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ARTICLE

Better Catch Curves: Incorporating Age-Specific Natural Mortality and Logistic Selectivity

James T. Thorson*
School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195-5020, USA

Michael H. Prager
Prager Consulting, 2333 Northeast 47th Avenue, Portland, Oregon 97213, USA

Abstract
Catch-curve analysis is one of the simplest methods for stock assessment and is widely applied in data-poor fisheries. Conventional catch-curve methods rely on the strong assumptions of constant fishing and natural mortality rates above some fully selected age that is usually estimated by visually inspecting a plot of catch at age. Here, we evaluate the performance of three catch-curve methods that relax or modify these assumptions by (1) estimating logistic selectivity parameters, (2) assuming Lorenzen-form natural mortality (natural mortality that decreases with weight), and (3) using both methods simultaneously. We used simulation modeling and decision tables to compare estimates of fishing mortality from four catch-curve methods, including the conventional method, across a variety of observable and unobservable data characteristics. We then applied the methods to catch-at-age data for Atlantic menhaden *Brevoortia tyrannus* from the U.S. South Atlantic fishery management region and compared the resulting estimates with published estimates of fishing mortality (*F*). In our simulation modeling, catch curves that estimated logistic selectivity parameters performed better than those derived by the conventional method when logistic selectivity was present. There was generally little difference in performance between estimates assuming constant natural mortality and those assuming Lorenzen natural mortality. The improvements from estimating selectivity parameters were particularly pronounced when the sample sizes for catch-at-age data were large: in those instances, estimating selectivity improved the estimation accuracy for *F* by nearly 20%. In our example involving Atlantic menhaden, estimates of *F* assuming logistic selectivity were most similar to those of published stock assessments, which had previously estimated logistic selectivity at age. We recommend our logistic-selectivity catch curve when selectivity is likely to be logistic because it improves accuracy at only a very small cost in terms of computational complexity.

Federal guidelines for management of fish stocks in the United States have become increasingly stringent (MSRA 2006). Interest has increased in assessment methods with minimal data requirements because annual catch limits will soon be required for all stocks, even those with limited data. Catch curves have been used for more than 50 years (Chapman and Robson 1960) to estimate total mortality from limited data, and Tuckey et al. 2007 have suggested they be used to manage local stock subunits because they require only an index of a cohort's relative abundance at various ages. Often the analysis is performed on all catch composition data for which natural and fishing mortality at age are assumed to be constant and is implemented using catch-at-age data from a synthetic cohort, i.e., data on catch at age in a single year or aggregated over several years (Quinn and Deriso 1999).

Conventional catch curves rely on several key assumptions: (1) no trend in recruitment over time, (2) no trend in the fishing mortality (F) rate over time, (3) constant natural mortality (M) at age for the analyzed ages, and (4) constant selectivity at age for the analyzed ages (Chapman and Robson 1960). Assumptions

*Corresponding author: jimthor@uw.edu
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(3) and (4) can be violated in many plausible circumstances. For example, selectivity at age of bottom trawls is sometimes assumed to follow a logistic model (e.g., Thorson and Simpfendorfer 2009), and this selectivity pattern can result in increasing selectivity over a broad range of ages (including the ages used in a catch-curve analysis). The assumption of constant M for ages used in a catch-curve analysis is also questionable because life history theory suggests that natural mortality will decrease with age as potential predators are outgrown (Lorenzen 2000), and this can contribute to a steady reduction of natural mortality even for mature individuals that are still slowly growing.

