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Performance of stock assessments with misspecified age- and time-varying natural mortality

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ABSTRACT

Natural mortality (*M*) in fish likely varies with age (size) and among years, and while *M* is often assumed constant over these factors in stock assessments, several methods have been applied to estimate age- or year-specific values. Including age- or time-varying *M* in stock assessments, however, may not produce less biased parameter estimates, despite the increased realism. Two generic fish populations (long- and short-lived) subject to size- and year-varying *M* were simulated, along with data used to fit statistical catch-at-age (SCAA) models. The SCAA models assumed *M* was constant, age-varying, or year-varying, and the bias in estimates of spawning stock biomass (*SSB*), fully selected fishing mortality (*F*), and recruitment was recorded. The scale and trends among years in the bias of parameter estimates were generally driven by how the true values of *M* varied among years and how *M* was treated in the SCAA model. Bias was unaffected by how fishing mortality rates varied among years. The scale and trends among years in the bias of parameter estimates were generally similar when specifying a constant *M* and an age-varying *M* in the SCAA model. Using an annually varying *M* in the SCAA model generally improved the scale, and reduced trends among years in the bias of parameter estimates relative to constant *M* and age-varying *M*. Trends among years in bias were generally more pronounced for estimates of *SSB* than recruitment for long-lived life history simulations, but the opposite was true for short-lived life history simulations. These results suggested that the biases induced by not accounting for age-variation in *M* are likely secondary to those caused by the misspecification of temporal trends (trend and annual fluctuations in this case) in *M*. More time should be dedicated to accounting for temporal shifts in *M* than accounting for age-variation in *M*. The consequences of misspecification of *M* may also partially depend on life history.

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1. Introduction

Natural mortality (*M*) in fish likely varies among ages (sizes) and years. Several analytical and empirical studies demonstrate that *M* likely declines with age (Chen and Watanabe, 1989; Lorenzen, 1996; Chu et al., 2008; McCoy and Gillooly, 2008). Natural mortality may also increase at some relatively older age of senescence, but this is rarely relevant in exploited populations (Chu et al., 2008). The theory behind a decline in *M* with age is that as fish get larger they are susceptible to predation by fewer predators (e.g., through gape width limitations). Swimming speed may also increase with size, permitting prey to better evade predators. Variation in *M* among years can be caused by changes in the abundance of predator or prey species (Overholtz et al., 2008; Tyrrell et al., 2011). Alternatively, temporal changes in the growth of a prey species might induce temporal changes in *M* because body size is related to *M* (Lorenzen, 1996; McCoy and Gillooly, 2008; Gislason et al., 2010).

Although *M* in stock assessments is often specified as constant among ages and years, several methods have been used to estimate age- and time-varying *M* (Vetter, 1988; Lee et al., 2011). Lorenzen (1996) estimated *M* as a negative power function of fish weight. Using data on weights-at-age, age- and year-specific natural mortality rates have been estimated using Lorenzen's relationship and input into stock assessments, such as for Gulf of Maine/George's Bank Atlantic herring *Clupea harengus* (Andrews and Mangel, 2012; NEFSC, 2012). Gislason et al. (2010) estimated *M* as a log-linear function of length and von Bertalanffy parameters. Using data on length-at-age, this relationship was used to develop age-specific values of *M* for sardine *Sardina pilchardus* in the northeast Atlantic (ICES, 2012). Empirical relationships such as those of Lorenzen (1996) and Gislason et al. (2010) have been criticized, however, as

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being imprecise and not accounting for species-specific variations in life history-traits (Brodziak et al., 2011; Maunder and Wong, 2011). Consequently, the estimates that come directly from the relationships given by Lorenzen (1996) and Gislason et al. (2010) are often rescaled to be more consistent with the life history of the species being assessed (Brodziak et al., 2011; ICES, 2012; NEFSC, 2012).

Methods to estimate age- and year-specific values of *M* have also involved multispecies modeling (e.g., multispecies virtual population analysis, MSVPA) or modeling estimates of predation mortality (e.g., predatory consumption) in ways analogous to models of fishing mortality (Hollowed et al., 2000; Moustahfid et al., 2009; A'mar et al., 2010; Garrison et al., 2010). Such methods have largely been applied to pelagic species that are significant sources of forage (Hollowed et al., 2000; Overholtz et al., 2008; Moustahfid et al., 2009). MSVPA has been applied to Atlantic herring, Atlantic mackerel *Scomber scombrus*, and Atlantic menhaden *Brevoortia tyrannus* (Tyrrell et al., 2008; Garrison et al., 2010). A stochastic multispecies model, similar to MSVPA, has also been applied to North Sea Atlantic herring (ICES, 2012). Overholtz et al. (2008) estimated age- and year-specific predation mortality rates for northwest Atlantic herring within the framework of a statistical catch-at-age model, and Moustahfid et al. (2009) applied similar methods to northwest Atlantic mackerel. These multispecies and predation mortality based approaches are subject to uncertainties in the age-based selectivities of the predator "fleets", estimates of predator abundance, food-habits data (e.g., stomach contents and predation rates), and shapes of functional responses (Hollowed et al., 2000; NEFSC, 2012).

Thus, although estimates of age- and year-specific natural mortality rates can be estimated using several methods, they are likely subject to imprecision and bias (Schnute and Richards, 1995; Cotter et al., 2004; Gislason et al., 2010; Lee et al., 2011; Maunder and Wong, 2011). Consequently, stock assessments that switch from using a constant *M* to age- and time-varying values of *M* may not produce less biased parameter estimates, despite the perception of increased biological realism and ecosystem perspective. The lack of a certain benefit to the stock assessment through the inclusion of age- or year-specific values of *M* may be why many assessments continue to use a constant *M* (Maunder and Wong, 2011).

Our objective was to evaluate the performance of stock assessments that have misspecified the true age- and year-specific values of *M* operating on a population of fish. Misspecification of *M* in stock assessments can generate biased estimates of biomass, fishing mortality, selectivity, and catchability (Ulltang, 1977; Lapointe et al., 1989, 1992; He et al., 2011). Misspecification of *M* can also cause spurious trends in abundance estimates and inflate interannual variation in recruitment estimates (Ulltang, 1977; Lapointe et al., 1989, 1992; Clark, 1999). Previous research, however, has generally not included error in input data other than *M* (e.g., catch, indices of abundance; but see He et al., 2011), has only evaluated instances where true *M* did not trend among years, and has generally been applied to virtual population analysis (VPA). Some previous research has also focused on the confounding between misspecified *M* and estimates of selectivity and catchability (Thompson, 1994; He et al., 2011). The present study extended the previous literature by incorporating noise in input data other than *M*, evaluating the effect of simultaneous temporal trends in fishing mortality and *M*, using a statistical catch-at-age framework, and testing the sensitivity of results to general life history (i.e., long- versus short-lived populations). This research also isolated the relative effects of including age-variation in *M* that was time invariant versus time-variation in *M* that was age invariant, rather than evaluating how such modeling choices about *M* are potentially confounded with other parameters (e.g., selectivity and catchability).

Table 1
Parameters defining the population dynamics of the long- and short-lived populations. Equations and detailed parameter definitions are provided in Appendix A.

Parameter	Life history	
	Long-lived	Short-lived
Maturity γ	0.1	1
Maturity τ (cm)	66	15
Recruitment α (R/SSB)	0.012	0.052
Recruitment β	0.06	0.00062
Recruitment CV	0.5	0.5
Growth L_∞ (cm)	90	30
Growth k (a^{-1})	0.24	0.42
Growth a_0	−0.03	−0.7
Growth st. dev.	1	1
Weight length $\ln(\alpha')$	−11.5	−12
Weight length β'	3.1	3.2

2. Methods

2.1. Overview

Simulation models were used to evaluate the extent of bias in parameter estimates from stock assessments with misspecified *M*. Simulation experiments were repeated for two generic fish populations representing two general life histories, long-lived and short-lived, and the characteristics of these populations were described below. To evaluate the effect of time varying dynamics and the sensitivity of results to the relative intensity of fishing and natural mortality rates, simulation experiments were repeated with the true fishing and natural mortality rates each varying among years in four ways (see below). For each unique combination of true dynamics, 1000 datasets each 30 years long were generated for use in fitting statistical catch at age (SCAA) models. Simulation experiments were repeated with *M* misspecified in the SCAA model in one of five ways (see below). The full factorial design resulted in 160 unique combinations (2 life histories × 4 true fishing mortalities × 4 true natural mortalities × 5 misspecified *M* scenarios in the SCAA model). The true population dynamics and datasets for the SCAA models were generated using the Population Simulator Version 7.5 (PopSim; Appendix A; NOAA, 2012). PopSim tracks the true populations by year, 1 cm length bins, and age (Appendix A). The SCAA model used for all simulations was the Age-Structured Assessment Program detailed in Legault and Restrepo (1999) and used for some assessments by the National Marine Fisheries Service (NMFS).

