically meaningful patterns for weakfish growth. Typically, Bayesian errors-in-variables regression can better approximate uncertainty in parameter estimates, with respect to variation in both the response (i.e. length) and predictor (i.e. age) (Carroll et al. 2006). In this instance, credible intervals for posterior estimates of L_∞ and k are lessened, as estimators consistently propose values for L_∞ near the upper boundary of the prior, reflecting perceived increases in asymptotic size as a consequence of incorporating ageing error during nonlinear growth curve analysis.

Measurement-error growth models can account for variability in age determinations, but may overestimate the variability in predicted lengths if multiple age reads per individual are unavailable. Calibration data allows the errors-in-variables approach to draw on information from multiple age reads to estimate and adjust for measurement error. Consequently, variance in predicted lengths appears to be overestimated if ageing error is not considered when fitting nonlinear growth curves, as the model is using discrepancies associated with age to amplify variability in predicted lengths (Figure 4). That being said, using repeated measures of age via different ageing structures to calibrate the measurement-error growth model assumes that both hard parts are unbiased estimators and multiple age reads will provide information on the true age for each individual. If multiple age reads are in any way biased or correlated, measurement-error growth curves will be unable to attenuate ageing error without validation data (i.e. reference collection), in which age for a subset of individuals is known (Punt et al. 2008). As such, it is recommended that otolith-estimated ages be used in conjunction with measurement-error growth models for weakfish, as scales tend to negatively bias age estimates (Lowerre-Barbieri et al. 1994). Moreover, scale-estimated ages were treated as unbiased during model fitting, which may have contributed to the large discrepancy between estimates for σ_A across models considering one versus two age reads (i.e. M3-M4 vs. M5 in Figure 5e).

The Bayesian errors-in-variables (EIV) approach avoids several issues associated with previous methods to account for measurement error in age estimates during nonlinear growth curve estimation. First, it avoids uncertainty in the specification of an error variance ratio necessary for errors-in-variables functional regression as proposed by Kimura (2000). Second, the Bayesian EIV approach allows for greater flexibility in modeling ageing uncertainty and can alleviate issues with calculating a coefficient of variation for ageing error when age-length data only constitute a single age read per individual (Cope and Punt 2007). Finally, estimation of growth curve parameters, while simultaneously considering measurement error, may improve model goodness-of-fit compared to the external, prior adjustment of observed ages before estimating regression coefficients (Spiegelhalter et al. 1996; Schwarz and Runge 2009).

While the main focus of this study was to investigate the contributions of age-reading error on weakfish growth, other sources of variability and bias need to be addressed. On purely empirical grounds, it appears that weakfish growth exhibits a strong linear component (see

Figure 4), although von Bertalanffy growth has been documented in the past (NEFSC 2009). This is likely a reflection of sampling bias, as weakfish age-length data came from multiple states over multiple years, which is further compounded by a protracted spawning season. Similarly, diffuse age-length distributions exhibited by weakfish likely contributed to the minimal improvement of measurement-error von Bertalanffy growth models over traditional methods. However, fish species that are relatively long-lived and whom exhibit less variation in length-at-age may be more inclined to incorporate ageing error during assessments of growth, as ageing error may play a larger role in perceived growth trajectories. Likewise, the von Bertalanffy growth function assumes continuous growth, yet age is often recorded in discrete time. While this shortcoming is not unique to weakfish, it may introduce some bias into parameter estimates, but this aspect is beyond the scope of the current study.

Adjustment for measurement error during model fitting is imperative, as growth models are often used to assess the relative effects of environmental factors on size (Jiao et al. 2010). By using a Bayesian EIV approach, the correlation between growth and environmental stochasticity can be discerned by removing the degrading effects of ageing error on the underlying age-length relationship. This becomes increasingly pertinent as more and more management agencies take a holistic approach to the conservation of commercial and recreational fisheries, with need to determine driving factors behind spatiotemporal trends in fish growth and productivity. Similarly, per-recruit models and the biological reference points derived from these methods are highly susceptible to variations in growth caused by ageing error (Tyler et al. 1989), which could potentially cause overexploitation of commercially viable fish stocks and eventually lead to fishery collapse. Bayesian EIV models, then, provide a comprehensive and flexible framework upon which measurement error in observed ages can be quantified and adjusted for during model fitting, so that more accurate descriptions of growth can be used in fisheries stock assessments.

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Legends of figures

Figure 1-1: Age-bias plot for weakfish *Cynosicon regalis* using otolith-estimated and scale-estimated ages obtained from Wenner and Gregory (2000). Numbers correspond to sample size. Dotted line indicates 1:1 agreement between ototlith- and scale-estimated age.

Figure 1-2: Percent agreement between otolith- and scale-estimated ages as a function of otolith-estimated age for weakfish *Cynoscion regalis*. Only ages 0-5 were used for comparison due to limited sample size of older individuals (see Figure 1). Dotted line indicates general trend.

Figure 1-3: Scatterplot of realized and predicted discrepancies used in calculating Bayesian posterior predictive *p*-values for models M1-M5. Solid line indicates zero difference between the discrepancy statistic evaluated at the observed and replicated data.

Figure 1-4: von Bertalanffy growth curves using a) otolith-estimated and b) scale-estimated ages. Solid lines correspond to median values of length-at-age from traditional von Bertalanffy growth models, whereas dashed lines correspond to median values of length-at-age from growth curves considering ageing uncertainty. The light-shaded regions correspond to 95% prediction intervals for traditional von Bertalanffy growth models, whereas the dark-shaded regions correspond to 95% prediction intervals for growth models considering ageing uncertainty. Circles correspond to observed data.

Figure 1-5: Marginal posterior distributions of the traditional (M1-M2) and measurement error (M3-M5) von Bertalanffy growth curve parameters: (a) L_{∞}; (b) k; (c) t_o; (d) σ_L; and (e) σ_A. M1, solid line; M2, small-dashed line; M3, dotted line; M4, dotted-dashed line; and M5, large-dashed line.

Legends of tables

Table 1-1: Summary of weakfish *Cynoscion regalis* age-length data used in constructing traditional and measurement error von Bertalanffy growth models (Wenner and Gregory 2000).

Table 1-2: Parameter estimates from von Bertalanffy (VBGF) and measurement error von Bertalanffy (MEVB) growth models using otolith-estimated and scale-estimated ages (i.e. M1-M4); including posterior mean and standard deviation (S.D.).

Table 1-3: Model comparison of traditional (VBGF) and measurement error (MEVB) von Bertalanffy growth models using posterior predictive *p*-values and deviance information criterion (DIC). See materials and methods section for descriptions of posited models. $\overline{D}$ is the posterior mean of the deviance and pD is the effective number of parameters.

Appendix

Table 1-1

	1989	1992	1995	1996	**Total**
New York	0	0	114	0	**114**
Delaware	0	0	1139	150	**1289**
Maryland	0	0	0	95	**95**
Virginia	83	74	0	0	**157**
North Carolina	0	0	142	521	**663**
Total	**83**	**74**	**1395**	**766**	**2318**

Table 1-2

			Otolith		Scale	
Model	Parameters	Prior	Mean	SD	Mean	SD
VBGF	L_∞	U(300,1200)	1177.780	21.982	1179.558	19.132
	k	U(0,1)	0.068	0.002	0.076	0.002
	t_o	U(-3,1)	-2.347	0.054	-2.116	0.045
	σ_L	U(0.0001,10)	0.190	0.003	0.180	0.003
MEVB	L_∞	U(300,1200)	1187.649	11.840	1187.139	12.671
	k	U(0,1)	0.062	0.001	0.068	0.001
	t_o	U(-3,1)	-2.596	0.053	-2.359	0.047
	σ_L	U(0.0001,10)	0.153	0.004	0.142	0.003
	σ_A	U(0.0001,10)	0.275	0.010	0.281	0.010

Table 1-3

Scenario	Data	Model	p-value	$\overline{D}$	pD	DIC
M1	Otolith	VBGF	0.05	25662	3	25665
M3		MEVB	0.31	24813	2112	26935
M2	Scale	VBGF	0.04	25419	3	25421
M4		MEVB	0.43	24145	2136	26281
M5	Otolith & Scale	MEVB	0.35	28651	2107	30759

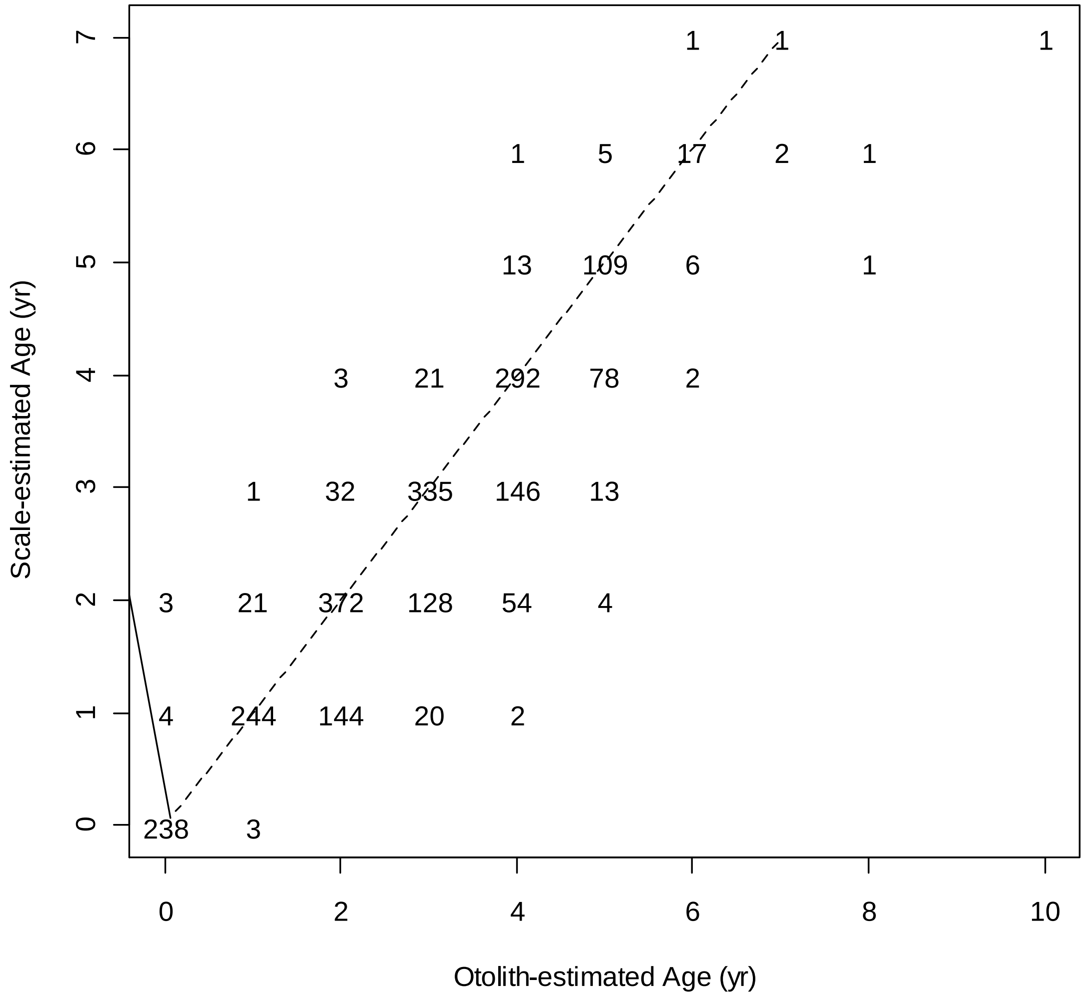
Scale-estimated Age (yr)
Otolith-estimated Age (yr)
0
1
2
3
4
5
6
7
0
2
4
6
8
10
238
3
4
244
144
20
2
3
21
372
128
54
4
1
32
335
146
13
3
21
292
78
2
13
109
6
1
1
5
17
2
1
1
1
1

Figure 1-1

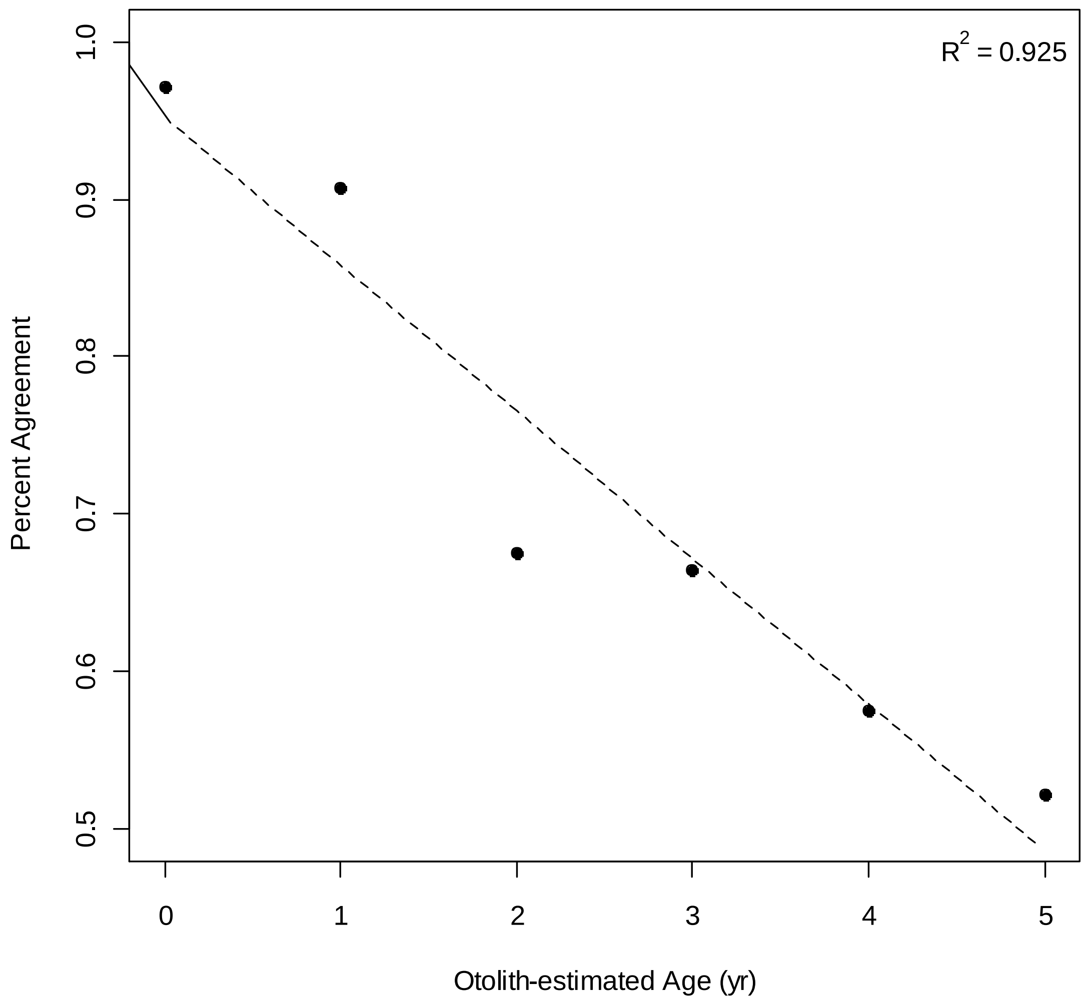
$R^2 = 0.925$
Percent Agreement
1.0
0.9
0.8
0.7
0.6
0.5
0
1
2
3
4
5
Otolith-estimated Age (yr)