Recent research has modified catch-curve methods to suit a variety of data circumstances and research goals. Recent modifications include relaxing the assumption of constant recruitment (Schnute and Haigh 2007) or exploring spatial hypotheses for fishing mortality (Tuckey et al. 2007). Catch curves have also been modified to explore environmental covariates of recruitment (Maceina 1997), use length-based data instead of age-based data (Rudershausen et al. 2008), and include gear selectivity (Schnute and Haigh 2007; Rudershausen et al. 2008; Wayte and Klaer 2010). Finally, harvest control rules have been developed for use with catch-curve analysis for managing data-poor fisheries (Wayte and Klaer 2010). However, the authors know of no studies that have compared the estimation accuracy of a catch-curve method incorporating age-specific selectivity with conventional catch-curve analysis or of studies exploring the effect of age-specific natural mortality on catch-curve analysis.

In this study, we demonstrate three catch-curve methods that differ from the conventional method by estimating logistic selectivity parameters, assuming Lorenzen mortality, or including both of those extensions. We compare the accuracy and precision of estimates of fishing mortality for fully selected ages from our three methods to those from the conventional method, using data simulated to represent plausible data and life history types. We present results using a decision analysis framework categorized by observable effects and averaged across unobservable effects. We also compare estimates of fishing mortality from all four methods with 2010 stock assessment estimates for Atlantic menhaden *Brevoortia tyrannus* in the U.S. South Atlantic fishery management region.

METHODS

Catch-curve models.—In conventional catch-curve methodology, total mortality (Z) for ages a greater than r is estimated from a linear regression of log-scaled catch at age (C_a) on those ages, where r is an age above which selectivity and natural mortality are assumed to be constant and thus $Z_a = Z_r$ for all ages for which a is greater than r (equation 1). Let $a' = a - r$; then

$$\log_e C_a = \log_e C_r - a'Z. \qquad (1)$$

In practice, r is often chosen as the age with highest catch at age.

We formulated four catch-curve methods as penalized likelihood models, so that future applications could implement likelihood estimation of confidence intervals, Bayesian estimation of parameters, or information-theoretic model comparison. The four models were

1. the standard catch-curve method, which assumes constant natural mortality at age and constant selectivity (CC_1);
2. a method based on constant natural mortality at age and logistic selectivity (CC_2);
3. a method based on Lorenzen natural mortality at age and constant selectivity (CC_3); and
4. a method based on Lorenzen natural mortality-at-age and logistic selectivity (CC_4).

A model for which all four estimation methods are special cases is listed in Table A.1 in the appendix; the parameters of the models are listed in Table 1. Depending on the model, certain parameters are estimated, assumed at fixed values, or required as data to calculate Lorenzen mortality (Table 1).

We represented the logistic selectivity at age (S_a) using two parameters, a_{50} (the age at 50% selection) and s (the slope at a_{50}). Under a logistic selectivity model, the probability of capture can increase over a wide range of ages, rather than abruptly

TABLE 1. Four catch-curve methods (CC_1–CC_4) and the parameters they estimate, assume to be fixed, or require for calculating Lorenzen natural mortality at age. Abbreviations are as follows: F = fishing mortality; σ = the coefficient of variation between predicted and observed catch-curve estimates; a_{50} = age at 50% selection; s = the slope at a_{50}; t_{max} = maximum observed age; k, t_0, and L_∞ = von Bertalanffy growth parameters; A and B = weight-at-age parameters; ξ = the Lorenzen parameter relating weight to natural mortality.

Method	Estimated parameters	Fixed parameters	Required values
CC_1: conventional	F and σ	$s = 1{,}000$ $a_{50} = -1{,}000$	None
CC_2: estimate selectivity at age	F, σ, s, and a_{50}	None	None
CC_3: estimate Lorenzen mortality at age	F and σ	$s = 1{,}000$ $a_{50} = -1{,}000$	t_{max}, k, t_0, L_∞, A, B, ξ
CC_4: estimate both	F, σ, s, and a_{50}	None	t_{max}, k, t_0, L_∞, A, B, ξ

at some particular age. Age-specific natural mortality was represented using the Lorenzen model (equation A1.7; SEDAR 2007; Lorenzen 1996, 2000), where mortality at age 0 (M_0) is set such that the proportion (usually 1%) of individuals reaching a maximum observed age (t_{max}) is equal to the proportion reaching the same age when natural mortality is assumed to be independent of age.