2.2. True underlying dynamics

2.2.1. General population dynamics

The long- and short-lived populations shared the same functional forms that defined their population dynamics, but with different parameters reflecting their life histories. The long-lived population had a maximum age of 50, while the short-lived population had a maximum age of 15. The parameters of a time invariant logistic maturity function of length were specified so that the long-lived population was 50% mature at approximately age-5.5 and the short-lived population at approximately age-1 (Table 1). Parameters of a time-invariant Beverton–Holt stock–recruitment curve were specified to correspond to a steepness of 0.6 for the long-lived life history and 0.85 for the short-lived life history (Table 1; Mangel et al., 2010). The coefficient of variation (CV) defining the noise about the recruitments from the underlying mean relationship equaled 0.5 for both life histories (Appendix A). Parameters of the von Bertalanffy growth equation for each life history differed, with a larger asymptotic size and slower rate of growth for the

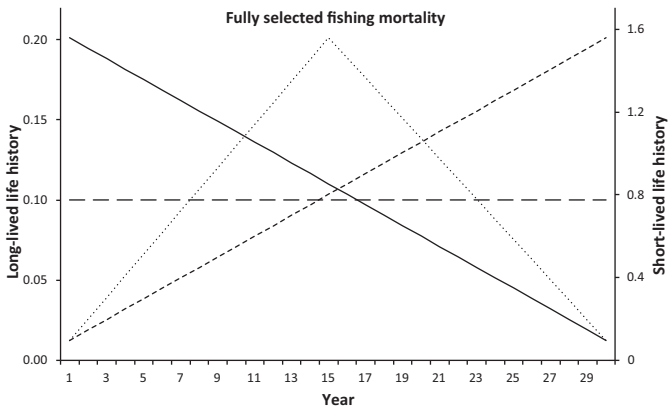

Fig. 1. True, fully selected fishing mortality rates for each year of the simulations for the long-lived and short-lived life histories.

long-lived than short-lived population (Table 1; Appendix A). The standard deviation defining the noise in the expected growth increment specified by the von Bertalanffy growth equation equaled 1.0 for both life histories (Appendix A). Parameters of weight–length relationships also differed between life histories, but were otherwise constant throughout the simulation experiments (Table 1; Appendix A).

2.2.2. True fishing mortality

The long- and short-lived populations were each subject to one fishing fleet. The fully selected fishing mortality rates (F) for this fleet trended among years in four ways: no trend, linear increase, linear decrease, and a linear increase followed by a linear decrease (Fig. 1). The simulation experiment was repeated for each trend in fully selected F. The scale of the mortality rates was lower for the long-lived population than the short-lived population, which reflects differences in their productivity (Fig. 1).

Fishery selectivity differed between long- and short-lived populations, but was otherwise constant throughout the simulation experiments. Long-lived population fishery selectivity was knife-edged at 52 cm, which approximately corresponded to age-3.5. Short-lived population fishery selectivity equaled 1.0 for all sizes and ages. Although perhaps unrealistic, time-invariant asymptotic fishery selectivity was deliberately chosen to simplify the analysis and isolate the effects of M. Time varying selectivity might confound the effects of time varying M.

2.2.3. True natural mortality

True M rates were simulated in a way analogous to a fishing fleet, with a fully selected mortality rate and an accompanying selectivity curve. The fully selected values of M trended among years in the same four ways as the true fully selected values of F and the simulation experiment was repeated for each trend. Unlike the F, the trends in fully selected M were not smooth, but were subject to annual variation that was meant to mimic factors such as changes in the predator field that might induce such noise. The same annual variations were used for all simulations (i.e., new random variables for each year were not drawn for each simulation). As with F, the values for fully selected M were lower for the long-lived population than the short-lived population (Fig. 2). The level of M for older fish that were not fully selected can be inferred from the selectivity curves described below (Fig. S1).

The M selectivity curves differed between long- and short-lived populations, but were otherwise constant throughout the simulation experiments. For both life histories, selectivity curves for M declined with size and increased to 1.0 at a relatively large size to imitate senescence (Fig. S1), which was a pattern supported by several analytical and empirical studies (Chen and Watanabe, 1989; Lorenzen, 1996; Chu et al., 2008; McCoy and Gillooly, 2008). Fish rarely survived to sizes where the selectivity for M increased to 1.0, and so this was a moot feature of the populations. Selectivity for M changed in steps so that a range of lengths had the same selectivity

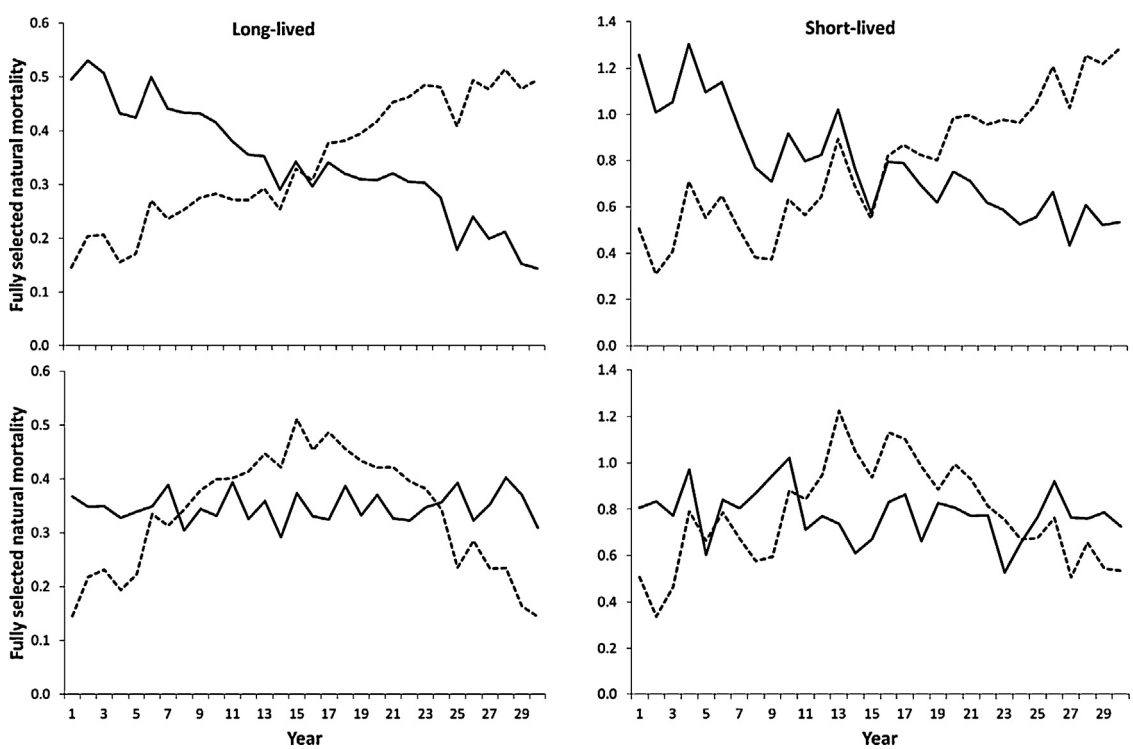

Fig. 2. True, fully selected natural mortality rates for each year of the simulations for the long-lived (left column) and short-lived (right column) life histories. The solid and dashed lines, and upper and lower panels, are only for ease of distinguishing between trends.

value, with each range of lengths approximating a single age (Fig. S1). This method was used so that correct age-specific values of *M* could be more easily approximated in the age-based stock assessment model (see Section 2.3.3.). Although unrealistic, this method represented a compromise between realism and greater control of the process errors in *M*, which this study sought to evaluate.

2.2.4. Initial population

Numbers at age in the first year of each simulation equaled the equilibrium abundances produced at the *F* in year one. For the purposes of determining the equilibrium abundances, *M* was held constant among years and the fully selected values equaled 0.34 yr^{-1} for the long-lived population and 0.78 yr^{-1} for the short-lived population. These fully selected *M* values for each life history type corresponded to the average fully selected *M* among years for any of the true *M* patterns considered (see Section 2.2.3).

2.3. Stock assessment model

2.3.1. Input data

Each simulation experiment included one fishery independent survey with all sizes and ages fully selected and constant catchability (Appendix A). Survey catches were subject to error with a CV of 0.3 for all simulation experiments (Appendix A). Although perhaps unrealistic, the time invariant properties of the survey were deliberately chosen to simplify the analysis and isolate the effects of *M*.