Figure 1-2

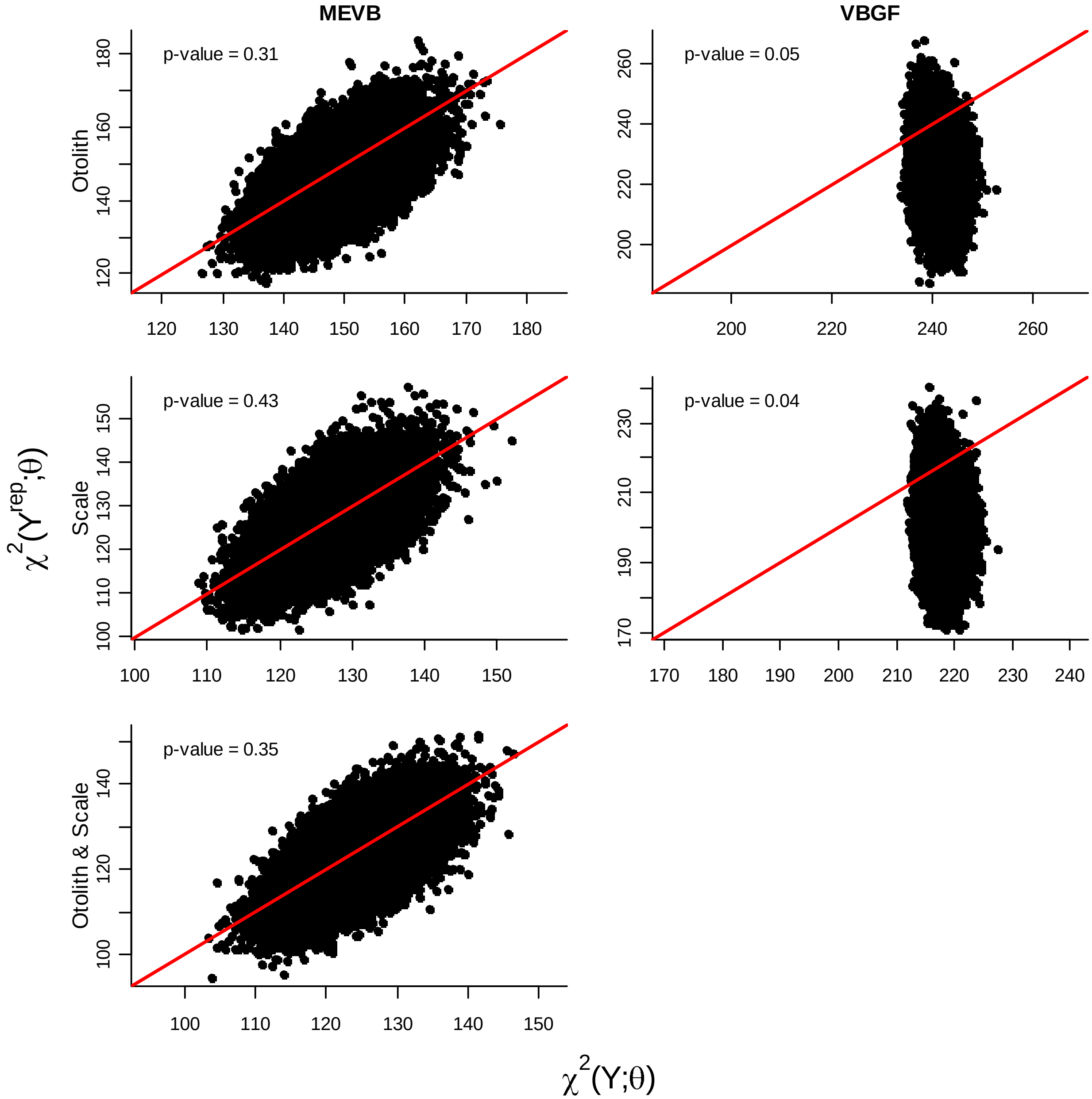
MEVB
VBGF
p-value = 0.31
p-value = 0.05
p-value = 0.43
p-value = 0.04
p-value = 0.35
Otolith
Scale
Otolith & Scale
$\chi^2(Y^{rep};\theta)$
$\chi^2(Y;\theta)$

Figure 1-3

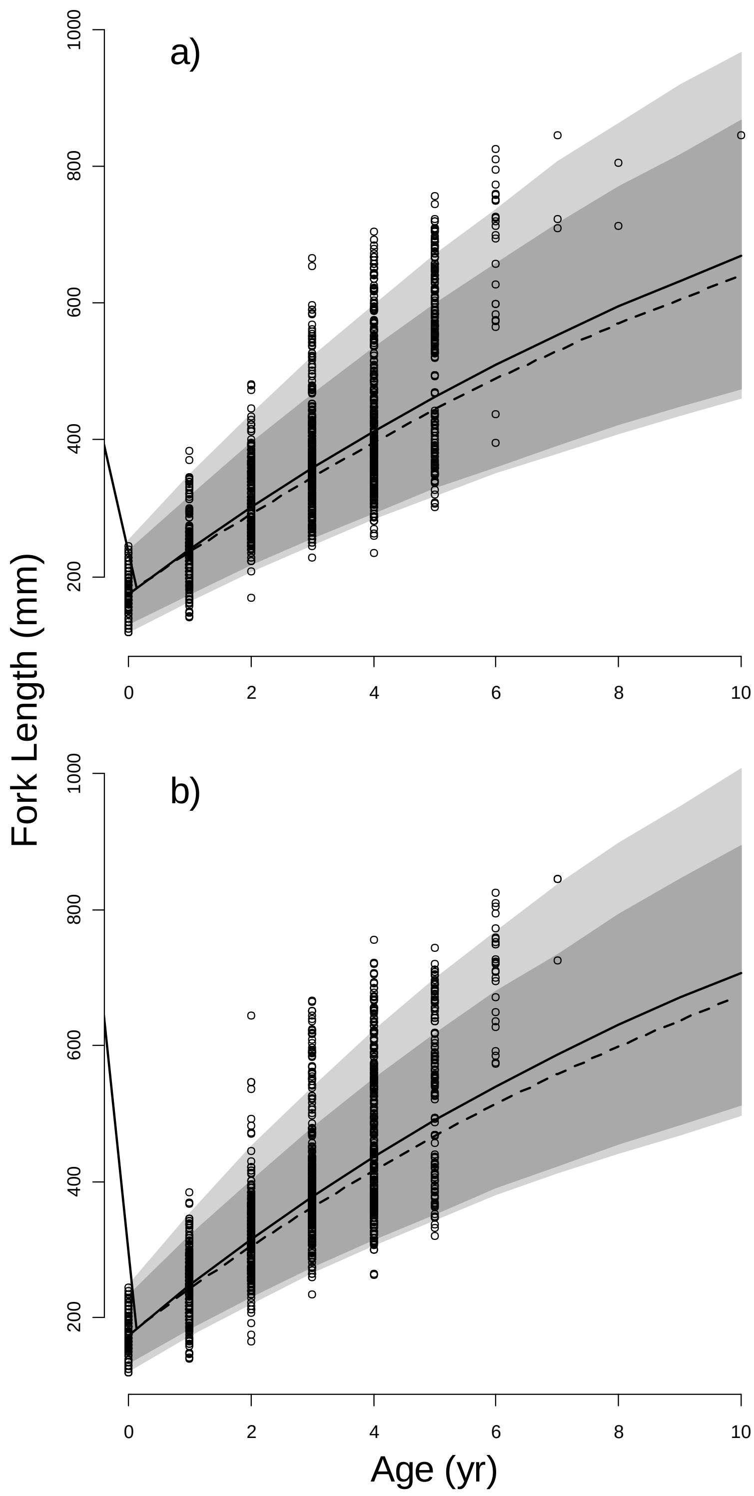

Figure 1-4

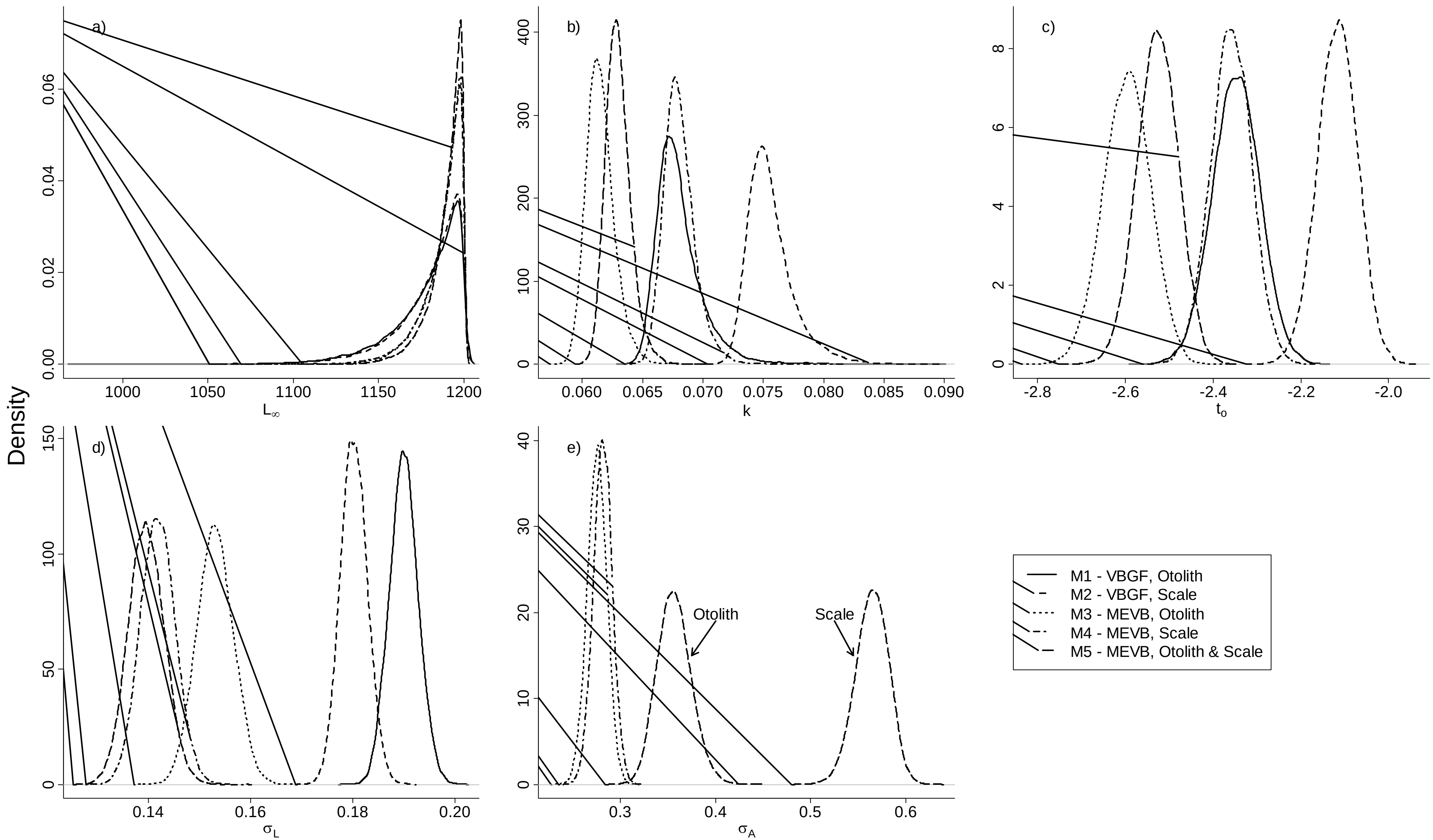
Density
a)
0.00
0.02
0.04
0.06
1000
1050
1100
1150
1200
L∞
b)
0
100
200
300
400
0.060
0.065
0.070
0.075
0.080
0.085
0.090
k
c)
0
2
4
6
8
-2.8
-2.6
-2.4
-2.2
-2.0
t_o
d)
0
50
100
150
0.14
0.16
0.18
0.20
σ_L
e)
0
10
20
30
40
Otolith
Scale
0.3
0.4
0.5
0.6
σ_A
M1 - VBGF, Otolith
M2 - VBGF, Scale
M3 - MEVB, Otolith
M4 - MEVB, Scale
M5 - MEVB, Otolith & Scale

Figure 1-5

Chapter 2: Integrated population dynamics modeling for age-based assessments with measurement error in observed ages

Abstract

Contemporary approaches for assessing fish populations include age-structured models that implicitly assume negligible uncertainty in catch at age. Ignoring measurement error in observed ages could bias estimation of key population parameters (full fishing mortality, age-specific selectivity, spawning stock size, and recruitment) and subsequent perceptibility of stock status (i.e. overfishing and/or overfished). Recent declines in weakfish abundance have raised concern among stakeholders, with respect to sensitivity of current stock assessment methods and violations of error-free catch at age. Population dynamics of weakfish were explored using Bayesian statistical catch-at-age models that explicitly incorporate ageing uncertainty into the analysis of the weakfish fishery. Several ageing error matrices were constructed to reflect various hypotheses concerning age estimation error, including unbiased and systematic over- and under-ageing. Absolute levels of spawning stock size and recruitment were influenced by age-reading error, although general patterns tended to be similar. The effects of ageing error on estimates of full fishing mortality were minimal, but large differences were observed for age-specific selectivity. Furthermore, the risk of overfishing and being overfished were altered by age-reading error, along with disparate estimates for biological reference points. In summary, relative support exists for negatively biased catch at age and differential ageing uncertainty for weakfish. Here, model comparison avoids overconfident statements regarding the "true" status of the weakfish fishery, especially when the exact form of age-reading error is uncertain. A model-averaging technique can help alleviate concerns for selecting a best model in this situation, and may provide robust inference for management advice.

1. Introduction

Weakfish *Cynoscion regalis* are a marine sciaenid found along the eastern coast of the United States, being most abundant within the Mid-Atlantic Bight (Shepherd and Grimes 1983; Lowerre-Barbieri et al. 1995). Estuarine dependent, weakfish migrate extensively from offshore, overwintering grounds to feed and spawn in nearshore habitats during protracted spawning seasons (Shepherd and Grimes 1983; Lowerre-Barbieri et al. 1995; Lowerre-Barbieri et al. 1996). Coupled with high variation in individual growth, early maturity, and indeterminate fecundity, weakfish exhibit diffuse length-at-age distributions and are relatively short-lived (Shepherd and Grimes 1983; Lowerre-Barbieri et al. 1995; Lowerre-Barbieri et al. 1996; Kahn 2002; Nye and Targett 2008). While weakfish demonstrate high spawning-site fidelity (Thorrold et al. 2001) and latitudinal clines in growth (Shepherd and Grimes 1983; Lowerre-Barbieri et al. 1995), they are currently considered a single unit stock by the Atlantic States Marine Fisheries Commission (ASMFC) (Graves et al. 1992; Cordes and Graves 2003; NEFSC 2009).