The candidate catch-curve models all maximize the likelihood corresponding to an estimate of fishing mortality, F. The likelihood is calculated by estimating the age structure that would arise from a given value for F in equilibrium and comparing this estimated age structure with the observed catch at age. Our catch curves also estimate a nuisance parameter σ, where σ is approximately equal to the coefficient of variation (CV) in catch-at-age data around levels that would be expected given true F. The catch-curve models that estimate selectivity at age also estimate two logistic parameters (s and a_{50}) and are based on all positive C_a data for which a is equal to or greater than 1 (we assume that, in practical applications, mortality on individuals when $a < 1$ will be highly variable and may thus degrade estimates of overall fishing mortality). We added a likelihood penalty when fitting catch-curve models with logistic selectivity (number A1.2 in Table A.1) to ensure that selectivity at age approaches (but can be slightly less than) unity for older individuals. In contrast, catch-curve models that assumed constant selectivity at age used fixed values of logistic-selectivity parameters (s = 1,000 and $a_{50} = -1{,}000$) to effect constant selectivity at age. Those catch-curves models were based on all positive C_a data for ages equal to or greater than the age of the greatest catch. Thus, catch-curve models that estimated logistic selectivity (CC_2 and CC_4) were able to use more data than those that assumed constant selectivity. To transform an estimate of total mortality Z into fishing mortality F, catch-curve analysis requires an estimate of the natural mortality rate M. Instead of specifying M directly, we specified the maximum observed age (t_{max}) and used that age to calculate $M_{constant}$ or M_0 for constant or Lorenzen natural mortality models, respectively. In addition, models CC_3 and CC_4 require specifying the parameters of the von Bertalanffy growth curve and the allometric weight-at-length relationship. The allometric parameter for calculating mortality at length was set to the value estimated by Lorenzen (1996). Thus, catch-curve models that assumed Lorenzen natural mortality (CC_3 and CC_4) required additional assumptions about life history parameters compared with catch curves that assumed constant natural mortality.

Simulated data.—We used simulation modeling to evaluate catch-curve model performance under a variety of observable and unobservable effects that are potentially important when estimating F. Data were simulated to resemble those for red snapper *Lutjanus campechanus*, with necessary life history parameters set to the median values listed on Fishbase (Froese and Pauly 2009; Allen 1985; values listed in Table A.2). Mortality parameters for constant ($M_{constant}$) and Lorenzen (M_0) configurations were calculated such that 1% of individuals would survive to t_{max} (Hoenig 1983). Recruitment was simulated with autocorrelated, lognormal process errors around a constant level, and fully selected fishing mortality was simulated with lognormal process errors around a level about twice that of constant or asymptotic natural mortality estimated from t_{max}. Selectivity at age was simulated at several values of a_{50} and r. Simulated catch was then subsampled in each year as a multinomial process without replacement (n_{sample}), catch-at-age samples were aggregated across recent years (n_{years}), and simulated catch at age was aggregated for all ages greater than a given value (A) above which aging methods were assumed to be unavailable.

Data were simulated in several combinations of four different biological and fishery parameters (Table 2). Two of these were observable parameters (i.e., could be ascertained by inspecting the data) and two were unobservable parameters (i.e., were unknown even when looking at data). Observable parameters included age at 50% selection (juvenile selection: $a_{50} = 2$; adult selection: $a_{50} = 6$) and data availability (low data availability: $n_{sample} = 200$, $n_{years} = 2$; high data availability: $n_{sample} = 1{,}000$, $n_{years} = 4$), while unobservable parameters included the functional form for natural mortality (constant or Lorenzen) and the slope of the selectivity curve at the age of 50% selection (rapid selectivity: $s = 2$; gradual selectivity: $s = 0.5$). Operating model values for selectivity at age are displayed in Figure 1. All combinations of observable and unobservable effects resulted in 16 model configurations (Table 2). We simulated 1,000 data sets for each configuration for a total of 16,000 simulated data sets, and fishing mortality for each data set was estimated by all catch-curve methods.