Commercial fishery catch was generated in a way that mimics the methods used by NMFS in the northeast U.S. (Appendix A). Catch was separated into market categories and fish from each market category were randomly sampled to estimate a length frequency. For the simulations here, only one market category was used. The number of fish sampled in each length bin was expanded up by the proportion of the total landings in weight to estimate total catch at length (Appendix A). The estimated total catches at length in each year were converted to estimated catches at age using the year-specific, true, population age-length key. The estimated catches at age may not match the true catches at age, however, because the random sampling of fish to estimate the length frequency for the market category may not match the true length frequency. The number of fish sampled to determine the observed length frequency depended on the amount of landings, and so the degree to which the observed length frequency differed from the true length frequency varied with fishing mortality and population abundance (Appendix A). Consequently, conveying the degree of variation in the age composition data was not straightforward, but sampling levels reflected realistic numbers of samples for some fisheries in the northeastern U.S. No other imprecision or bias was included in the aging process for catches at age.

Total fishery yield was estimated as the sum among lengths of the product of estimated total catches at length, the true weight-at-length (from the weight–length relationship; see above), and a lognormal random error. The errors had a CV of 0.01 for all simulation experiments (Appendix A).

2.3.2. Assessment model configuration and parameters

The SCAA model was configured for both life histories so that the only significant model misspecification was for *M*. This modeling choice was intended to isolate the effects of *M* on parameter bias and avoid confounding with other model misspecification. For both life histories, the SCAA model was given the correct maturity-at-age vector and matrices of mean weights-at-age. The assessment model used a plus group of age-20+ for the long-lived population and age-13+ for the short-lived population.

The input data used to fit the SCAA model were the fishery-independent survey trend, fishery catch age composition, and total fishery yield. The likelihood components for each data source were equally weighted during model fitting. Age-specific selectivity for the fishery independent survey was correctly specified as 1.0 for all ages in all simulations. The annual survey catches were correctly assumed to be linearly related to fish abundance and catchability was estimated using the correct catchability as the initial guess. The true knife-edged selectivity of the fishery at 52 cm for the long-lived population was approximated in the assessment model by assuming knife-edged selectivity at age-4, and results of preliminary simulations were not sensitive to this approximation. The fishery selectivity was correctly specified as 1.0 for all ages for the short-lived population.

The fully selected *F* in the first year of each run of the SCAA model equaled the true value and was not estimated. Fully selected fishing mortality rates in subsequent years were estimated in log space as multiplicative deviations from the *F* in the previous year. No restrictions were placed on the annual *F* deviations, so that each deviation was effectively a free parameter and fishing mortality could continually increase, decrease, or fluctuate throughout the time series. Age specific fishing mortality rates were determined as the product of the year specific, fully selected *F*, and the age based selectivities described above.

The SCAA model also estimated numbers at age in the first year and parameters related to stock–recruitment. Numbers at age in the first year were estimated using the correct values as initial guesses. Steepness and unexploited spawning stock biomass were estimated as parameters using the correct values as initial guesses and defined a Beverton–Holt stock–recruitment relationship (Mangel et al., 2010). Annual recruitment deviations were permitted to deviate from this underlying mean stock–recruitment relationship with a CV of 0.40. Additional details of the SCAA model can be found in Legault and Restrepo (1999).

2.3.3. Natural mortality

Natural mortality in the SCAA model was treated five ways and each treatment misspecified *M* in some fashion. The simulation experiment was repeated for each of the five treatments. Three treatments used a value of *M* that was constant among ages and years: a high, medium, and low value. The long-lived life history simulations used high, medium, and low values of 0.12 yr^{-1}, 0.08 yr^{-1}, and 0.04 yr^{-1}, and the short-lived life history simulations used values of 0.60 yr^{-1}, 0.40 yr^{-1}, and 0.20 yr^{-1}.

One treatment included age-varying *M* that was constant among years (Fig. S2). The age-specific values of *M* were determined by assuming a fully selected *M* of 0.34 yr^{-1} for the long-lived population and 0.78 yr^{-1} for the short-lived population (see Section 2.2.4). The fully selected values of *M* were multiplied by age-specific selectivity values to determine the age-specific *M* values used for all years. The age-specific selectivity values were approximated by converting the true length-specific selectivities to age-specific selectivities using the expected lengths-at-age from the von Bertalanffy growth equation (see Section 2.2.3). Because the growth increments between years defined by the von Bertalanffy equation contained error and the true *M* values were length-specific and not age-specific, some fish in each age group were subjected to an incorrect level of *M*. So, although this method was intended to provide the assessment model with the correct pattern in age-specific *M*, some process error was inevitable.

The final treatment of *M* included annually varying values that were constant among ages (Fig. S3). To determine the annual values, the true fully selected *M*s in each year were multiplied by the approximated age-specific selectivities described above. This process produced a matrix of age- and year-specific *M* values. The annual value input into the assessment was the geometric mean *M* among ages in each year. A geometric mean was used rather than an arithmetic mean so that the annual values for *M* were not

skewed toward young ages that had relatively high *M* values. Thus, the SCAA model was provided with the correct temporal trends in *M*, although with incorrect scaling caused by ignoring the age-variation.

2.4. Output metrics

Relative error (*RE*) was used as a measure of bias in estimates of spawning stock biomass (*SSB*), fully selected *F*, and recruitment (i.e., age-1 abundance) in each year of each simulation:

$$RE = \frac{estimated - true}{true} \times 100$$

(e.g., Wilberg and Bence, 2006). Boxplots were constructed to summarize the results for each year, with bold horizontal lines at the median *RE* among the 1000 simulations, boxes displaying the first and third quartiles (i.e., interquartile range), and whiskers extending to 1.5 times the difference between the third and first quartiles (McGill et al., 1978; Frigge et al., 1989).

Boxplots were qualitatively examined for trends among years in the median *RE*s and the inclusion of 0.0 in the range of the boxes or whiskers. The effect of modeling choices on the results was controlled for by providing the SCAA model with as much correct information as possible within each treatment of *M* (e.g., the approximately correct pattern in age-specific *M* when *M*