Historically, weakfish have supported important commercial and recreational fisheries from Massachusetts to Florida, with approximately 70-90% of commercial harvest occurring in New Jersey, Virginia, and North Carolina (NEFSC 2009). Declining trends in weakfish abundance and subsequent reductions in commercial and recreational landings have been attributed to increases in natural mortality rates, with unknown mechanisms inhibiting the translation of age-0 recruits into exploitable biomass (NEFSC 2009; Jiao et al. 2012). Furthermore, concern has been raised regarding the use of traditional stock assessment methods for estimating weakfish abundance and instantaneous fishing mortality, with particular emphasis on ageing error within the catch-at-age matrix (NEFSC 2009).

Contemporary approaches for assessing fish populations include age-structured models that implicitly assume negligible uncertainty in catch-at-age data (e.g. ADAPT-VPA). These methods are collectively referred to as Virtual Population Analysis (VPA) and utilize recursive algorithms to sequentially calculate abundance at age given catch by age and year and an index of relative abundance from fishery-dependent and/or -independent surveys (Megrey 1989; Hilborn and Walters 1992). Unlike VPA, statistical catch-at-age models (SCA) allow for the incorporation of measurement error in catch and relative abundance indices and provide a flexible framework to incorporate multiple data sources (Fournier and Archibald 1982; Megrey 1989; Hilborn and Walters 1992). In addition, SCAs allow for uncertainty in estimated age compositions, while simultaneously considering stochasticity imposed by the sampling process on relative age frequencies observed within the fishery (Fournier and Archibald 1982; Conn and Diefenbach 2007).

Ageing error matrices (AEM) are often used to account for ageing uncertainty during fisheries stock assessment and define age misclassification rates for the observed age range from sub-sampled harvest (Richards et al. 1992; Punt et al. 2008). Basically, ageing error matrices define the probability of being aged a', given the individual is true age a. Ageing uncertainty arises from the inability of ageing structures to accurately record true age (i.e. process error) and/or the inability of readers to provide accurate and consistent age estimates (i.e. interpretation error) (Campana 2001). Prior to 1990, weakfish were aged using scale samples, until it was discovered that scales tend to negatively bias age estimates (Lowerre-Barbieri et al. 1994). Since then, otoliths have been the primary ageing structure used to infer growth and relative age frequencies for weakfish (NEFSC 2009). Unfortunately, various sources of error still confound the assignment of age to individual fish and incorporating ageing uncertainty into catch-at-age analyses may still be necessary (Kimura and Lyons 1991; Neilson 1992; Pepin et al. 2001; Buckmeier 2002).

The effects of ageing error on age-structured population dynamics can be considerable, especially on the ability to estimate current stock status and subsequent biological reference points used for management. Generally, ageing error leads to comparable trends in key outputs from stock assessment models (e.g. spawning stock biomass (SSB), instantaneous fishing mortality (F), recruitment), but affects absolute levels of estimated population parameters and has the potential to prejudice management actions (Reeves 2003; Bertignac and Pontual 2007). Reeves (2003) found that ageing error had little impact on estimates for SSB and mean F, but could lead to the underestimation of overall recruitment and consequently bias catch forecasts. This has the potential to hinder stock rebuilding programs, as the risk in evaluating alternative management strategies is misrepresented. In contrast to Reeves (2003), Bertignac and Pontual (2007) found that systematic over-ageing led to differing trajectories for SSB, with relative trends in mean F and recruitment being broadly similar. Hence, the potential effects of ageing error on fisheries stock assessment appear context-specific, with respect to data structure and how individual population parameters are treated during estimation.

The propagation of ageing uncertainty into catch-at-age data is not unique, and in fact many inputs for stock assessment models are likely to be impacted by age-reading errors. For example, age-structured indices of relative abundance, lengths at age, weights at age, and maturity at age may all be affected by the misallocation of individuals to erroneous age classes. However, the influence of ageing error on estimates of auxiliary information is dependent upon data sources and whether or not these biological parameters are treated as fixed constants during model fitting. While ageing uncertainty in age-structured indices of relative abundance may play a significant role in driving the population dynamics of age-based assessments, the magnitude of these errors is likely to be survey-specific and information on ageing error for different states and/or laboratories is currently unavailable for weakfish.

The possible effects of ageing uncertainty on estimating historical trends in weakfish abundance and exploitation rates were explored using Bayesian statistical catch-at-age (SCA) models. Empirical and theoretical ageing error matrices were constructed to reflect various hypotheses concerning the role of age estimation error on weakfish stock assessment. Posited models include 1) a statistical catch-at-age model not considering ageing error in catch at age, 2) an SCA model considering ageing error in catch at age using an empirically derived ageing error matrix, 3) an SCA model considering unbiased ageing error in catch at age using a theoretically derived ageing error matrix, 4) an SCA model considering positively biased ageing error in catch at age using a theoretically derived ageing error matrix, and 5) an SCA model considering negatively biased ageing error in catch at age using a theoretically derived ageing error matrix. Model performance was compared using deviance information criterion (DIC) and posterior predictive *p*-values, which attempt to determine model adequacy through discrepancies in observed and predicted values.

2. Materials and methods

2.1 Data

Data used in this study were obtained from the Weakfish Stock Assessment Report of the Atlantic States Marine Fisheries Commission Weakfish Technical Committee (NEFSC 2009). Detailed information on the catch-at-age matrix and relative abundance indices are available from the same report and are only summarized here for brevity.

2.1.1 Catch at age

Catch-at-age data were available for years 1982-2007, including commercial and recreational harvest and discard. Landings were high in the early 1980s, but declined steadily after 1998, reaching an all time low of 1.1 million pounds in 2008. Catch at size was converted to catch at age using appropriate age-length keys developed from biological sub-sampling of landed harvest. Error within ageing techniques, used to assess relative age frequencies within commercial and recreational catches, is considered to be a major source of uncertainty within the catch-at-age matrix (NEFSC 2009).

2.1.2 Relative abundance indices

Seventeen fishery-dependent and -independent surveys were available for weakfish, of which six provided age-structured information, ten provided indices for tuning recruitment (i.e. age 1), and one provided an age-aggregated measure of relative abundance. Out of all the fishery-dependent and -independent surveys available, the National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center (NEFSC) Bottom Trawl Survey was deemed inappropriate for use as an index of weakfish abundance by the Weakfish Technical Committee (WTC) and was excluded. Similarly, the Massachusetts Division of Marine Fisheries (DMF) Trawl Survey was determined to be a poor index of year class strength and was not included in the stock assessment for weakfish.

2.2 Statistical catch-at-age model

The statistical catch-at-age model based on available weakfish fishery data can be written as:

(1) $N_{a+1,y+1} = N_{a,y}e^{-F_{a,y}-M}$

$$N_{A,y+1} = N_{A,y}e^{-F_{A,y}-M} + N_{A-1,y}e^{-F_{A-1,y}-M}$$

$$C_{a,y} = \frac{F_{a,y}}{F_{a,y+M}}N_{a,y}(1-e^{-F_{a,y}-M})$$

$$log_e(C_{a',y}) = log_e\left(\sum_{a'} C_{a,y}p(a'|a)\right) + \varepsilon_C$$

$$F_{a,y} = f_y s_a$$

$$log_e(I_{j,a,y}) = log_e(q_{j,a}N_{a,y}) + \varepsilon_j$$

where *a'* is observed age , *a* is true age, *A* is maximum true age, *y* is year, and *j* is the *j*th relative abundance index. *N* is population size, *C* is catch, *f* is full fishing mortality, *s* is gear selectivity, and *M* = 0.25 is the natural mortality rate (NEFSC 2009). *I* is the relative abundance index and *q* is the catchability coefficient used to describe the proportion of total weakfish caught per unit effort by fishery-dependent or -independent surveys. *p(a'|a)* denotes the ageing error matrix and characterizes the probability of being aged *a'*, given the individual is true age *a*. Observed catch at age and indices of relative abundance were assumed to be log-normally distributed, $\varepsilon_C \sim N(0, \sigma_C^2)$ and $\varepsilon_j \sim N(0, \sigma_j^2)$, as this is a standard assumption in statistical catch-at-age analyses (Quinn and Deriso 1999).

Selectivity-at-age and recruitment were treated as free parameters to be estimated within the statistical catch-at-age models. This avoids any false perceptions in model output from functional misspecification of age-specific selectivity and the stock-recruitment relationship (Butterworth and Rademeyer 2008). Similarly, only measurement error in catch (i.e. observation and ageing uncertainty) and relative abundance indices (i.e. observation uncertainty) were considered, so as to avoid confounding effects of process error in weakfish abundance on discerning the influence of ageing uncertainty during fisheries stock assessment.

2.3 Fishery status evaluation

Relative indicators of stock status were computed according to the method of Shepherd (1982), which combines spawner- and yield-per-recruit models with a stock-recruitment relationship to elicit biological reference points from age-structured analyses (i.e. F_{MSY} and N_{MSY}). In this study, spawning stock size (SSN) was assumed to be the product of age-specific maturity and yearly abundance, while age-1 fish were treated as recruits. The risk of overfishing and being overfished were evaluated using the joint posterior distribution for full fishing mortality (f_y) relative to F_{MSY} and spawner abundance (SSN_y) relative to N_{MSY}, respectively (Jiao et. al 2010). Model comparison was further augmented by contrasting biological reference points obtained from each scenario and their associated risks for stock status (i.e. overfishing and/or overfished).

A key determinant of biological reference points used for fishery evaluation is the underlying stock-recruitment (S-R) relationship that attempts to describe the link between spawning stock size (SSN) and ensuing recruits (R). However, various environmental factors may also drive fluctuations in year class strength, which is further confounded by mis-measurement of spawner abundance and limited contrast in S-R estimates. Misspecification of the stock-recruit functional form can have considerable effects on derived reference points used for management advice. To circumvent this issue, a model-averaging approach was used to provide robust inference with respect to uncertainty in estimates of spawner abundance and recruitment from stock assessment output. Ricker and Beverton-Holt stock-recruitment relationships were fitted to annual estimates of SSN and R drawn from the joint posterior distribution for each scenario (i.e. M1-M5). Fits were obtained by using maximum likelihood estimation assuming a log-normal error structure. The Akaike information criterion (AIC) was then calculated for each S-R relationship to determine the "best" fit for each of the simulated SSN and R values, from which F_{MSY} and N_{MSY} were calculated. If model selection uncertainty was high for a given set of SSN and R estimates (i.e. $\Delta AIC_i < 5$), then Akaike weights were computed and the resultant F_{MSY} and N_{MSY} values were model-averaged at that iteration.

2.4 Ageing error matrices (AEM)

An ageing error matrix characterizes the uncertainty in observed ages by outlining the misclassification rates for fish aged *a'*, given true age *a*. Typically, fish must be aged multiple times in order to estimate an ageing error matrix, with "true age" being defined as the mode or mean of multiple, independent age determinations (Heifetz et al. 1998). Unfortunately, this method ignores the error imposed by assigning "true age" based on multiple observations of an ageing structure. A Bayesian errors-in-variables (EIV) approach can incorporate uncertainty into the estimation of true age, given the observed age readings (Chapter 1). Similar to the ageing error analysis proposed by Richards et al. (1992), the Bayesian EIV approach cannot reliably detect a systematic difference between observed and true age without prior knowledge on the distribution of the bias, as determined through known-age individuals (Heifetz et al. 1998; Punt et al. 2008; Schwarz and Runge 2009). In this study, five ageing error matrices were developed to reflect various hypotheses regarding age-reading errors during weakfish stock assessment (Table 1).

2.4.1 Empirical AEM

Weakfish age-length data were obtained from Wenner and Gregory (2000), where age for the same individual was determined using saggital otolith and scale readings. Assuming otolith-estimated ages provide a more accurate and precise representation of true age, percent agreement between ageing structures was calculated and normalized for ages predominating commercial and recreational harvest (i.e. ages 1-6). While otolith-estimated ages are thought to produce more accurate and precise age estimates, the prevalence of interpretation error during production ageing is not without influence (Kimura and Lyons 1991; Buckmeier 2002).

2.4.2 Theoretical AEM

Richards et al. (1992) proposed a statistical method to estimate ageing error matrices based on the likelihood of observing age a', given true age a and a parameter vector θ. In the commonly used "normal model", θ specifies the age-reading error standard deviation (σ_A) or the parameters used in modeling σ_A. In order to avoid true age estimates that deviate heavily from the observed age reading, the authors penalized the likelihood by the probability of true age for each individual within the aged sample. From a Bayesian perspective, the penalty term becomes the prior and reflects the distribution of true ages in the sampled fish population. Given the parameter vector θ=σ_A and the observed age classes a', the ageing error matrix is defined as

$$(2)\ p(a'|a) = \frac{x_{a',a}(\theta)}{\sum_{a=1}^{A} x_{a',a}(\theta)}$$

where $x_{a',a}(\theta)$ is the discrete log-normal density function. This approach is easily extended to incorporate known biases, although relatively few studies have utilized this technique (Heifetz et al. 1998; Punt et al. 2008).

Following Richards et al. (1992), theoretical ageing error matrices were derived by discretizing the log-normal distribution over the age range currently observed in catch at age for weakfish, constraining $\sum_{a'} p(a'|a) = 1$. Uncertainty in estimating the age-reading error standard deviation (σ_A) was incorporated into the analysis by integrating over the marginal posterior distribution for σ_A, which was obtained from Chapter 1. The marginal posterior distribution for σ_A was estimated using a Bayesian measurement-error growth model in conjunction with otolith-estimated ages assuming unbiased, log-normally distributed ageing errors (Wenner and Gregory 2000; Chapter 1). For models considering a systematic difference between observed and true age (i.e. bias), a constant (i.e. 1) was added to (i.e. over-ageing) or subtracted from (i.e. under-ageing) the known age during construction of the ageing error matrix (Coggins and Quinn 1998).

Inclusion of observed-age plus groups into theoretical ageing error matrices is relatively straightforward, and entails summing the proportion of $p(a'|a)$ that is greater than or equal to the maximum observed age considered in the matrix, up to a pre-specified cutoff (i.e. longevity). However, the paucity of older individuals within aged samples for weakfish precludes this complexity (Chapter 1), as including an observed-age plus group slightly diminishes the potential for under-ageing in the oldest age class. For similar reasons, true-age plus groups were not considered during construction of theoretical ageing error matrices. In this case, considering plus groups within theoretical ageing error matrices is unlikely to change general conclusions, as only $p(a'|a)$ for the oldest age class is substantially altered.