Evaluation of simulation results.—The four catch-curve methods were applied to all 16,000 simulated data sets. Catch-curve methods were assumed to have perfect information regarding the life history parameters used by the operating model, including t_{max}, which could be used to calculate either $M_{constant}$ or M_0 (one of which would be identical to the operating model). Each catch curve estimated F, and estimated F was compared with the true average F over the final n_{years} for each of 1,000 simulations.

The performance of alternative catch-curve methods depended on both observable quantities (i.e., sample size) and unobservable qualities (i.e., the functional form of natural mortality). Decision analysis (Punt and Hilborn 1997) was used to assess the expected performance of different catch-curve models given different combinations of observable and unobservable effects. In this application, the performance of catch-curve methods was displayed for each combination of observable parameters while averaging across unobserved qualities (which were each assigned an equal likelihood of occurrence). We summarized performance of the methods in a table of average relative unsigned error (ARUE) and relative bias (RB) in estimates of fishing mortality, as well as ARUE and RB averaged across unobservable effects for each combination of observable effects (Table 1). The averaged values are presented so that researchers, after deciding which combination of observable effects

TABLE 2. Simulation modeling configurations and their parameter values. See Table 1 for definitions of variables.

	Observable effects		Unobservable effects	
Configuration	Age at 50% selection	Data quantity	Mortality type	Steepness of selection curve
1	$a_{50} = 2$	$n_{\text{years}} = 2$, $n_{\text{sample}} = 200$	M_{constant}	$s = 0.5$
2	$a_{50} = 2$	$n_{\text{years}} = 2$, $n_{\text{sample}} = 200$	M_{constant}	$s = 2$
3	$a_{50} = 2$	$n_{\text{years}} = 2$, $n_{\text{sample}} = 200$	M_{Lorenzen}	$s = 0.5$
4	$a_{50} = 2$	$n_{\text{years}} = 2$, $n_{\text{sample}} = 200$	M_{Lorenzen}	$s = 2$
5	$a_{50} = 2$	$n_{\text{years}} = 4$, $n_{\text{sample}} = 1{,}000$	M_{constant}	$s = 0.5$
6	$a_{50} = 2$	$n_{\text{years}} = 4$, $n_{\text{sample}} = 1{,}000$	M_{constant}	$s = 2$
7	$a_{50} = 2$	$n_{\text{years}} = 4$, $n_{\text{sample}} = 1{,}000$	M_{Lorenzen}	$s = 0.5$
8	$a_{50} = 2$	$n_{\text{years}} = 4$, $n_{\text{sample}} = 1{,}000$	M_{Lorenzen}	$s = 2$
9	$a_{50} = 6$	$n_{\text{years}} = 2$, $n_{\text{sample}} = 200$	M_{constant}	$s = 0.5$
10	$a_{50} = 6$	$n_{\text{years}} = 2$, $n_{\text{sample}} = 200$	M_{constant}	$s = 2$
11	$a_{50} = 6$	$n_{\text{years}} = 2$, $n_{\text{sample}} = 200$	M_{Lorenzen}	$s = 0.5$
12	$a_{50} = 6$	$n_{\text{years}} = 2$, $n_{\text{sample}} = 200$	M_{Lorenzen}	$s = 2$
13	$a_{50} = 6$	$n_{\text{years}} = 4$, $n_{\text{sample}} = 1{,}000$	M_{constant}	$s = 0.5$
14	$a_{50} = 6$	$n_{\text{years}} = 4$, $n_{\text{sample}} = 1{,}000$	M_{constant}	$s = 2$
15	$a_{50} = 6$	$n_{\text{years}} = 4$, $n_{\text{sample}} = 1{,}000$	M_{Lorenzen}	$s = 0.5$
16	$a_{50} = 6$	$n_{\text{years}} = 4$, $n_{\text{sample}} = 1{,}000$	M_{Lorenzen}	$s = 2$

(sample size and a_{50}) applies to a given data set, can use the corresponding decision table to account for uncertainties in the form of natural mortality and the value of s. Estimation properties were further illustrated with box plots of $\hat{F} - F$ for all configurations.