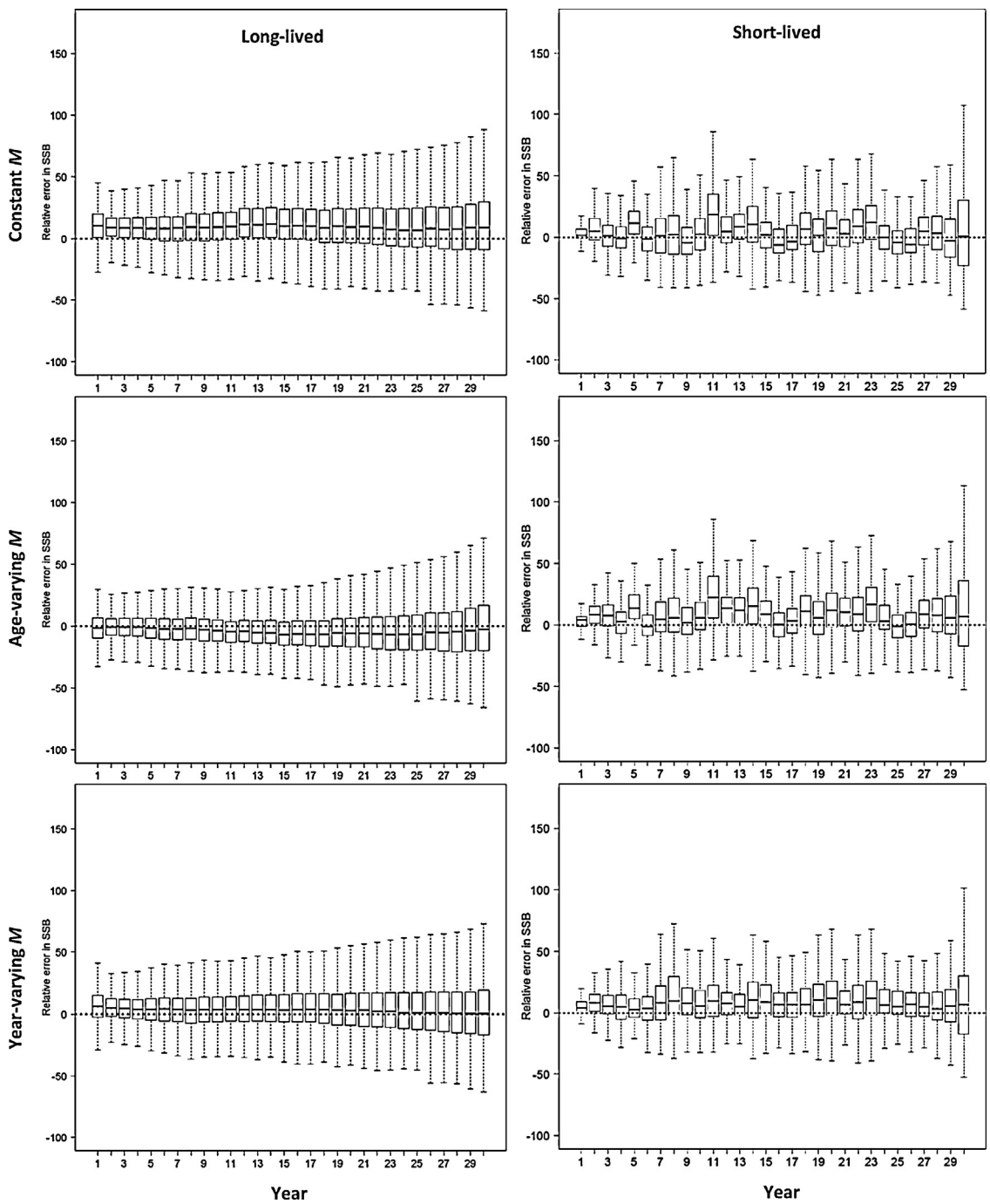

Fig. 3. Box plots of relative errors in estimates of spawning stock biomass from SCAA models using natural mortality rates constant among ages and years (top row), age-specific natural mortality rates constant among years (middle row), and year-specific (i.e., correct trend and fluctuation) natural mortality rates constant among ages (bottom row), for long-lived (left column) and short-lived (right column) life histories. The true fully selected natural mortality rates did not trend among years.

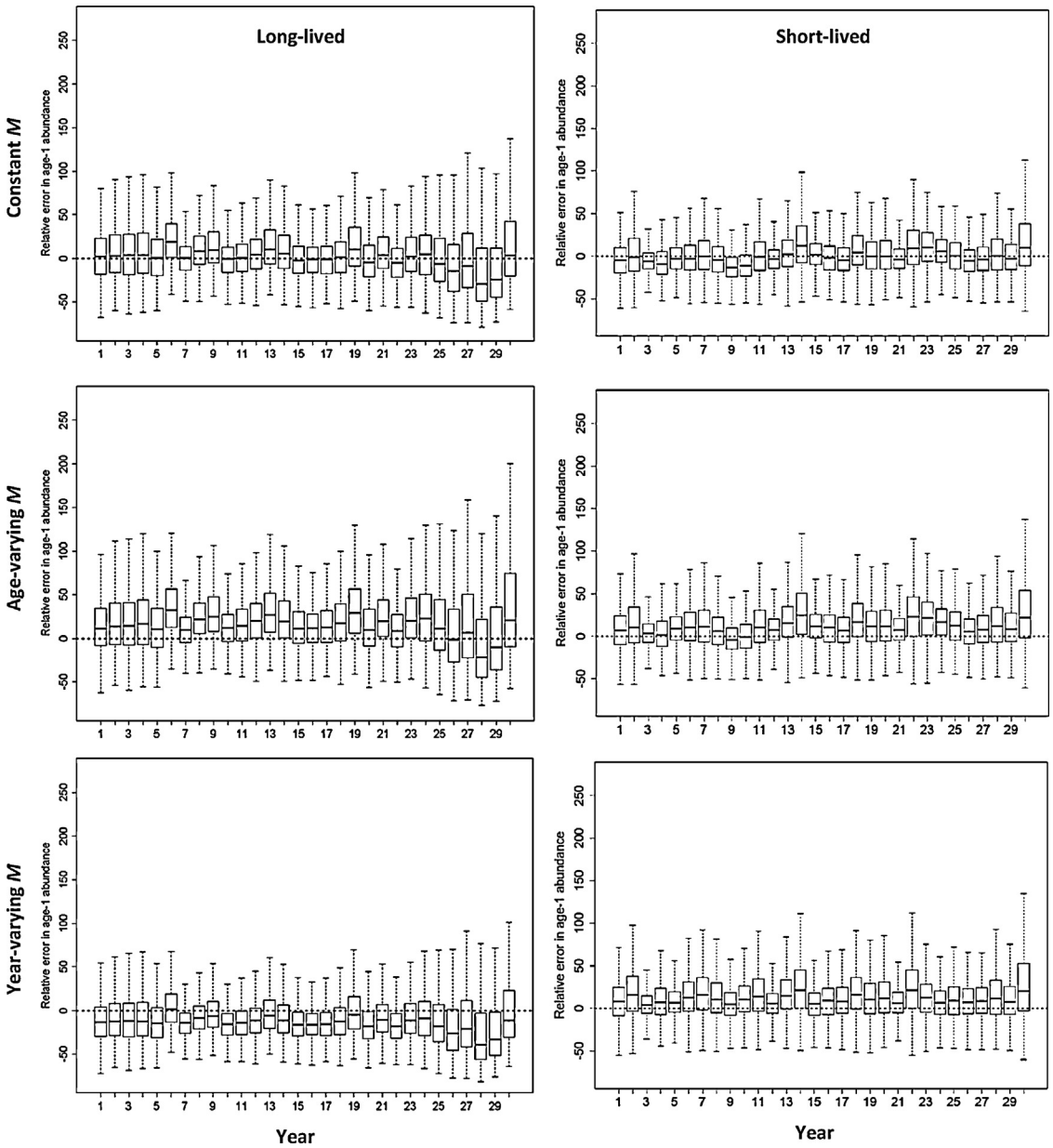

Fig. 4. As for Fig. 3, except for relative errors in estimates of age-1 abundance.

varied with age). The values of *RE*, however, would scale up or down with the values of *M* input to the SCAA model. So, especially the results related to the inclusion of 0.0 in the range of the boxes may depend on the methods used to determine the age- or year-specific values used in the SCAA model. Conclusions, however, would likely be robust to alternative, reasonable modeling choices.

3. Results

3.1. Overview of results not presented in detail

The trend across years in the true *F* had little effect on the *RE*s of the parameter estimates. For example, with all else equal, the trend across years and the scale of the *RE*s were similar regardless of the temporal trend in the true *F*. Consequently, only results for simulations with no trend among years in the fully selected, true *F* are presented below.

Similarly, with all else equal, the *RE*s for simulations with increasing and decreasing true *M*s across years were similar in scale but with inverse sign and opposite trends among years. Consequently, only results for simulations with an increasing trend among years in the fully selected, true *M*s are presented below.

With all else equal, when *M* in the SCAA model was constant among ages and years, only the scale of the *RE*s differed among the high, medium, and low values. So, only the results for high *M* constant across ages and years are presented relative to the alternatives with age- or time-varying *M* in the SCAA model.

3.2. Detailed results

When the fully selected true *M* values had no trend across years, results were generally similar regardless of life history and how *M* was treated within the SCAA model (Figs. 3 and 4 and Fig. S4). Generally, the median *RE*s for *SSB*, fully selected *F*, and recruitment