2.5 Statistical estimator

A Bayesian approach was used to construct the joint posterior probability distribution for parameters in the aforementioned statistical catch-at-age models. Prior distributions were assumed to be vague and uninformative, with bounds being defined by biological expectations. For example, age-specific selectivity (s_a) was constrained to be between 0 and 1. The full conditional distribution for the parameter vector θ, where $\theta = R_y$, $N_{a,y=1982}$, f_y, s_a, $q_{j,a}$, σ_j, σ_C, can be written as

$$(3)\ p\left(\theta \middle| C_{a,y}, I_{j,a,y}\right) \propto \prod_y \prod_a \prod_j \mathcal{L}\left(C_{a,y} | R_y, N_{a,y=1982}, f_y, s_a, \sigma_C\right) \mathcal{L}\left(I_{j,a,y} | R_y, N_{a,y=1982}, f_y, s_a, q_{j,a}, \sigma_j\right) \pi(\theta)$$

where $p(\cdot)$ denotes the posterior probability, $\mathcal{L}(\cdot)$ denotes the likelihood function, and $\pi(\cdot)$ denotes the prior distribution.

All models were run with three Markov chains for 20,000 simulations per chain using the software packages WinBUGS version 1.4.3 and R version 2.13.1. Convergence of the Markov chains to the stationary distribution was determined by monitoring trace plots and computing Gelman and Rubin diagnostics. The first 10,000 iterations from each chain were discarded to allow for adequate burn-in and a thinning interval of 5 was used to reduce autocorrelation among iterative samples and improve computational efficiency. A total number of 6,000 iterations were used to summarize the posterior distribution for each model. A summary of prior distributions can be found in Table 2.

2.6 Model performance

2.6.1 DIC

Deviance information criterion (DIC) was used to compare model goodness-of-fit (Spiegelhalter et al. 2002; Ward 2008) and has been shown to be a reliable means of discrimination in catch-at-age analyses (Wilberg and Bence 2008; Jiao et al. 2012). Like other information-theoretic approaches (e.g. AIC), DIC penalizes overparamaterization and descriptive accuracy in order to select effective models with high explanatory power. The DIC can be written as

$$(4)\ DIC = \overline{D} + p_D$$

$$p_D = \overline{D} + D(\bar{\theta})$$

$$D(\cdot) = -2\log\left(\mathcal{L}(y|\theta)\right)$$

where $D(\cdot)$ is the deviance defined as -2 times the log-likelihood of the data y given the unknown parameter vector θ, $\overline{D}$ is the posterior mean of the deviance, $D(\bar{\theta})$ is the deviance evaluated at the posterior mean of θ, and p_D is the effective number of parameters in the Bayesian model as formulated by Spiegelhalter et al. (2002).

2.6.2 Posterior predictive model checks

Posterior predictive p-values were used to conduct posterior predictive model checks in evaluating the ability of posited models to replicate data similar to that observed. Generally, a discrepancy statistic is used to assess model goodness-of-fit based on observed data and the posterior predictive distribution, where the posterior predictive distribution is defined as

$$(5)\ p(y^{rep}|y) = \int p(y^{rep}|\theta)p(\theta|y)d\theta$$

where $p(y^{rep}|\theta)$ is the data distribution for replicated observations y^{rep} and $p(\theta|y)$ is the posterior distribution of the unknown parameter vector θ given the observed data y. The discrepancy measure utilized in this study was the Bayesian residual sum of squares (Gelman et al. 1996), which can be written as

$$(6)\ \chi^2(y;\theta) = \sum_{i=1}^{n} \frac{[y_i - E(y_i|\theta)]^2}{Var(y_i|\theta)}$$

where $E(\cdot)$ is the expectation, $Var(\cdot)$ is the variance, and y_i is the ith observation of the data y or simulated data y^{rep}. The posterior predictive p-value, then, is simply the proportion of times $\chi^2(y^{rep}; \theta) \geq \chi^2(y; \theta)$. The closer the posterior predictive p-value is to 0.50, the more adequate the model is at replicating data similar to that observed.

3. Results

According to the DIC statistic, considering ageing error in catch at age did not increase model goodness-of-fit for weakfish (Table 3). Resultant DIC values were comparable for statistical catch-at-age models utilizing theoretically derived ageing error matrices (M3-M5), while M1 and M2 produced smaller, and albeit, similar DIC estimates. Still, hypotheses suggesting negatively biased catch at age (i.e. M2 and M5) appear to be the most supported, relative to other models incorporating ageing uncertainty. Unfortunately, DIC was unable to identify whether or not considering ageing error in catch at age is beneficial for weakfish stock assessment, as the difference between DIC values for M1 and M2 is trivial ($\Delta DIC_i = 0.9$).

Model performance was further examined using posterior predictive model checks, where discontinuities between observed and predicted catch at age were determined through comparisons with expected values. Scenarios M1 and M4 produced posterior predictive *p*-values closest to 0.50, suggesting improved adequacy of these models to demonstrate posterior predictions in accordance with observed catch at age for the weakfish fishery. However, *p*-values for all models reflect typical discrepancies between observed and posterior predicted catch at age (Table 3), being unable to corroborate substantial improvements in model structure by accounting for age-reading error during statistical catch-at-age analysis for weakfish.

Trends in spawning stock size, recruitment, and fishing mortality were broadly similar for all 5 models, but absolute levels in weakfish abundance differed considerably (Figure 2). Comparable trajectories for population size across scenarios was expected, as all models were calibrated using the same set of relative abundance indices, of which none were assumed to have ageing uncertainty. Statistical catch-at-age models utilizing theoretical ageing error matrices (M3-M5) suggest a decline in spawning stock size (SSN) within the last year of the time series (i.e. 2007), as indicated by the posterior mean for SSN_{2007}, while M1 and M2 denote an increase. Although, there is some congruency among models as to the status of the weakfish stock in 2007, as indicated by the substantial overlap in 95% credible intervals for population size in the last year covered by the assessment. Trends in recruitment were fairly analogous amongst models, with annual changes in year class strength hallmarking the difference between fits. This is especially relevant during the early portion of the time series, where recruitment dynamics appear to be more variable for models incorporating ageing error in catch at age, regardless of the scenario considered (i.e. unbiased, over-ageing, or under-ageing) (Figure 3).

Estimates of full fishing mortality were fairly consistent across scenarios, with similar patterns being produced for selectivity-at-age, except for M4 (Figures 2 and 4). Adjusting for systematic over-ageing (M4) resulted in higher estimates for selectivity of younger ages and lower estimates for selectivity of older ages, excluding the plus group (i.e. age-6+). Still, models considering theoretical ageing error matrices generally allocated wider credible intervals for age-specific selectivity, as well as other population parameters (Figures 2 and 4). This is likely an artifact of greater ambiguity in observed age frequencies for theoretical ageing error matrices, which is perpetuated into posterior estimates of key outputs from stock assessment models, thereby reflecting uncertainty in age compositions as a consequence of age-reading error.

Relative indicators for stock status differed substantially among scenarios, with M1 and M2 resulting in lower posterior median estimates for F_{MSY} and higher posterior median estimates for N_{MSY} (Table 4). Conversely, estimates for F_{MSY} were more variable for M3-M5, while M1 and M2 proposed more precise values for N_{MSY} (Table 4). The greater precision in N_{MSY} values for M3-M5 is likely a reflection of poor S-R fits to posterior estimates of SSN and R for M1-M2, resulting in higher variability for N_{MSY}. The risk of overfishing was high for all five scenarios, but declined for a short period during the mid-1990s (Figure 5). Generally, M3-M5 demonstrated a lower risk of overfishing throughout the time horizon, although all models were in strong agreement for year 2007. The associated risk of the weakfish stock being overfished was more variable across scenarios, although all models were fairly congruent for the most recent years (i.e. 2002-2007). Again, M1 and M2 generally resulted in a higher risk of the weakfish population being overfished, relative to M3-M5.

4. Discussion

The most recent assessment of the weakfish stock inherently assumes negligible uncertainty in catch at age, namely as a consequence of age-reading error. While otolith-based readings have been validated to provide more accurate estimates of age (Lowerre-Barbieri et al.

1994), within- and between-reader variability can still bias inference on population dynamics and exploitation rates (Kimura and Lyons 1991; Reeves 2003; Bertignac and Pontual 2007). Furthermore, ageing uncertainty has the potential to impact our perception of stock status and associated risks of overfishing and being overfished.

Although ageing error leads to comparable trends in weakfish abundance, the estimates for spawning stock size and recruitment differ substantially in terms of magnitude. Generally, incorporating unbiased or systematic under-ageing led to more optimistic outlooks for population numbers, as well as higher uncertainty in the absolute level of the weakfish stock. Recruitment dynamics also tended to be more variable, as statistical catch-at-age models considering ageing error strengthened cohorts formerly displaced over adjacent ages. This is particularly relevant given the contemporary emphasis on climate change and ecosystem-based approaches to marine fisheries management, with need to identify correlative links between environmental covariates and the driving factors behind spatiotemporal patterns in fish productivity (Bradford 1991; Jiao et al. 2010; Jiao et al. 2012).

The effects of ageing uncertainty on estimates of full fishing pressure were minimal, with comparison among models yielding qualitatively similar patterns. While annual exploitation rates (i.e. f_y) appear to be unaffected by age estimation error, large differences in age-specific selectivity were observed. For instance, systematic over-ageing led to relatively inflated estimates for year class strength and subsequent overestimation of spawning stock size. Basically, the model is associating higher numbers of recruits with lower fishing mortality via decreased age-specific selectivity, so as to reflect inability of fishers to effectively land age-1 individuals. However, adjusting for positively biased catch at age led to anomalous patterns for selectivity-at-age (Figure 4d), with increases in fishing mortality for younger ages. This suggests systematic over-ageing could potentially mask unsustainable fishing practices, as fishers preferentially select for younger ages as a result of declines in older individuals, although M4 was not preferred in this case. The effect of ageing uncertainty on selectivity-at-age is less pronounced for random and negatively biased scenarios, with M2, M3, and M5 producing similar selectivity patterns as M1. At least for weakfish, the nominal effect of ageing uncertainty on estimates of yearly fishing mortality is promising, and harvest control rules that utilize annual exploitation rates may be relatively robust to error in age determinations.

Overall, there appears to be general concordance for negatively biased catch at age and concurrent differential ageing error for weakfish. Scales were the primary ageing structure utilized for construction of age-length keys prior to 1990 and in effort to confer otolith-based age frequency to scale-estimated catch at age, a scale-otolith conversion matrix was applied to historical harvest (NEFSC 2009). Unfortunately, weakfish age- and size-structure fluctuates extensively (Shepherd and Grimes 1983; Lowerre-Barbieri et al. 1995) and the ototlith-scale conversion matrix may have been misrepresentative of past stock dynamics. It is possible that the model considering the empirical ageing error matrix (M2) is better able to reflect the underlying age-structure of the weakfish population, adjusting for measurement error imposed by former scale-estimated ages. Although, the empirical ageing error matrix is merely a comparison between otolith- and scale-estimated ages and does not constitute a "true" ageing error matrix. As such, the empirical ageing error matrix may be preferred over scenarios utilizing theoretical ageing-error matrices, as it more closely resembles relative age frequencies already observed in the weakfish fishery.

When deriving theoretical ageing error matrices, uncertainty in estimated ages was assumed to be age-invariant, although the magnitude of the error was allowed to increase with age (i.e. multiplicative error structure). Results from the current study indicate that ageing uncertainty is likely a function of age, and exploration into more flexible relationships for modeling the ageing error variance is suggested (Richards et al. 1992, Heifetz et al. 1998, Punt et al. 2008). Furthermore, connotation exists for negatively biased catch at age (i.e. M2), and while assuming age-independent bias for weakfish would be reasonable (Francis et al. 2010), hypotheses integrating systematic over- or under-ageing were unsubstantiated (i.e. M4-M5). Attempts to model bias as a function of age appear promising (Punt et al. 2008), although caution should be used when applying these methods without known-age individuals.

Implications from the current study on effects of age estimation error for fisheries stock assessment are not without due concern. The assumption of time-invariant ageing uncertainty is likely unrealistic, as well as assuming constant ageing error for spatially-disaggregated landings and the potential influence of spatial variation in weakfish growth on the interpretability of ageing structures (Shepherd and Grimes 1983; Lowerre-Barbieri et al. 1995). In addition, this study assumed a constant vector for maturity at age and ignored the possible mitigating influence of ageing uncertainty on estimates of weight-at-age in calculating spawning stock biomass (Reeves 2003). Recent stock assessments and projections for the weakfish fishery assume that maturity at age is fixed and ignoring ageing error during estimation of weight at age is likely unreasonable, especially in calculating long-term yield and subsequent biological reference points. In order to avoid this issue, weight at age was not used for fishery evaluation and relative indicators of stock status were re-parameterized in terms of absolute numbers.

While the findings presented here are consistent with those acquired by Reeves (2003) and Bertignac and Pontual (2007), their conclusions regarding age estimation error and management advice seem premature. Unrealistic assumptions of model structure often preclude the use of absolute values in setting management targets, with decision-making being informed by relative trends in key population parameters. However, even with precautionary reference points and risk-averse harvest control rules, our ability to perceive stock status and associated risks can be hindered by age-reading error. Not to mention, ageing uncertainty has the potential to influence our ability to evaluate the efficacy of former management strategies on meeting conservation objectives. Model averaging is one method to provide robust inference for management advice when model selection uncertainty is high, as is the case here (Jiao et al. 2008). Whether or not age estimation error should be integrated into statistical catch-at-age analysis for weakfish is still unclear and it is recommended that Bayesian model-averaging be applied to circumvent ambiguity in weakfish population dynamics as a result of measurement error in observed ages.

The overarching goal of this study was to investigate the sensitivity of current stock assessment methods to unrealistic assumptions of error-free catch at age. However, it is also worth mentioning that changes in age frequency could be attributed to non-stationary population dynamics or time-varying age-specific selectivity. Concurrent research suggests that changes in natural mortality, and to a lesser extent selectivity-at-age, are contributing factors for declining trends in weakfish abundance (Jiao et al. 2012). Moreover, perceived trajectories in population size are likely a culmination of ageing error and annual changes in natural mortality rates, both of which have severe repercussions on the ability to estimate age-specific selectivity (He et al. 2011). Future consideration should be given to the ability of statistical catch-at-age analyses to effectively estimate age-specific selectivity and natural mortality in the presence of ageing uncertainty, along with the ability of model selection criterion to select for analyses integrating ageing error when it is appropriate to do so.

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Legends of figures

Figure 2-1: Commercial and recreational harvest for weakfish.

Figure 2-2: Marginal posterior distributions for weakfish spawning stock size (SSN), recruitment, and full fishing mortality. Solid line indicates the posterior mean, while grey regions correspond to 95% credible intervals.

Figure 2-3: Coefficients of variation (CVs) for recruitment estimated from the Bayesian statistical catch-at-age models.