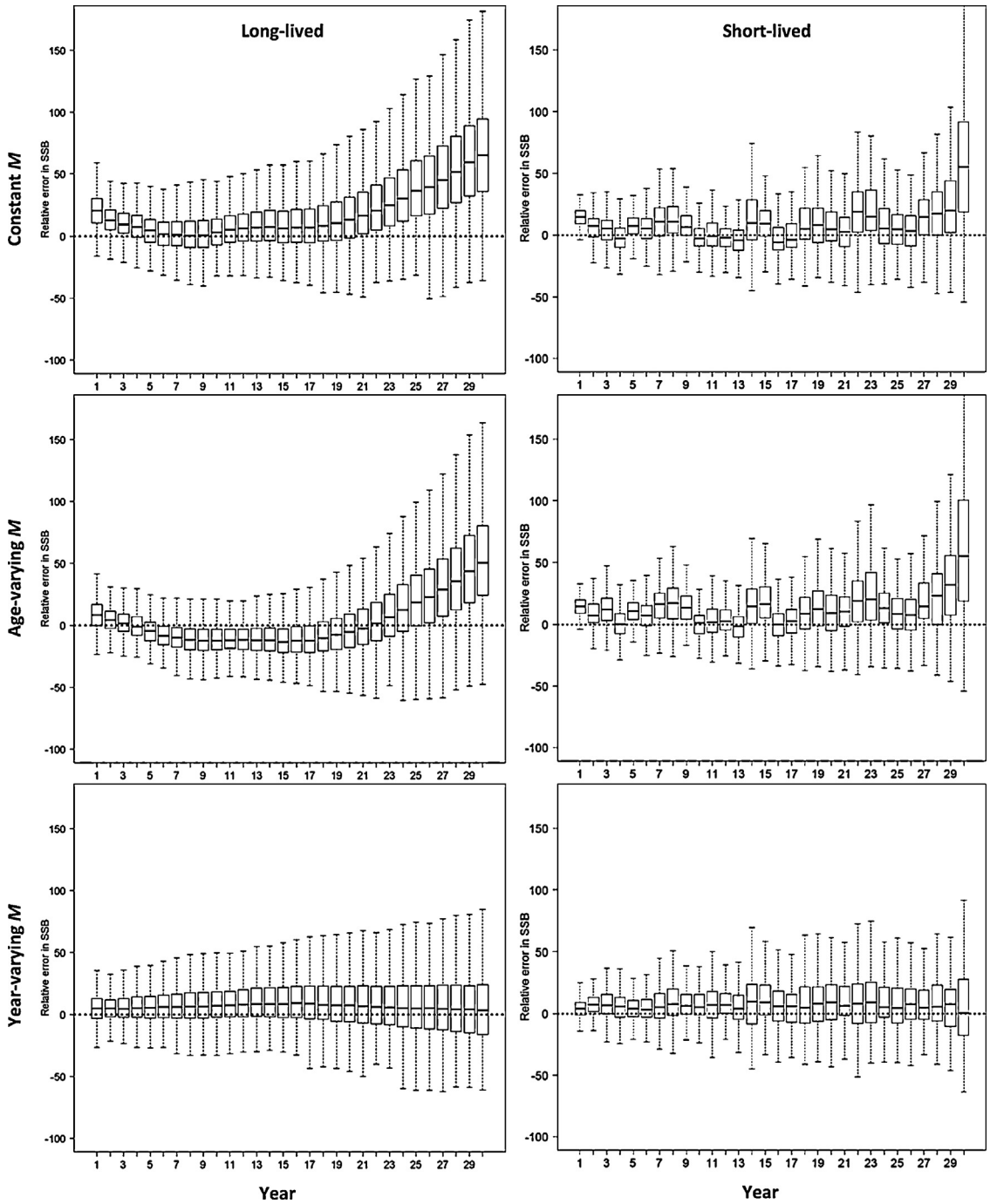

Fig. 5. As for Fig. 3, except the true fully selected natural mortality rates had an increasing trend among years.

did not trend among years and the interquartile ranges included zero.

When the fully selected true values of *M* had an increasing trend among years, results depended on how *M* was treated in the SCAA model (Figs. 5 and 6 and Fig. S5). When *M* in the SCAA model was constant among ages and years or age-variable, the median *REs* for *SSB* increased among years and the interquartile ranges included zero early in the time series but not late in the time series (Fig. 5). This pattern was more pronounced for the long-lived life history. Results for fully selected *F* were similar to *SSB*, except the median *REs* decreased among years (Fig. S5). The median *REs* for recruitment decreased among years and interquartile ranges only included zero for several years in the middle of the time series (Fig. 6). Conversely, when *M* in the SCAA model varied annually (i.e., had the correct trend and annual fluctuations) the median *REs* for *SSB*, fully selected *F*, and recruitment did not trend among years and the interquartile ranges generally included zero (Figs. 5 and 6 and Fig. S5).

When the fully selected true values of *M* had an increasing trend followed by a decreasing trend among years, results depended on life history and how *M* was treated in the SCAA model (Figs. 7 and 8 and Fig. S6). When *M* in the SCAA model was constant among ages and years or age-variable, the median *REs* for *SSB* followed an S-shape among years and this pattern was more pronounced for the long-lived life history (Fig. 7). Results for fully selected *F* were similar to *SSB*, except with inverse sign and opposite trends among years

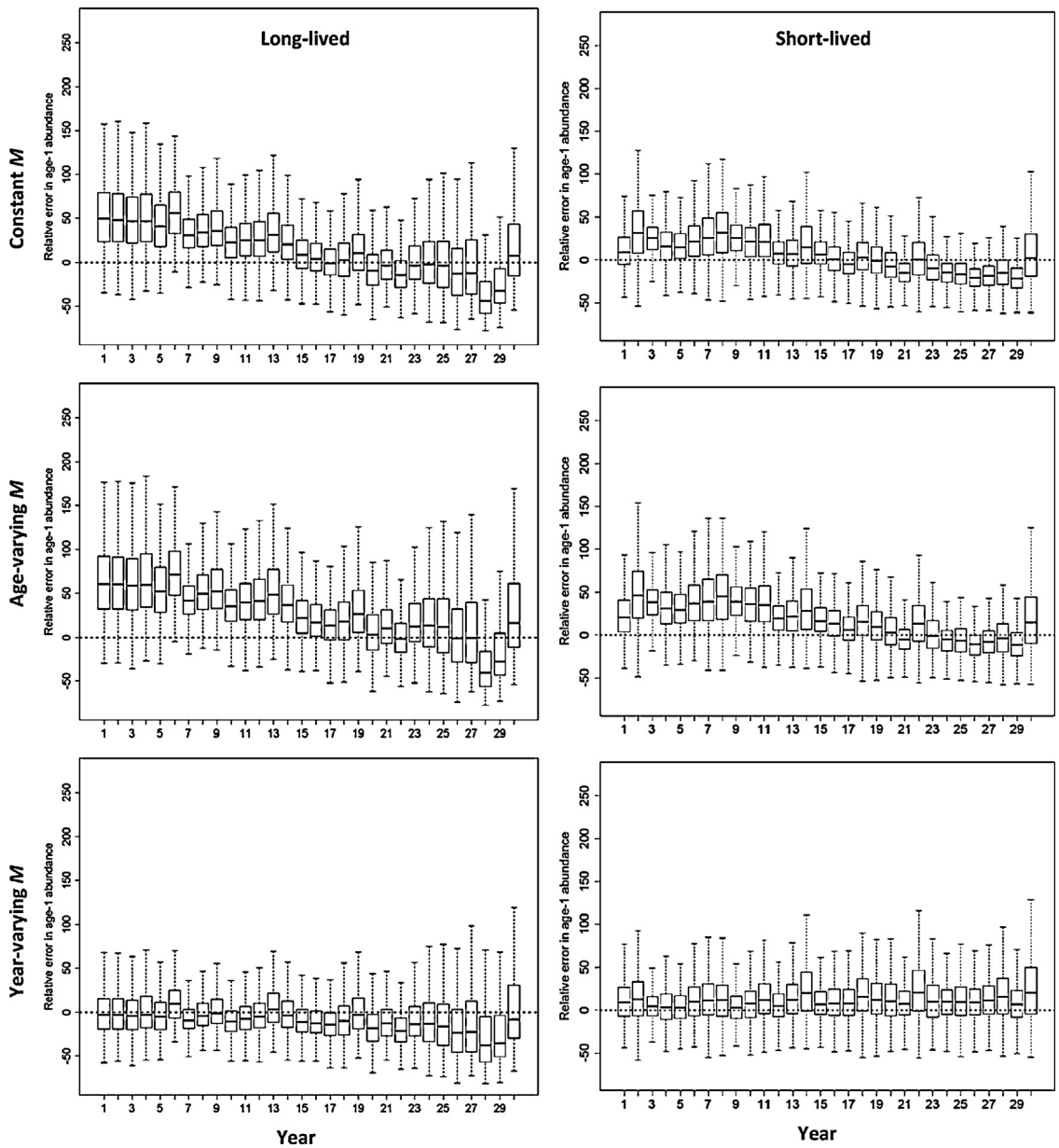

Fig. 6. As for Fig. 3, except for relative errors in estimates of age-1 abundance and the true fully selected natural mortality rates had an increasing trend among years.

(i.e., if *RE*s of *SSB* were positive then *RE*s for fully selected *F* were negative; Fig. S6). The temporal trend in the median *RE*s for recruitment depended on life-history (Fig. 8). For the long-lived life history simulations, the *RE*s for recruitment declined during the first several years but remained relatively stable for the remainder of the time series. For the short-lived life history simulations, the *RE*s for recruitment declined during the first several years but increased for the remainder of the time series. Due to the temporal trends in the *RE*s for *SSB*, fully selected *F*, and recruitment, the interquartile ranges of the *RE*s included zero during some time periods but not others. Conversely, when *M* in the SCAA model varied annually the median *RE*s for *SSB*, fully selected *F*, and recruitment did not trend among years and the interquartile ranges generally included zero for both life histories (Figs. 7 and 8 and Fig. S6).

4. Discussion

In this study, results were robust to the temporal trends in the true, fully selected fishing mortality rates. Lapointe et al. (1989) found that trends among years in the true fishing mortality rate generated spurious trends in recruitment when *M* was misspecified in a VPA, but noted that such spurious trends may not be produced by SCAA type models, such as the one used here. The results of this study did contradict with Lapointe et al. (1989) because the biases in estimates of recruitment were generally robust to the trends in the true fishing mortality rate. If the results of Lapointe et al. (1989) applied in this study, the trend among years in the median *RE*s for recruitment would have differed among the trends considered for the true fishing mortality rates. The reason for this contradiction is likely that *M* was the only parameter misspecified by Lapointe et al. (1989) and so solving the VPA only allowed bias to be placed in the estimates of recruitment. In SCAA type models, such as the one used here, the bias can be spread among various parameters, including recruitment and annual fully selected fishing mortality rates. The inclusion of observation error in this study and the use of auxiliary survey information, which were not included in Lapointe et al. (1989), may also reduce any spurious trends in recruitment estimates.

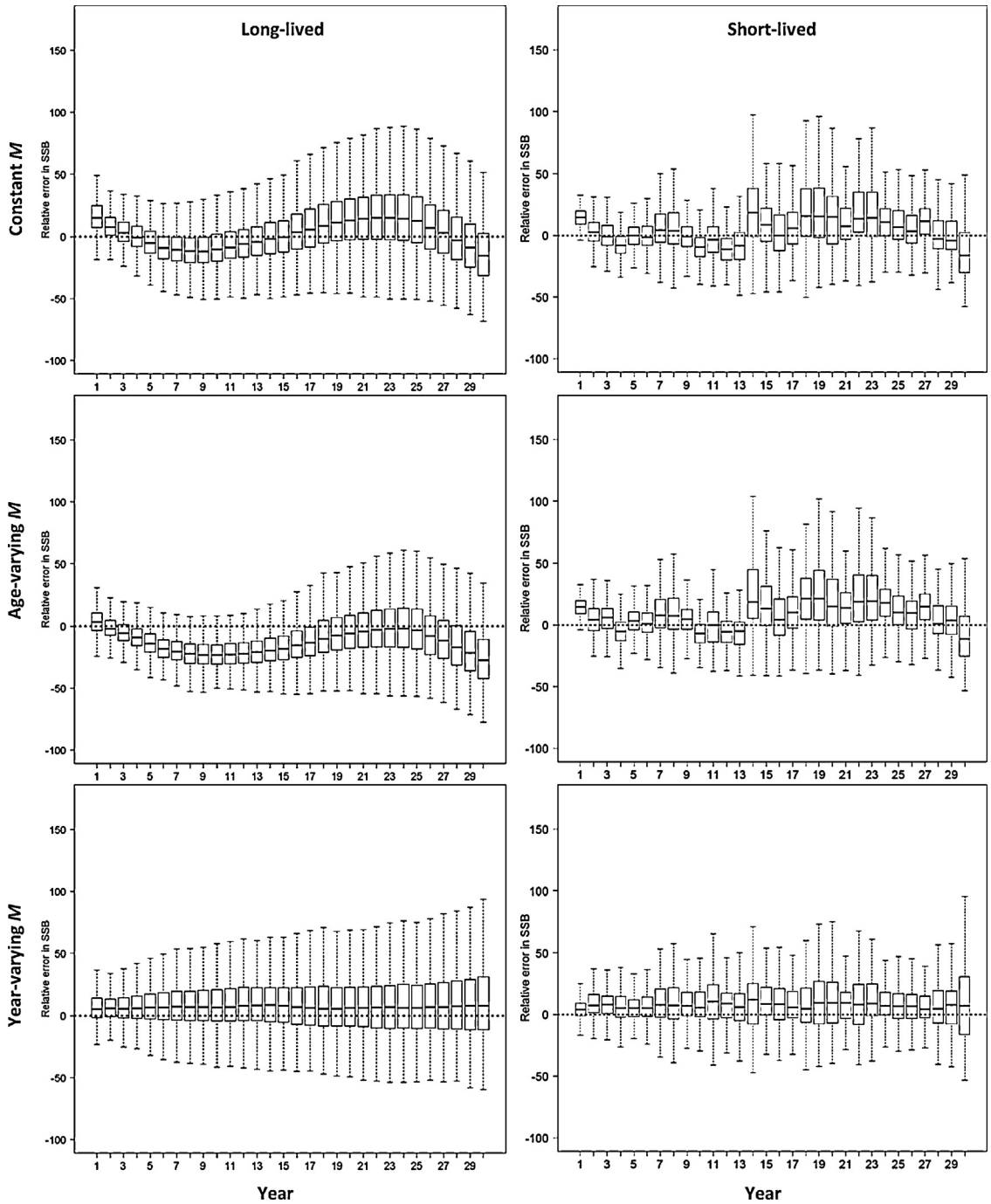

Fig. 7. As for Fig. 3, except the true fully selected natural mortality rates had an increasing trend followed by a decreasing trend among years.

When true *M* varied without trend among years, the three treatments of *M* in the stock assessment (i.e., constant *M*, age-varying *M*, or time-varying *M*) performed about equally well, with no trend in the *RE*s among years and generally unbiased estimates (i.e., interquartiles included zero). Similarly, Lapointe et al. (1992) found that estimates of recruitment were nearly unbiased when true *M* varied among years without trend and a constant *M* was assumed in a VPA. Lapointe et al. (1992) also found, however, that not accounting for the interannual variation in *M* decreased the power to detect correlations between recruitment and environmental covariates. Although unbiased estimates might be produced when interannual variation in *M* is ignored, accounting for such variation may still be beneficial. These conclusions also require specifying an *M* in the stock assessment similar in scale to the true *M*.

The inclusion of age-varying *M*s in the stock assessments in this study performed about equally to using a value of *M* that was constant among ages and years (i.e., similar trends among years in the *RE*s and interquartiles including zero), but including annually varying *M*s that had the correct trend and yearly fluctuations generally improved the *RE*s. The inclusion of age-varying *M* in stock assessments might be expected to improve estimates of recruitment, in particular, because the lifetime mortality of each cohort is more realistically represented, and previous research has found that ignoring age variation in *M* would produce biased