Figure 2-4: Age-specific selectivity patterns from models M1-M5. (a) M1, (b) M2, (c) M3, (d) M4, and (e) M5. Lines correspond to 95% credible intervals. See Table 1 for specification of models M1-M5.

Figure 2-5: Fishery status evaluation for differing ageing error scenarios (see Table 1 for specification of models M1-M5).

Figure 2-6: Coefficients of variation (CVs) for catch-at-age from the Bayesian statistical catch-at-age models for ages 1-6+.

Legends of tables

Table 2-1: Ageing error matrices (AEM). M1) Ignore ageing error, M2) empirical AEM, M3) unbiased-theoretical AEM, M4) positively-biased-theoretical AEM, and M5) negatively-biased-theoretical AEM.

Table 2-2: Summary of prior distributions used in solving the Bayesian statistical catch-at-age models.

Tables 2-3: Bayesian statistical catch-at-age model performance using deviance information criterion (DIC) and posterior predictive *p*-values for catch at age. See Table 1 for specification of models M1-M5.

Table 2-4: Summary of posterior distributions for biological reference points F_{MSY} and N_{MSY} (in 1E6 fish), including posterior median, standard deviation (S.D.) and 95% credible intervals.

Appendix

Table 2-1

Model 1

	True Age					
Observed Age	1	2	3	4	5	6
1	1.000	0.000	0.000	0.000	0.000	0.000
2	0.000	1.000	0.000	0.000	0.000	0.000
3	0.000	0.000	1.000	0.000	0.000	0.000
4	0.000	0.000	0.000	1.000	0.000	0.000
5	0.000	0.000	0.000	0.000	1.000	0.000
6	0.000	0.000	0.000	0.000	0.000	1.000

Model 2

	True Age					
Observed Age	1	2	3	4	5	6
1	0.917	0.261	0.040	0.004	0.000	0.000
2	0.079	0.675	0.254	0.106	0.019	0.000
3	0.004	0.058	0.665	0.287	0.062	0.000
4	0.000	0.005	0.042	0.575	0.373	0.080
5	0.000	0.000	0.000	0.026	0.522	0.240
6	0.000	0.000	0.000	0.002	0.024	0.680

Model 3

	True Age					
Observed Age	1	2	3	4	5	6
1	0.979	0.064	0.001	0.000	0.000	0.000
2	0.021	0.750	0.244	0.032	0.004	0.000
3	0.000	0.169	0.484	0.290	0.104	0.033
4	0.000	0.016	0.210	0.377	0.313	0.198
5	0.000	0.001	0.052	0.217	0.348	0.377
6	0.000	0.000	0.010	0.085	0.233	0.391

Model 4

	True Age					
Observed Age	1	2	3	4	5	6
1	0.064	0.001	0.000	0.000	0.000	0.000
2	0.750	0.244	0.032	0.004	0.000	0.000
3	0.169	0.484	0.290	0.104	0.033	0.011
4	0.016	0.210	0.377	0.313	0.198	0.116
5	0.001	0.052	0.217	0.348	0.377	0.348
6	0.000	0.010	0.085	0.233	0.391	0.524

Model 5

	True Age					
Observed Age	1	2	3	4	5	6
1	1.000	0.979	0.064	0.001	0.000	0.000
2	0.000	0.021	0.750	0.244	0.032	0.004
3	0.000	0.000	0.169	0.484	0.290	0.104
4	0.000	0.000	0.016	0.210	0.377	0.313
5	0.000	0.000	0.001	0.052	0.217	0.348
6	0.000	0.000	0.000	0.010	0.085	0.233

Table 2-2

Parameter	Prior
f_y	U(0.001,2)
s_a	U(0,1)
Ln(R_y)	U(-20,20)
Ln($N_{a,y=1982}$)	U(-20,20)
Ln($q_{j,a}$)	U(-30,30)
σ_C	U(0.001,10)
σ_j	U(0.001,10)

Table 2-3

Model	*p*-value	pD	$\bar{D}$	DIC
1	0.745	103.5	849.6	953.1
2	0.721	103.1	859.9	954.0
3	0.891	99.8	889.5	989.3
4	0.253	96.9	982.7	1079.6
5	0.874	100.3	880.8	981.1

Table 2-4

	F_{MSY}				N_{MSY} (10^6 Fish)			
Scenario	Median	S.D.	0.025	0.975	Median	S.D.	0.025	0.975
M1	0.604	0.234	0.340	1.143	62.934	58.966	33.808	119.202
M2	0.709	0.318	0.325	1.483	55.646	56.569	32.642	89.638
M3	1.381	0.398	0.747	2.000	31.437	6.138	23.349	44.794
M4	1.176	0.336	0.753	1.909	26.552	5.767	17.527	38.808
M5	1.410	0.509	0.565	2.000	49.887	10.388	37.393	72.877

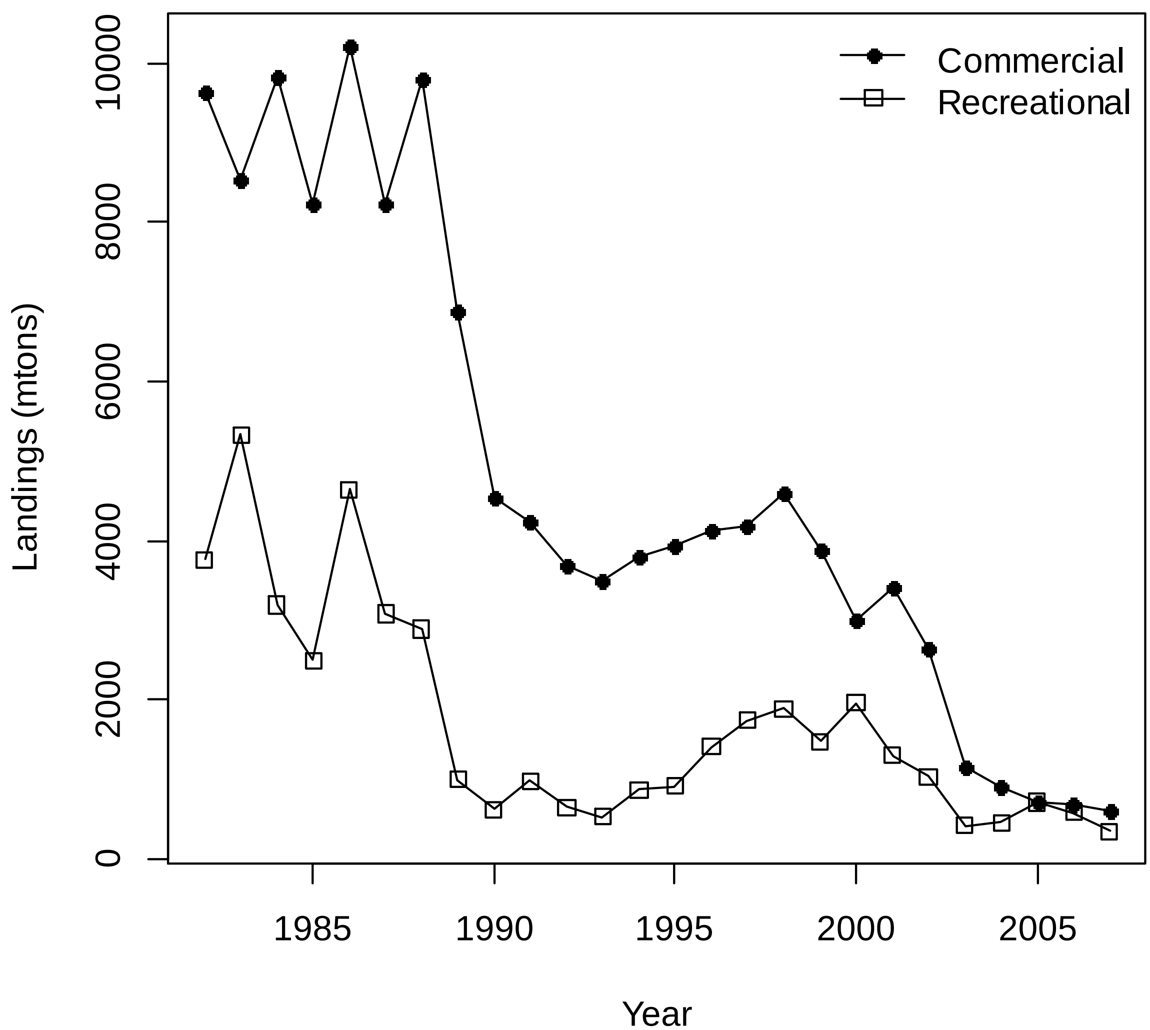
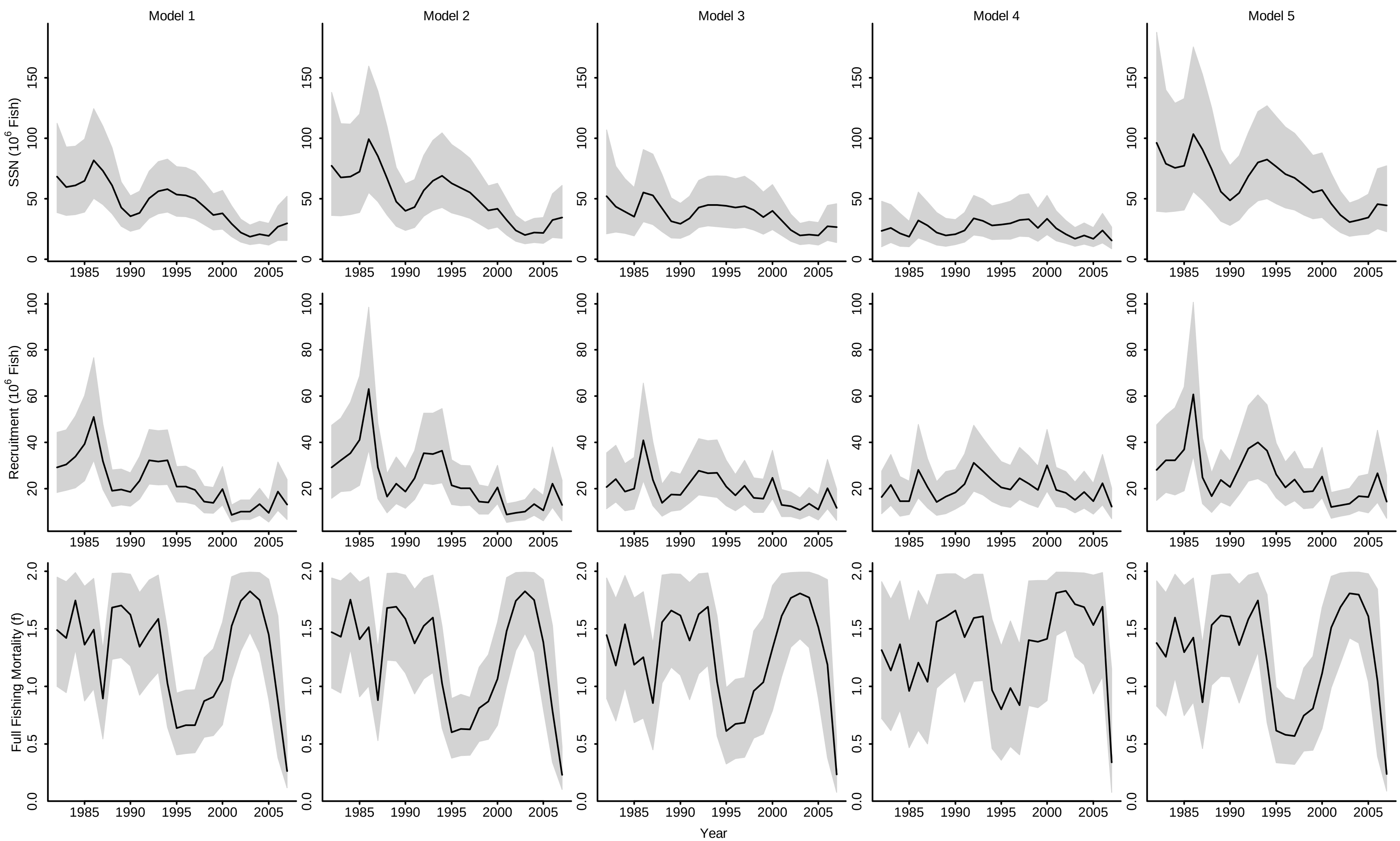

Commercial
Recreational
Landings (mtons)
0
2000
4000
6000
8000
10000
1985
1990
1995
2000
2005
Year

Figure 2-1



Model 1
Model 2
Model 3
Model 4
Model 5
SSN (10^6 Fish)
Recruitment (10^6 Fish)
Full Fishing Mortality (f)
Year

Figure 2-2

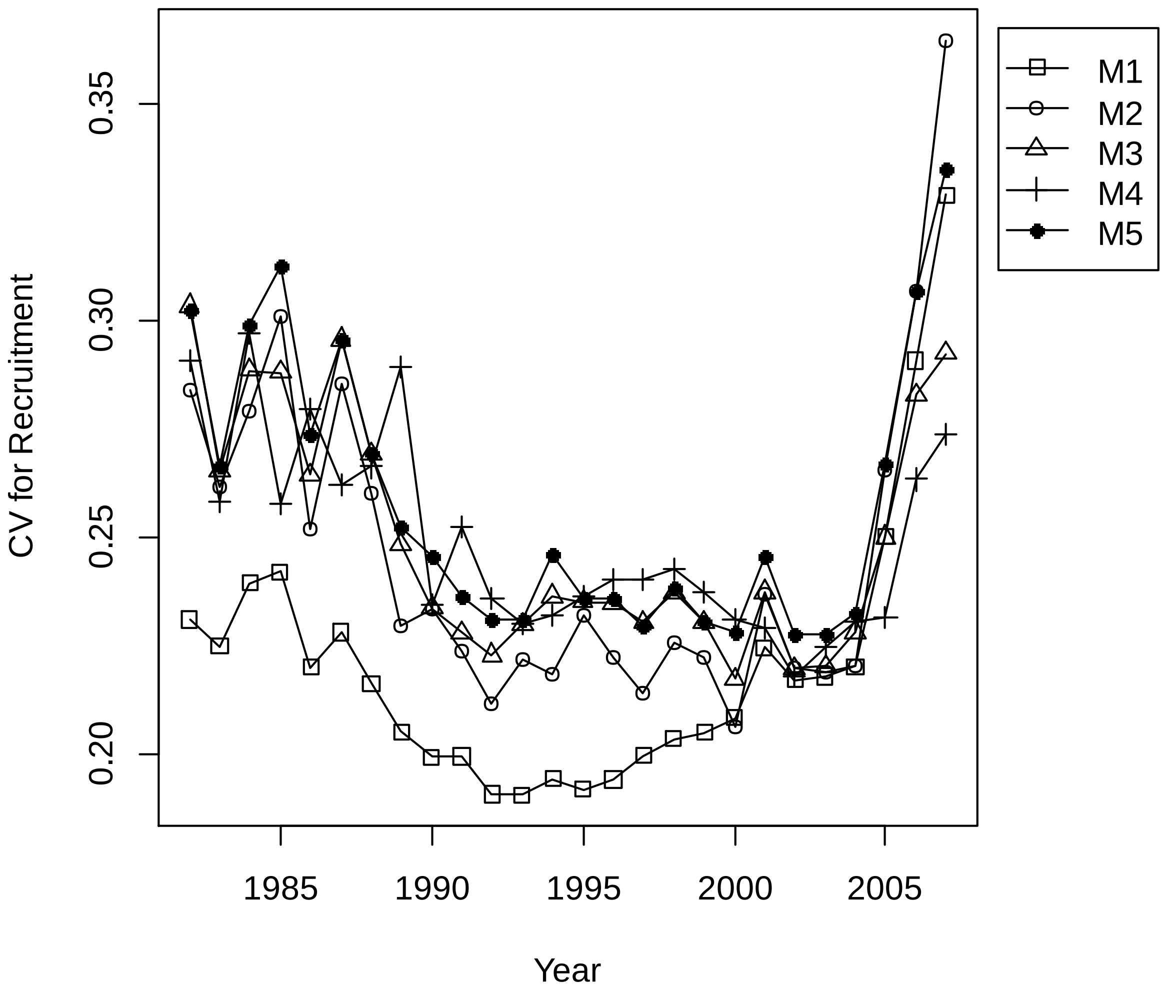

M1
M2
M3
M4
M5
CV for Recruitment
0.20
0.25
0.30
0.35
1985
1990
1995
2000
2005
Year