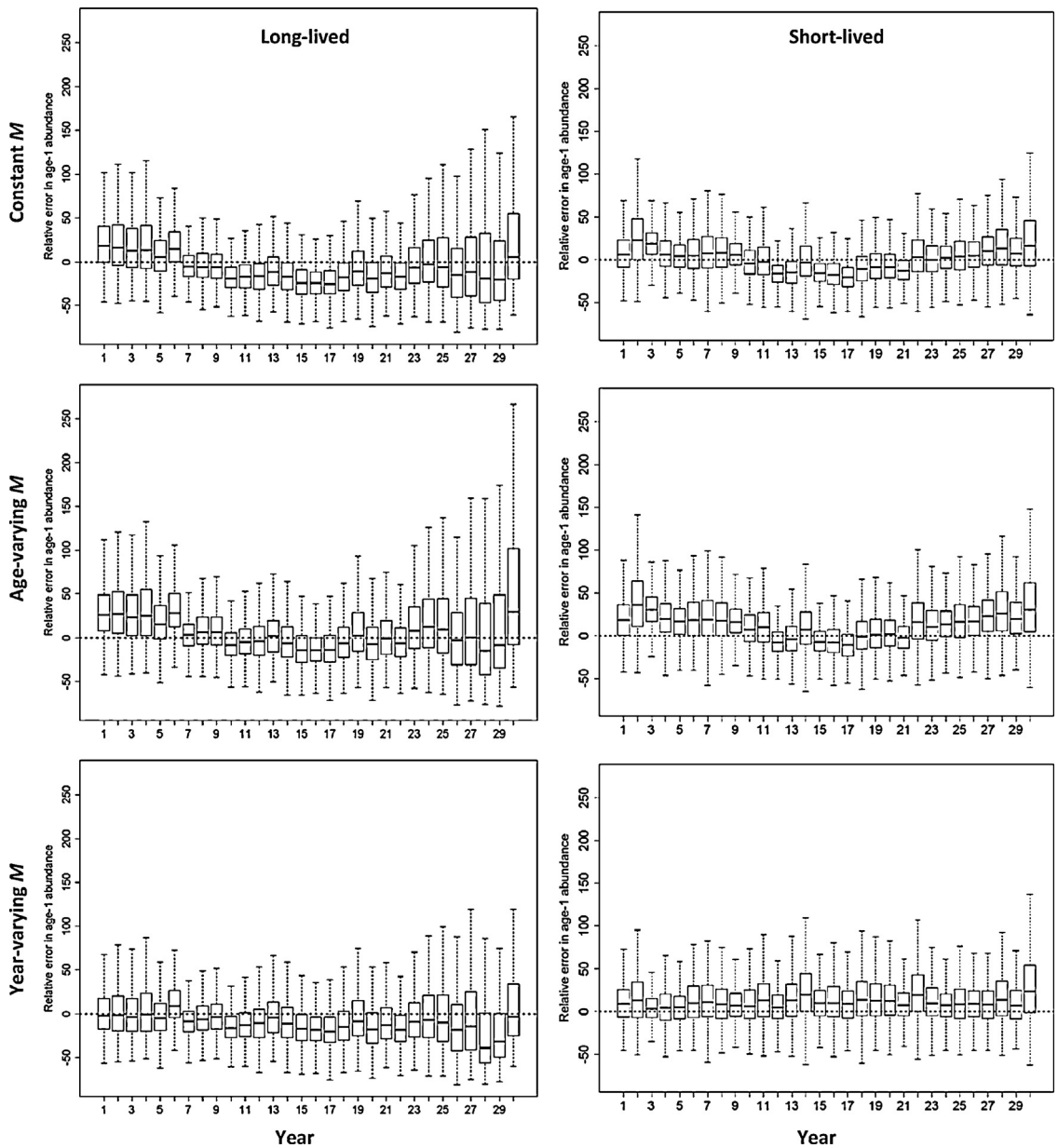

Fig. 8. As for Fig. 3, except for relative errors in estimates of age-1 abundance and the true fully selected natural mortality rates had an increasing trend followed by a decreasing trend among years.

estimates of abundance and fishing mortality rates (Ulltang, 1977; Tyler et al., 1985). He et al. (2011) also found that using a value of *M* that was constant among ages when the true *M* varied by age produced biased estimates of selectivity, catchability, and *SSB*, especially when the true *M* was higher at young ages and the assessment utilized a juvenile survey. The results of this study suggested that a constant value of *M* that approximates the average *M* among ages will perform about as well as accounting for the age variation in *M* explicitly. The likely explanation for this apparent contradiction between He et al. (2011) and this study is that this study fixed the selectivity parameters and did not include a survey specifically for young ages, which is in contrast to He et al. (2011). Thus, including age-variation in *M* can produce benefits in some situations, but the results of this study suggested that the benefits of including age variation in *M* are likely secondary to accounting for temporal trends in *M*. Thus, stock assessment scientists time would be better spent attempting to get the scale of a constant value of *M* correct than trying to estimate age-specific *M*s. Furthermore, more time should also be dedicated to quantifying temporal trends in *M*, or at least examining data for large temporal shifts in *M* among years, as suggested by Lapointe et al. (1992). A recent Gulf of Maine/George's Bank Atlantic herring stock assessment recently increased *M* for a period of years based on evidence from estimates of predatory consumption of herring (NEFSC, 2012). Stock assessment scientists could also use stomach contents data, predator abundance estimates, multi-species modeling, tagging data, or growth to inform decisions about temporal shifts in *M* (Lorenzen, 1996; Hollowed et al., 2000; Overholtz et al., 2008; Gislason et al., 2010).

Although the potential to reduce bias in parameter estimates is substantial through the inclusion of time-varying *M* in a stock assessment, falsely including a temporal change in *M* will worsen bias and affects reference point calculations and subsequent stock status determinations (e.g., maximum sustainable yield; NEFSC,

2012). Consequently, the evidence for temporal shifts in *M* should be relatively strong, with the exact requirements being case specific.

Some results in this study depended on life history. Generally, trends among years in the *RE*s for estimates of *SSB* were more prominent for the long-lived life history than the short-lived life history. In contrast, trends among years in the *RE*s for estimates of recruitment were more prominent for the short-lived life history than the long-lived life history, especially when the variation among years in the true *M* was non-monotonic. This result was likely caused by incoming recruits comprising a larger portion of the total population for the short-lived life history. Similarly, Lapointe et al. (1992) concluded that accurately characterizing variability in recruitment and detecting correlations between recruitment and environmental covariates would be more difficult for short-lived, high *M* stocks than for long-lived stocks. These results suggest that misspecification of *M* in stock assessments will have different consequences for different life histories under certain conditions (e.g., when variation among years in true *M* is non-monotonic).

In this study, the only significant misspecification was in *M*, but the effect of a misspecified *M* can also be confounded with other parameters. In a delay-difference model, Tyler et al. (1985) found that errors in *M* could be counteracted with a misspecification of a growth parameter in the opposite direction. So, the assessment produced unbiased estimates of biomass even though multiple parameters were misspecified. Conversely, if *M* and growth parameters were misspecified so that they did not counteract, bias in estimates of biomass was often large. The degree to which bias in parameter estimates might be offsetting likely depends on the parameters being estimated, data availability, and selectivity patterns (He et al., 2011).

This study treated *M* as an input to a stock assessment and did not address the possibility of estimating *M* as a parameter. Although determining a value for *M* external to the stock assessment is a common approach (Andrews and Mangel, 2012), various methods have been proposed to estimate a constant *M* or *M*s that vary with age or time (Hollowed et al., 2000; Catalano and Allen, 2010; Lee et al., 2011; Jiao et al., 2012). The conclusions of this study may not be applicable to situations where *M* is estimated because estimates of *M* are often confounded with other parameters (Thompson, 1994; Lee et al., 2011; Maunder and Wong, 2011). The degree of bias in estimates of biomass, fishing mortality, or recruitment will depend on the degree of confounding between *M* and other parameters and the relative weights given to various data sources (e.g., age compositions and indices of abundance; Lee et al., 2011; Maunder and Wong, 2011). So, the relative benefit in terms of the bias of estimates of biomass, fishing mortality, or recruitment when estimating a constant *M*, age-varying *M*, or time-varying *M* should be a topic of future research. Results of such research are also likely to depend on the data used to inform estimates of *M* and selectivity patterns (He et al., 2011). For example, informative length- or age-composition data have been shown to produce reliable estimates of *M* (Catalano and Allen, 2010; Lee et al., 2011), while predatory consumption data have also been used (Hollowed et al., 2000). Conversely, *M* may be more difficult to estimate if the true *M* is higher on older ages and selectivity is dome-shaped (He et al., 2011).

Results related to bias in reference points and relative stock status when *M* is misspecified might also be of interest to scientists and managers. Reference points, however, depend on assumptions about *M* and no standard methods have been developed for reference point calculation when *M* varies through time. Consequently, this study purposefully avoided reporting results related to reference point calculation, but this should be a topic of future research.

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Appendix A.

These are the details of the Population Simulator Version 7.5 (PopSim; NOAA, 2012). Symbols are defined in Table A1.

Table A1
Symbols and descriptions of parameters or variables used in the simulation model.

Symbol	Description
l	Length
y	Year
N	Abundance
S	Selectivity
ϑ	Denotes values associated with a survey
q	Catchability
C	Catch
ε	Error in survey catch, yield, growth, or recruitment
σ^2_ϑ	Survey error variance
a	Age
θ	Denotes values associated with a fishery
F	Fishing mortality
M	Natural mortality
Z	Total mortality
L	Landings (catch converted to units of weight)
W	Weight
α'	Parameter of weight–length relationship
β'	Parameter of weight–length relationship
$\hat{Y}$	Observed (estimated) yield
σ^2_δ	Error variance of observed yield
B	Numbers of sub-sampled fish from fishery catches
A	Expansion factor applied to sub-sampled fish for estimating catch
$\hat{C}$	Observed (estimated) catch
D	Maturity
γ	Parameter of maturity at length function
τ	Parameter of maturity at length function
$\ddot{N}$	Number of mature fish
SSB	Spawning stock biomass
Z'	Total mortality discounted for the proportion of fishing and natural mortality that occurred prior to spawning
f_F	Proportion of fishing mortality that occurred before spawning
f_M	Proportion of natural mortality that occurred before spawning
N'	Number of surviving fish
X	Probability of being in a length bin in the first year
$\bar{L}$	Mean length
σ^2_α	Age specific variance of lengths around a mean length in the first year
$l1$	Minimum length of a length bin
$l2$	Maximum length of a length bin
L_∞	Parameter of the von Bertalanffy growth equation
k	Parameter of the von Bertalanffy growth equation
a_0	Parameter of the von Bertalanffy growth equation
Q	Probability of being in a length bin for all years other than the first
σ^2_δ	Variance of lengths around a mean length for all years other than the first
R	Recruitment
α	Parameter of the stock–recruitment relationship
β	Parameter of the stock–recruitment relationship
σ^2_τ	Error variance of the stock–recruitment relationship