Figure 2-3

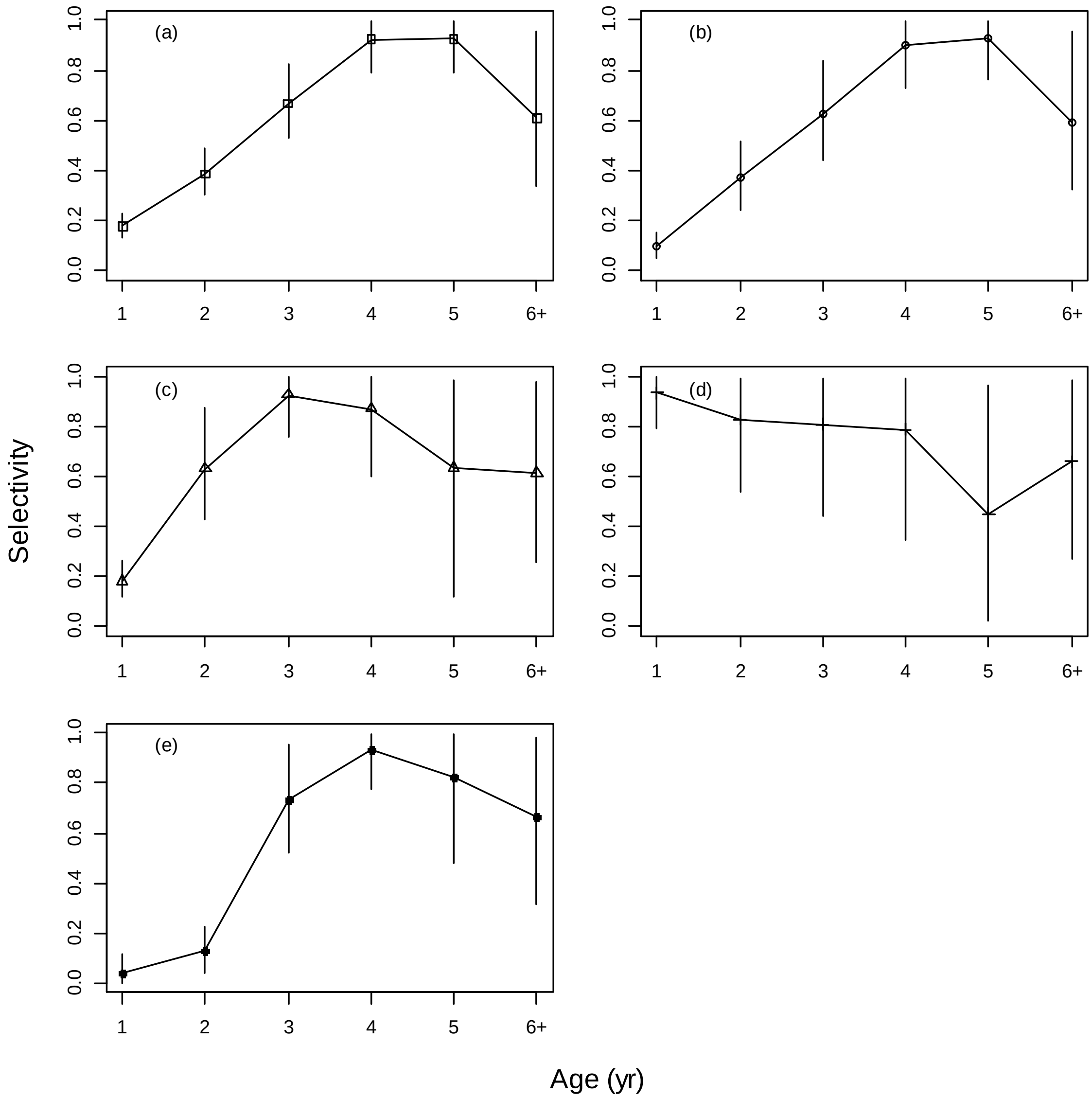
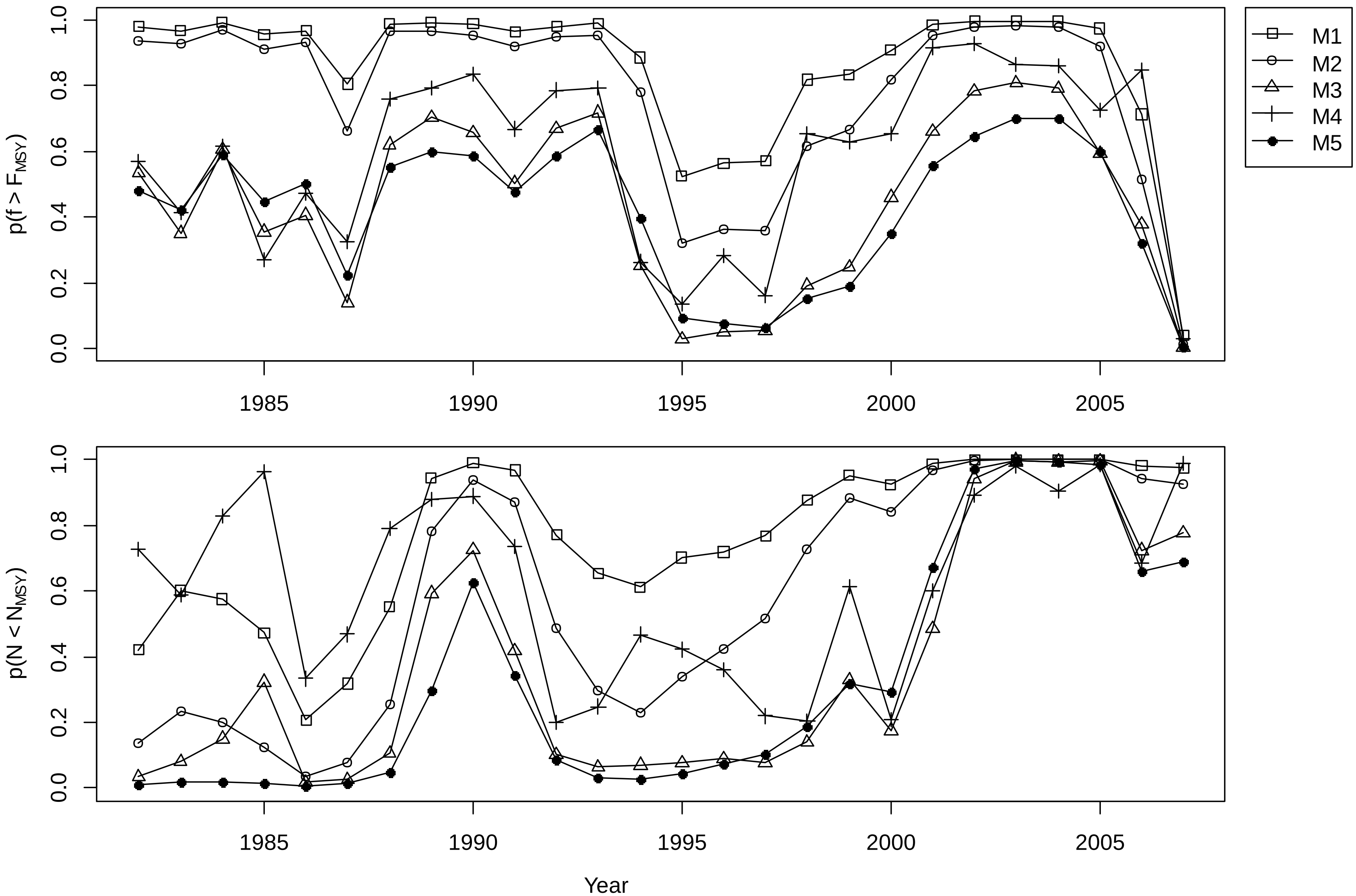


Figure 2-4



M1
M2
M3
M4
M5
p(f > F_{MSY})
p(N < N_{MSY})
0.0
0.2
0.4
0.6
0.8
1.0
1985
1990
1995
2000
2005
Year

Figure 2-5

Chapter 3: Stochastic simulation concerning the effects of ageing error during fisheries stock assessment for weakfish *Cynoscion regalis*

Abstract

Current methods for assessing weakfish stock dynamics assume negligible uncertainty in catch-at-age, as well as ancillary information used to calibrate estimates of population abundance. Unfortunately, error within ageing techniques, used to assess relative age frequencies within commercial and recreational harvest, is considered to be a major source of uncertainty for weakfish. Monte Carlo simulations were used to gauge the robustness of ignoring this type of uncertainty during weakfish stock assessment, as well as the influence of ageing error on relative indicators of stock status. Overall, implications for age-reading error on weakfish stock assessment are varied, depending upon the type ageing uncertainty considered, as well as the underlying structure of the stock assessment model. While ageing error has the potential to impact absolute levels of estimated population parameters (e.g. fishing mortality and spawning stock size), it plays a lesser role on relative trends of those parameters over time. As such, our ability to correctly allocate the weakfish stock to its appropriate status (i.e. overfishing and/or overfished) is relatively unaffected, regardless of the type of ageing error assumed. Furthermore, assuming negligible ageing uncertainty within age-structured indices of relative abundance appears reasonable, as simulations incorporating age-reading error within fishery-independent surveys showed minor deviations from situations only considering observation noise.

1. Introduction

Productivity of fish populations is largely determined by reproductive output, growth and mortality rates, all of which can vary with age (Caswell 1989). Hence, statistical catch-at-age models have been widely applied and prerequisites for many stock assessment methods include age-structured data (Campana & Thorrold 2001). Age estimation, then, plays a key role in providing scientific advice for management decision-making, with need to evaluate age-structured models in the presence of measurement error in observed ages. Not to mention, effects of age-reading error appear fishery-specific (Reeves 2003; Bertignac and Pontual 2007), requiring case-by-case understanding of ageing uncertainty and its influence on perceived population dynamics and stock status (i.e. overfishing and/or overfished).

Age-based assessments typically portray fish stocks as individual cohorts and consider the effects of age- and year-specific recruitment, growth, and total mortality on underlying population structure (Megrey 1989; Hilborn and Walters 1992). Age-length keys (ALKs) are commonly used to confer age frequency to total catch and entail reliable age determinations from sub-sampled harvest. Error in observed ages will be propagated into stock assessment through misallocation of catch at age and various ancillary information used for calibrating population dynamics and/or elicitation of biological reference points. Consequently, the quality, and to a lesser extent quantity (Coggins and Quinn 1998), of aging information may drive the performance of fisheries stock assessment and influence subsequent management advice.

Variability in age estimates is largely a function of misinterpretation by readers or inability of ageing structures to accurately record true age (Campana 2001). The former and latter sources of ageing uncertainty are referred to as interpretation and process error, respectively, with interpretation error being more prevalent in age determinations, owing to the fact that age validation methods are fundamental to production ageing programs (Campana 2001). The subjective assignment of age to individual fish is largely dependent upon preparation and interpretation of periodic increments innate to ageing structures, and can vary within and between readers, as well as laboratories (Campana and Moksness 1991; Kimura and Lyons 1991; Reeves 2003). The ability to quantify and adjust for ageing error, then, is an important aspect of fisheries stock assessment, as well as the application of Monte Carlo simulations to evaluate consequences of ignoring this type of uncertainty during model fitting.

Currently, stock assessment methods for weakfish assume no error in catch at age, as well as age-structured indices of relative abundance. Prior to 1990, scales were the primary ageing structure utilized for construction of age-length keys, until it was discovered that scales tend to negatively bias age estimates for older individuals (Lowerre-Barbieri et al. 1994). However, using otolith-estimated ages does not guarantee age determinations will reflect true age for sampled fish, as variation within and between readers, as well as laboratories, can still bias inference. Recent declines in weakfish abundance have raised concern among stakeholders, as to the potential ramifications of unrealistic model assumptions on stock assessment performance. Error within ageing techniques, used to assess relative age frequencies within commercial and recreational harvest, is considered to be a major source of uncertainty for weakfish stock assessment (NEFSC 2009).

Implications for violating error-free assumptions of statistical catch-at-age models, with respect to ageing uncertainty, were assessed using Monte Carlo simulations emulating the weakfish fishery. Four ageing error scenarios were investigated, each with a subset of situations that mimic potential realizations of age-reading error within fisheries stock assessment for weakfish. Uncertainty in observed ages was introduced into the simulation by applying ageing error matrices to age-structured catch and relative abundance indices, thereby reflecting age-misclassification rates for weakfish. Ageing error matrices were constructed using the methods of Richards et al. (1992) and Coggins and Quinn (1998), see Hatch et al. (*in preparation*) for more detailed information concerning ageing error matrix construction. We would further like to emphasize that this study is not meant as a critique on the current stock assessment or management approach for weakfish, but simply an investigation into the sensitivity of age-structured methods to issues with data quality.

2. Methods and materials

A Monte Carlo simulation was used to evaluate the effects of age-reading error on fisheries stock assessment within a statistical catch-at-age framework. Simulated data sets were generated based on the weakfish stock (Hatch et al. *in preparation*), although general conclusions should be applicable to fisheries with similar characteristics. Output from the data-generating model included true catch- and abundance-at-age, as well as known age-structured indices of relative abundance. True catch at age and indices of relative abundance were then manipulated to reflect various scenarios of ageing uncertainty, as well as observation error in fisheries stock assessment. Key population parameters were estimated jointly from generated assessment data using a Bayesian statistical catch-at-age model, and performance measures were calculated by comparing estimates with known, true values. Performance measures were then summarized across simulation replicates to provide an overall, relative measure of ageing uncertainty and its influence on stock assessment quality. Full descriptions of the simulation approach used in this study are presented below.

2.1 Statistical catch-at-age model

The same set of equations was used in generating assessment data, as well as estimating population parameters, and can be written as

(1) $N_{a+1,y+1} = N_{a,y}e^{-F_{a,y}-M}$

(2) $N_{A,y+1} = N_{A,y}e^{-F_{A,y}-M} + N_{A-1,y}e^{-F_{A-1,y}-M}$

(3) $F_{a,y} = f_y s_a$

(4) $C_{a,y} = \frac{f_y s_a}{f_y s_a + M} N_{a,y}\left(1 - e^{-f_y s_a - M}\right)$

(5) $I_{j,a,y} = q_{j,a} N_{a,y}$

where $N_{a,y}$ is the population size of age *a* fish in year *y*, $C_{a,y}$ is the catch of age *a* fish in year *y*, f_y is the full fishing mortality in year *y*, s_a is the age-specific selectivity, and $M = 0.25$ is the natural mortality rate (NEFSC 2009). $I_{j,a,y}$ is the jth relative abundance index for age *a* fish in year *y* and $q_{j,a}$ is the catchability coefficient of age *a* fish used to scale weakfish abundance to the *j*th relative abundance index ($j \in \{1, 2\}$). Catch at age and age-structured indices of relative abundance were further manipulated to represent situations in which ageing error influences misallocation of relative age frequencies (i.e. $C'_{a,y} = \sum_a C_{a,y} p(a'|a)$), where $p(a'|a)$ denotes the ageing error matrix and characterizes the probability of being aged *a'*, given the individual is true age *a*.

Variability in recruitment, initial abundance, fishing mortality, age-specific selectivity, catchability, and measurement error were incorporated into the simulation by drawing known, true values from their joint posterior distribution (Hatch et al. *in preparation*). The joint posterior distribution for key population parameters was obtained from a Bayesian statistical catch-at-age model assuming negligible error within estimated age compositions (Hatch et al. *in preparation*). In this way, a broad range of potential outcomes was simulated to ensure an adequate representation of the influence of ageing error on the stock assessment performance for weakfish.

2.2 Biological reference points

The method of Shepherd (1982) was used to calculate the true and estimated biological reference points (BRPs) for simulated datasets. The posterior medians of estimated abundance-at-age and age-specific selectivity were input for elicitation of F_{MSY} and N_{MSY} values from the age-structured stock assessment model. As recruitment and selectivity-at-age were assumed to be free parameters and not constrained by pre-defined functions, both Beverton-Holt and Ricker stock-recruitment relationships were used in obtaining true and estimated BRPs. Either Ricker or Berverton-Holt stock-recruitment functions were used to calculate BRPs for each simulation replicate (i.e. ΔDIC > 5). If model selection uncertainty was high, then both stock-recruitment relationships were used to calculate BRPs, with the final BRPs being model-averaged at that iteration (Jiao et al. 2008).

2.3 Scenarios and situations

Four ageing error matrices were constructed to simulate various scenarios of age-reading error during weakfish stock assessment (Table 1). An empirical ageing error matrix was assembled based on comparison between scale- and otolith-estimated ages, with the understanding that otolith-estimated ages are more reflective of true ages for weakfish. Three theoretical ageing error matrices were also developed based on the methods of Richards et al. (1992) and Coggins and Quinn (1998), which represent unbiased and biased (over- or under-ageing) ageing-error scenarios. See Hatch et al. (*in preparation*) for a more in depth discussion on the methods used to construct ageing error matrices.

Within any given ageing-error (AE) scenario, six situations were explored to assess the relative contribution of ageing uncertainty in age-structured catch and relative abundance indices on estimating population parameters and biological reference points during fisheries stock assessment. These included no AE (1), AE in catch only (2), AE in one relative abundance index (3), AE in both relative abundance indices (4), AE in catch and one relative abundance index (5), and AE in catch and both relative abundance indices (6). Throughout the course of this study, scenario will refer to the type of ageing error (e.g. over- or under-ageing) and situation will determine how that ageing uncertainty influenced construction of simulated datasets.

2.4 Convergence and performance measures

Inference of ageing error during fisheries stock assessment was based on 100 simulations per scenario, with 2,400 simulations in total. All MCMC samplers were run for 5,000 iterations, with the first 2,500 being discarded, using 3 chains for each simulation. Convergence of the estimator to the posterior distribution was determined by monitoring trace plots for every 10th simulation and ensuring that the $\sqrt{\hat{R}}$ $(\mathrm{i.e.\,potential\ scale\ reduction\ factor})\ < 1.05$ for all parameters in every simulation. Extensive pilot runs were conducted *a priori* to determine appropriate details of MCMC samplers necessary to achieve efficient convergence.

The performance measure utilized in this study was relative estimation error (REE), as defined by

$$REE = \frac{1}{n}\sum_{j}\frac{\hat{\theta}_{j,i} - \theta_{j,i}}{\theta_{j,i}} * 100$$

where j is either age or year and n is the number of simulations. $\theta_{j,i}$ and $\hat{\theta}_{j,i}$ are the true and estimated parameter values for simulation i, respectively. An REE closer to zero indicates an estimation procedure or situation that performs well, relative to all others considered.

2.5 Summary

A Monte Carlo simulation was implemented to examine the effects of ageing error on weakfish stock assessment through the following steps:

1. Draw true values for R_y, $N_{a>1,y=1982}$, f_y, s_a, $q_{j,a}$, σ_C, and σ_j from their joint posterior distribution, thereby emulating uncertainty in estimates of current stock status.
2. Calculate weakfish abundance by age (i.e. 1-6+) and year (i.e. 1982-2007) using equations 1-3, assuming $M = 0.25$.
3. Observe catch at age and age-structured relative abundance indices by drawing log-normal random deviates, with log-means equal to the logarithms of equations 4 and 5, respectively. Set corresponding measurement error variances to those obtained from step 1.
4. Apply ageing error matrix to observed catch at age and/or relative abundance indices to reflect uncertainty in observed age compositions.
5. Estimate key population parameters using equations 1-5, ignoring ageing error in age-structured catch and relative abundance indices, and compute performance measures for stock assessment quality. Only catch at age and age-structured indices of relative abundance are assumed to be log-normally distributed during estimation.
6. Repeat steps 1-5 for N simulation replicates.

3. Results

The stochasticity imposed on simulations by drawing true values from their joint posterior distribution, derived from Bayesian statistical catch-at-age analysis of the weakfish fishery, precludes comparison across simulated scenarios on the implications for ageing error during fisheries stock assessment. As a result, valid inference is restricted within a particular ageing-error scenario and is further influenced by random generation of simulated data sets, requiring careful interpretation of results. Because of the limited number of simulations per situation and scenario, deviations of estimated parameters from their true values may be slightly exaggerated and not truly reflective of all potential outcomes for age-reading error during weakfish stock assessment. Regardless, general conclusions should remain applicable and comparison across scenarios is achieved through evaluation of changes relative to situations with only observation noise (i.e. no ageing error).

It is commonly assumed that trends in fishery-independent surveys are proportional to overall abundance, and as such error within observed age compositions should affect estimates of population numbers. However, assuming negligible ageing uncertainty within age-structured indices of relative abundance appears reasonable, as simulating age-reading error within fishery-independent surveys had little effect on stock assessment performance (as defined by relative estimation error of parameter estimates). This is likely a function of increased variation in trends of relative abundance over time, such that any bias introduced by ageing error is confounded by overall uncertainty in changes of relative population numbers (i.e. bias-variance tradeoff). That being said, ageing error within catch-at-age has a profound effect on the performance of fisheries stock assessment, impacting estimates of age-specific selectivity, recruitment, and, to a lesser extent, full fishing mortality (i.e. f_y) (see Figure 1).

At least for full fishing mortality, the type of ageing error had little effect on general trends in estimates across scenarios, resulting in consistent and less pronounced underestimation, relative to other population parameters (Figure 1). The effect of age-reading error on selectivity and recruitment was more variable, depending upon the type of ageing uncertainty and the resultant fishing mortality estimate (i.e. $F_{a,y} = f_y s_a$), at least for recruitment. The empirical and under-ageing scenarios tended to inflate estimates for fishing mortality, likely a consequence of skewed catch-at-age toward younger ages, resulting in lower estimates for recruitment and spawning stock size, as fishers are perceived to be putting higher pressure on younger ages through increased age-specific selectivity, resulting in fewer individuals throughout the lifetime of a cohort. Conversely, systematic over-ageing and unbiased ageing-error scenarios tended to result in negatively biased estimates for fishing mortality, producing grossly overoptimistic numbers for abundance (relative estimation error for SSN was ~51%, averaged across both unbiased and over-ageing scenarios, relative to the noise only situation). Overestimates for abundance can generally be explained by the perceived shift in selectivity-at-age toward older individuals via unbiased and systematic over-ageing, resulting in lower fishing mortality for younger ages and subsequently increasing estimates for recruitment and spawning stock size.

Elicitation of biological reference points from age-structured models relies heavily on estimates for age-specific selectivity, abundance, and the corresponding stock-recruitment relationship. With that in mind, only minimal effects were observed for relative indicators of stock status, regardless of the type of ageing uncertainty considered (Figure 2). Generally speaking, systematic over-ageing led to slightly inflated levels of fishing pressure, typically beyond that which could be sustained by the fishery, resulting in depleted estimates for abundance and the potential loss of harvest opportunities by fishers. On the other hand, empirical, unbiased, and systematic under-ageing tended to produce slightly optimistic relative indicators of stock status, potentially leading to overexploitation of the weakfish stock. The small deviation in estimates for biological reference points is encouraging, suggesting age-reading error may play a minor role in the management of marine fish populations, relative to impacts of non-stationary population dynamics, selectivity, and/or catchability.

4. Discussion

The effects of age-reading error on weakfish stock assessment are varied, and often depend on the underlying ageing error matrix, reflecting the direction and magnitude of ageing uncertainty within age-structured catch and fishery-independent surveys. While age-reading error has the potential to impact estimates of key population parameters, its influence on biological reference points is minimal, generally resulting in correct assignment of weakfish stock status (Figure 2). Furthermore, it appears that ignoring ageing uncertainty within age-structured indices of relative abundance may be reasonable, although further consideration should be given to the role of ageing error on estimates of relative abundance over time, especially with varying degrees of observation noise.

To some extent, the results presented here are merely a reflection of how simulations were developed, as well as the assumed, underlying model structure of the stock assessment. Observed catch-at-age for weakfish is heavily dominated by younger ages (Figure 3), and as such larger discrepancies are expected for ageing-error scenarios that preferentially influence these age classes. Basically, simulated ageing error works to misallocate individuals into neighboring age groups, but not so far as to traverse the true age range. In other words, observed ages are lower and upper bounded by age-1 and age-6+ respectively, with changes in age frequencies of younger individuals driving most of the conclusions for this simulation. As shown in Table 1, age-reading error for older ages tended to be more uncertain, but more consistent across scenarios, while age-reading error for younger ages was more precise, allowing for a larger impact of ageing bias on estimates for fishing mortality and recruitment. This may also explain why our study showed a clear distinction between unbiased and biased ageing-error scenarios, as opposed to the findings of Reeves (2003), although our results are consistent with those obtained by Coggins and Quinn (1998) and Bertignac and Pontual (2007). This discrepancy may be further explained by the order of magnitude in ageing bias considered across studies (Bertignac and Pontual 2007), and the fact that we modeled population numbers, instead of population biomass, which has been shown to smooth differences in estimates of spawning stock size across age-reading error scenarios, although this phenomenon is likely fishery-specific depending upon how growth is modeled (Reeves 2003). Similarly, some of the results presented here may be an artifact of using posterior medians to reflect parameter estimates across simulations.

Empirical and under-ageing scenarios tended to produce similar results, while parameter estimates for unbiased and over-ageing scenarios were also comparable. This is likely a result of similarity amongst ageing error matrices, due in part to the assumed skewed nature of age-reading error for weakfish. Age-reading error was assumed to be log-normally distributed, resulting in stronger underestimation of observed ages for older age classes, which is somewhat reflected in empirical observations between scale- and otolith-estimated ages (Table 1). For younger ages, underestimation is less pronounced, allowing unbiased and over-ageing error scenarios to be more alike, relative to the empirical and under-ageing error scenarios. On a similar note, unbiased and over-ageing scenarios tended to result in larger deviations for estimates of key population parameters, relative to empirical and under-ageing scenarios. Again, this is likely a consequence of unbiased and over-ageing error matrices more heavily re-distributing predominate age-classes within age-structured catch, which causes larger departures of parameter estimates from their true values.

Several other caveats of the simulation need to be addressed before adequate implications from this study can be drawn for use in a management-oriented context. First, plus groups were not considered during construction of ageing-error matrices, largely in part because their inclusion would greatly diminish the potential for under-ageing of age-6 individuals. However, this would likely decrease ageing uncertainty for older ages, allowing for a stronger impact of ageing bias on stock assessment results, and further investigation into its effect is recommended. Secondly, ageing error was applied directly to catch-at-age, instead of adjusting relative age frequencies within given length intervals (i.e. age-length keys), which are used to confer age composition to total weakfish landings. If growth changes over time or space, effects of age-reading error may be confounded by spatiotemporal trends in the age-length relationship and subsequent derivation of age-length keys. Similarly, age-reading error was assumed to be static over time, although this is likely a reasonable assumption given the strict protocols of many ageing programs for quality control and assurance (Morison et al. 1998).

The influence of age-reading error on weakfish stock assessment largely depends on the type of ageing uncertainty considered, although there is little effect on relative perceptions in key population parameters over time. This appears promising for management, as the role of ageing error in formulating policy may be relatively small, although adjusting for ageing error during fisheries stock assessment is still recommended, as it will allow for a better understanding of population dynamics. Furthermore, age-reading error may have severe repercussions on the ability to predict outcomes of alternative management strategies on future trends in abundance (Reeves 2003; Bertignac and Pontual 2007). As such, it is recommended that a more in-depth management strategy evaluation be undertaken for weakfish, especially in the presence of ageing uncertainty.

While the results from this simulation study appear promising, the general conclusions and inferences regarding ageing error within fisheries stock assessment are limited to the weakfish fishery, as well as fisheries with similar characteristics. The role of age-reading error on estimation of key population parameters and subsequent biological reference points will depend, in large part, on how those population parameters were treated during estimation and whether or not certain parameters were modeled by pre-defined functions. Similarly, ageing error matrices constructed for this study are specific to the weakfish stock, and will likely influence the sign and/or magnitude of over- and/or under-estimation of key population parameters as a result of misallocating individuals to erroneous age classes. As such, caution should be used in extrapolating the results from this study to fisheries whose characteristics are dissimilar to that of weakfish.

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Legends of figures

Figure 3-1: Boxplot of relative estimation error (REE) for full fishing mortality, selectivity, and recruitment. Colors correspond to age-reading error scenarios (i.e. white = empirical, light grey = unbiased, dark grey = over-ageing, and black = under-ageing). See Methods and Materials section for a more in-depth discussion of situations explored during this study. Outliers not shown.