A.1. Fishery independent surveys

True numbers at length l in each year γ of the population $N_{y,l}$ are summed over lengths and multiplied by catchability q and a lognormal error to obtain the total number of fish that will be sampled in the survey $C_{\vartheta,y}$, where ϑ distinguishes survey catches from fishery catches (described below):

$$C_{\vartheta,y} = \sum_l N_{y,l} q e^{\varepsilon_y}; \quad \varepsilon_y \sim N(0, \sigma_\vartheta^2)$$

$C_{\vartheta,y}$ random variables representing probabilities from the cumulative length frequency distribution of the survey are randomly drawn from a uniform distribution bounded by zero and one. The length corresponding to each probability is recorded and the distribution of these lengths represents an observed length frequency based on $C_{\vartheta,y}$ number of samples. This process is analogous to drawing $C_{\vartheta,y}$ samples from a multinomial distribution. The observed length frequency is converted to an age frequency via the true, year specific, population age-length key. Subsequent age specific indices of abundance, for input into age based stock assessments, are calculated as the product of the age frequency and $C_{\vartheta,y}$. Errors will persist through the age-length key and the survey indices at age will also contain error because the length composition of the survey will not exactly match the true length composition. The user inputs a coefficient of variation that defines σ_ϑ^2.

A.2. Fishery catch

True catch at length and age a, $C_{\theta,y,l,a}$, is calculated using Baranov's catch equation, the input fully selected fishing mortality F_y, length selectivity S_l, natural mortality $M_{y,l}$, and true numbers at length and age $N_{y,l,a}$, where θ distinguishes fishery catches from survey catches:

$$C_{\theta,y,l,a} = \frac{F_y S_l}{Z_{y,l}} N_{y,l,a}(1 - e^{-Z_{y,l}})$$

$$Z_{y,l} = F_y S_l + M_{y,l}.$$

Catch at length equals the sum across ages:

$$C_{\theta,y,l} = \sum_a C_{\theta,y,l,a}.$$

Catches at length are converted to landings L_y by multiplying by weight at length W_l and summing across lengths:

$$L_y = \sum_l C_{\theta,y,l} W_l$$

$$W_l = \alpha' l^{\beta'};$$

where α' and β' are parameters of the weight–length relationship. Observed total yield $\hat{Y}_y$ is calculated as the summation of catches across lengths, multiplied by weight and lognormal error:

$$\hat{Y}_y = \sum_l C_{\theta,y,l} W_l e^{\varepsilon_y}; \quad \varepsilon_y \sim N(0, \sigma_\varphi^2);$$

where φ was used to distinguish this variance from others in this manuscript. A number of random variables representing probabilities from the cumulative length frequency distribution of each market category are randomly drawn from a uniform distribution bounded by zero and one. The length corresponding to each probability is recorded and the distribution of these lengths represents an observed length frequency for each market category. The number of samples used to determine the observed length frequencies is based on annually specified input sampling rates (i.e., as a function of L_y; input as the number of fish sampled per 100 mt). This process is analogous to drawing samples from a multinomial distribution. The numbers of sub-sampled fish at length $B_{y,l}$ are multiplied by an expansion factor to estimate the total number of fish at length $\hat{C}_{\theta,y,l}$:

$$\hat{C}_{\theta,y,l} = B_{y,l} A_y;$$

where

$$A_y = \frac{\hat{Y}_y}{\sum_l B_{y,l} W_l}.$$

Observed catches at length are then converted to catches at age $\hat{C}_{\theta,y,a}$ using the true, year specific, population age-length key. These catches at age are provided to the selected age structured assessment model. As with the surveys, this sampling method creates an observed length composition that does not exactly match the true length composition, and this error carries forward through the age length key to the age composition. These errors in sampling, however, affect the length and age composition, and therefore the observed trends in cohort strength sent to an assessment. In contrast, the lognormal errors in the equation for $\hat{Y}_y$ generate measurement errors within years.

The user inputs the values for F_y, $M_{y,l}$, parameters of the weight–length relationship (α', β'), sampling rates (see above), and a coefficient of variation that defines σ_φ^2.

A.3. Maturity

The user specifies the parameters of a logistic maturity at length D_l function:

$$D_l = \frac{1}{1 + e^{-\gamma(l-\tau)}};$$

where γ is the slope parameter and τ is the length at 50% maturity. Maturity at length is used to define the proportion of the mature population in each age, $D_{y,a}$:

$$\ddot{N}_{y,l,a} = D_l N_{y,l,a};$$

$$D_{y,l,a} = \frac{\ddot{N}_{y,l,a}}{\sum_l \sum_a \ddot{N}_{y,l,a}}$$

$$D_{y,a} = \sum_l D_{y,l,a};$$

where $\ddot{N}_{y,l,a}$ is the number of mature fish at each year, length, and age. Although maturity at length is constant among years, this method can lead to temporal variation in maturity at age as the population length at age distributions change in response to selective fishing pressures. For example, abundance at each length and age $N_{y,l,a}$ is affected by fishing mortality and length based selectivity. Consequently, $D_{y,a}$ is also determined by these factors, such that if all age-4 fish were harvested from the population, then $D_{y,a=4}$ would be zero.

A.4. Spawning stock biomass

Spawning stock biomass was calculated as the sum of the product of abundance, maturity, and weight, discounted for the proportion of fishing and natural mortality that occurred prior to spawning:

$$SSB_y = \sum_l \sum_a \ddot{N}_{y,l,a} W_l e^{-Z'_{y,l}};$$

where

$$Z'_{y,l} = F_y S_{y,l} f_F + M_{y,l} f_M;$$

f_F and f_M were the fraction of fishing and natural mortality that occurred before spawning and are input by the user. All other symbols were defined as above.

A.5. Population abundance

PopSim assumes that fish die at an instantaneous exponential rate:

$$N'_{y,l,a} = N_{y,l,a} e^{-Z_{y,l}};$$

where $N'_{y,l,a}$ is the number of fish in each year, length, and age that survive, and:

$$Z_{y,l} = F_y S_{y,l} + M_{y,l}.$$

A.6. Growth

The initial population (i.e., in year $y = 1$) numbers at age are specified by the user. These numbers of fish at age are normally distributed among lengths based on the mean length at age defined by the user input von Bertalanffy growth parameters and age specific standard deviations:

$$N_{y=1,l,a} = N_{y=1,a} X_{l,a};$$

where $X_{l,a}$ is the probability of being in length bin l and:

$$X_{l,a} = \int_{l1}^{l2} x\,dx; x \sim N(\bar{L}_a, \sigma_a^2);$$

where $l1$ is the minimum length and $l2$ is the maximum length in the length bin, σ_a^2 is the age specific variance calculated as the square of the standard deviations at age input by the user, and $\bar{L}_a$ is mean length at age defined by the von Bertalanffy growth equation:

$$\bar{L}_a = L_\infty (1 - e^{-k(a-a_0)});$$

where L_∞, k, and a_0 are parameters input by the user. The standard deviation specified for the first age class (age-1) of the initial population is also used to distribute recruits among length bins in all years.

After the initial year, the numbers of surviving fish in each length bin at each age are assigned to length bins in the following year and age based on the increment defined by the von Bertalanffy growth equation and additional error:

$$N_{y+1,a+1,l} = \sum_l N'_{y,a,l} Q_{y+1,a+1,l};$$

where $Q_{y+1,a+1,l}$ is the probability of being in length bin l and:

$$Q_{y+1,a+1,l} = \int_{l1}^{l2} i\,di; i \sim N(\bar{L}_{a+1,l}, \sigma_\delta^2);$$

$$\bar{L}_{a+1,l} = l + (\bar{L}_{a+1} - \bar{L}_a)$$

where the variance σ_δ^2 is calculated as the square of the standard deviation input by the user and δ was used to distinguish this variance from others in this manuscript. Fish in each length bin are not permitted to get smaller as they age or exceed a user defined maximum length and the integral of the probability distribution among all lengths at a given age is normalized to equal one.

A.7. Recruitment

Recruitment followed Beverton–Holt dynamics:

$$R_y = \frac{\alpha \times SSB_y}{\beta + SSB_y} e^{\varepsilon_y}; \quad \varepsilon_y \sim N(0, \sigma_\tau^2);$$

where α and β are parameters defined by the user, σ_τ^2 is defined by a user input coefficient of variation, and τ was used to distinguish this variance from others in the document.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2013.03.015.

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