Figure 3-2: Boxplot of relative estimation error (REE) for relative indicators of stock status. Relative estimation error was calculated relative to the situation with no ageing error, so as to remove influences of measurement noise on discerning the overall contribution of age-reading error to estimates of biological reference points. Colors correspond to age-reading error scenarios (i.e. white = empirical, light grey = unbiased, dark grey = over-ageing, and black = under-ageing). See Methods and Materials section for a more in-depth discussion of situations explored during this study. Outlier not shown.

Figure 3-3: Bubble plot of observed catch-at-age for weakfish, as well as total catch over time.

Legends of tables

Table 3-1: Ageing error matrices (AEM). M1) Ignore ageing error, M2) empirical AEM, M3) unbiased-theoretical AEM, M4) positively-biased-theoretical AEM, and M5) negatively-biased-theoretical AEM.

Table 3-2: Summary of prior distributions used in solving the Bayesian statistical catch-at-age models.

Appendix

Table 3-1

Scenario 1

	True Age					
Observed Age	1	2	3	4	5	6
1	0.917	0.261	0.040	0.004	0.000	0.000
2	0.079	0.675	0.254	0.106	0.019	0.000
3	0.004	0.058	0.665	0.287	0.062	0.000
4	0.000	0.005	0.042	0.575	0.373	0.080
5	0.000	0.000	0.000	0.026	0.522	0.240
6	0.000	0.000	0.000	0.002	0.024	0.680

Scenario 2

	True Age					
Observed Age	1	2	3	4	5	6
1	0.979	0.064	0.001	0.000	0.000	0.000
2	0.021	0.750	0.244	0.032	0.004	0.000
3	0.000	0.169	0.484	0.290	0.104	0.033
4	0.000	0.016	0.210	0.377	0.313	0.198
5	0.000	0.001	0.052	0.217	0.348	0.377
6	0.000	0.000	0.010	0.085	0.233	0.391

Scenario 3

	True Age					
Observed Age	1	2	3	4	5	6
1	0.064	0.001	0.000	0.000	0.000	0.000
2	0.750	0.244	0.032	0.004	0.000	0.000
3	0.169	0.484	0.290	0.104	0.033	0.011
4	0.016	0.210	0.377	0.313	0.198	0.116
5	0.001	0.052	0.217	0.348	0.377	0.348
6	0.000	0.010	0.085	0.233	0.391	0.524

Scenario 4

	True Age					
Observed Age	1	2	3	4	5	6
1	1.000	0.979	0.064	0.001	0.000	0.000
2	0.000	0.021	0.750	0.244	0.032	0.004
3	0.000	0.000	0.169	0.484	0.290	0.104
4	0.000	0.000	0.016	0.210	0.377	0.313
5	0.000	0.000	0.001	0.052	0.217	0.348
6	0.000	0.000	0.000	0.010	0.085	0.233

Table 3-2

Parameter	Prior
f_y	U(0.001,2)
s_a	U(0,1)
Ln(R_y)	U(-30,30)
Ln($N_{a,y=1982}$)	U(-30,30)
Ln($q_{j,a}$)	U(-30,30)
σ_C	U(0.001,10)
σ_j	U(0.001,10)

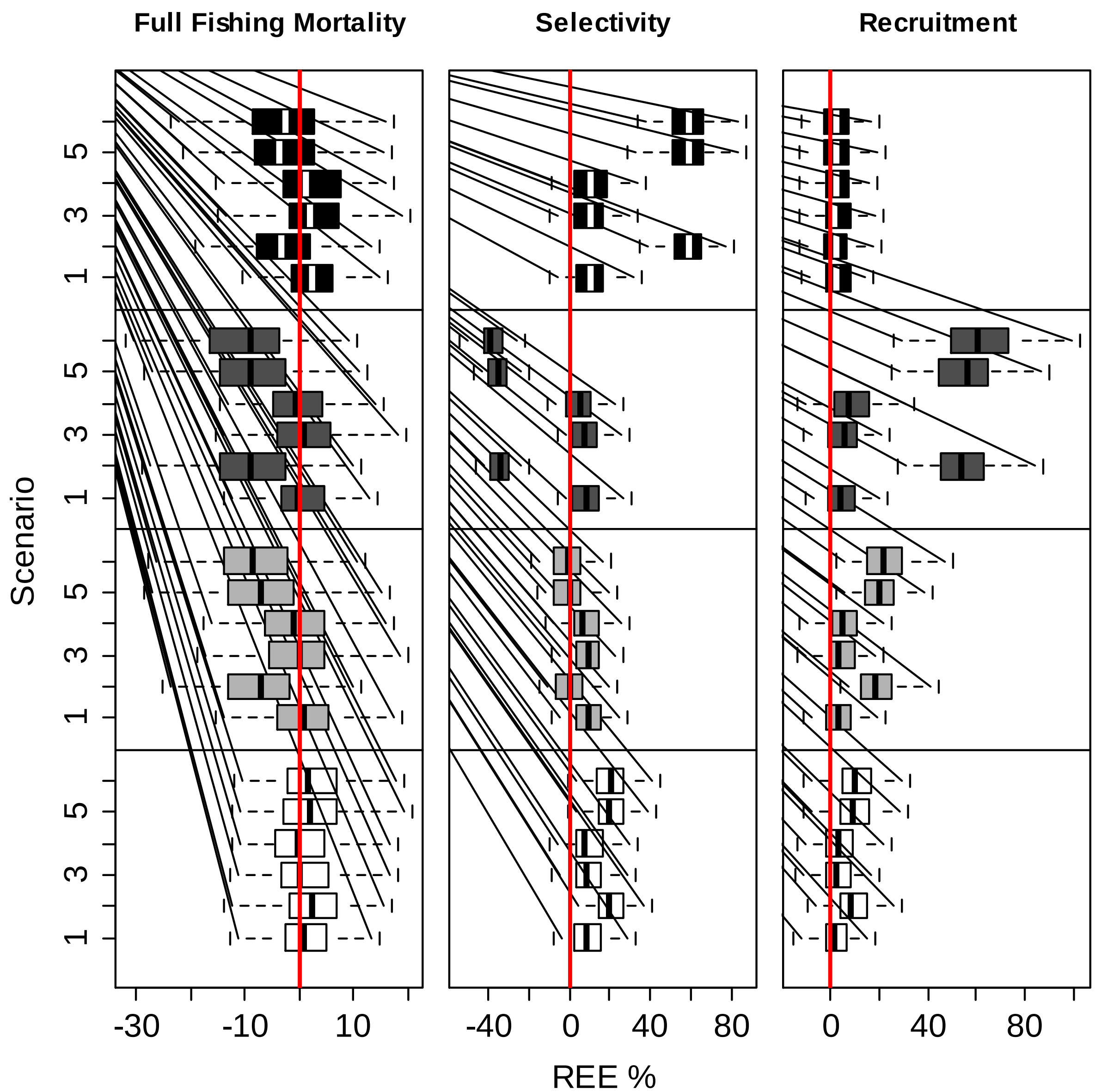
Full Fishing Mortality
Selectivity
Recruitment
Scenario
1
3
5
-30
-10
10
-40
0
40
80
REE %

Figure 3-1

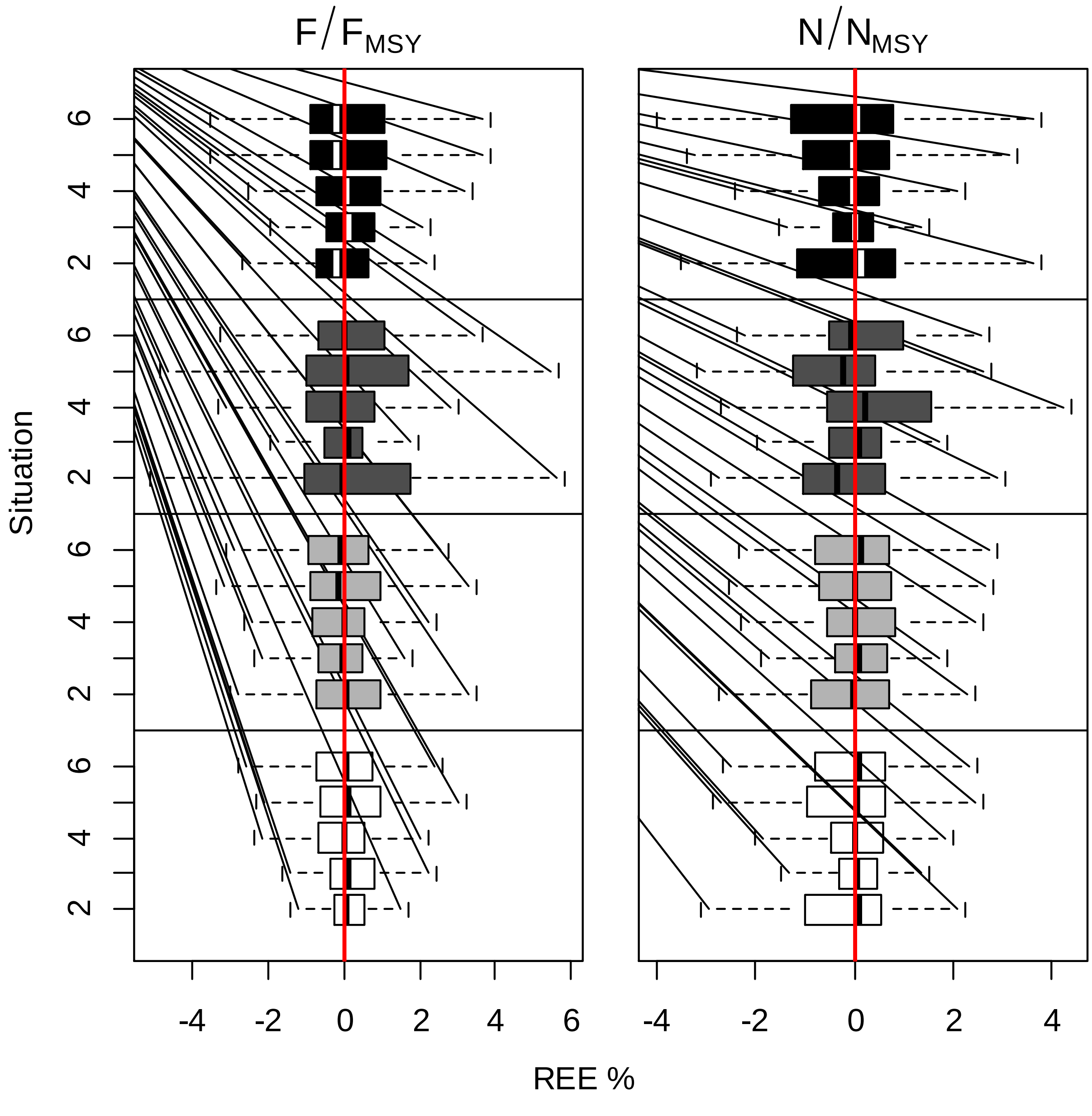

Figure 3-2

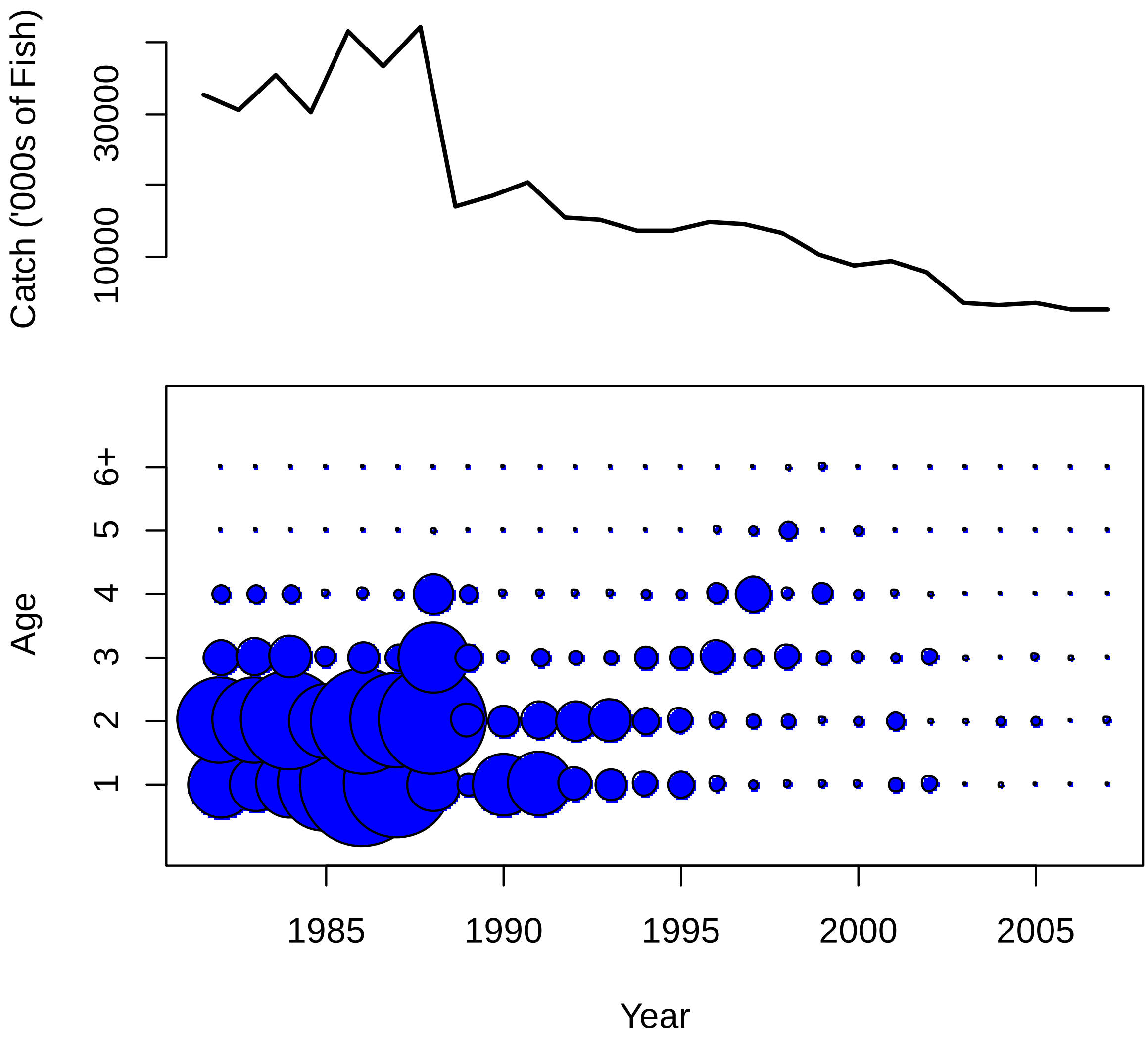
Catch ('000s of Fish)
10000
30000
Age
1
2
3
4
5
6+
1985
1990
1995
2000
2005
Year

Figure 3-3