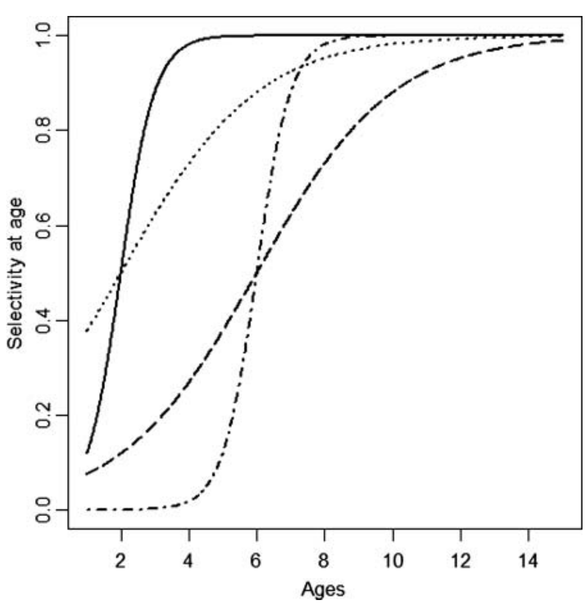

FIGURE 1. Selectivity at age for all four simulated combinations of the age at 50% selection (a_{50}) and the slope at a_{50} (s) (solid line: $a_{50} = 2$, $s = 2$; dotted line: $a_{50} = 2$, $s = 0.5$; dotted–dashed line: $a_{50} = 6$, $s = 2$; and dashed line: $a_{50} = 6$, $s = 0.5$).

Demonstration using field data.—We also illustrate our methods by applying them to catch-at-age data for Atlantic menhaden from the U.S. South Atlantic fisheries management region. This data set was chosen because (1) it contains over 20 years of catch-at-age data, (2) the latest stock assessment estimates that selectivity is logistic, and (3) the assessment provides estimates of fishing mortality to which catch-curve estimates can be compared (D. S. Vaughan, personal communication). This and recent assessments for Atlantic menhaden have incorporated estimates of natural mortality that were age- and year-specific, which were calculated using multispecies virtual population analysis (Garrison and Link 2003), but our catch-curve methods assume constant or Lorenzen natural mortality that does not change over time. We used median values of length-at-age and weight-at-length parameters from Fishbase to parameterize the Lorenzen-form natural mortality (Henry 1971; Pauly 1978; Whitehead 1985; Froese and Pauly 2009), although constant natural mortality was set to a value that has been used by past Atlantic menhaden stock assessments (0.45/year) and is similar to multispecies virtual population analysis estimates of natural mortality for mature individuals (ASMFC 2006; D. S. Vaughan, personal communication). Maximum age ($t_{\max}$) was calculated from this assumed value of constant natural mortality such that 1% of individuals would reach $t_{\max}$, and this age was then used to calculate M_0 for the Lorenzen estimating models. "True" fishing mortality was assumed to be equal to the 2010 assessment estimates of fully selected fishing mortality, and was compared with estimates of fishing mortality from each of the four catch-curve methods (CC_1–CC_4).

RESULTS

Simulation Modeling

A randomly selected set of C_a and $\hat{C}_a$ for all 16 configurations fitted by all four models (Figure 2) confirms that, in general, it is difficult to distinguish visually between the values of parameters we have designated as unobservable (Figure 2, rows) but that it is relatively easy to distinguish between the values of parameters we have designated as observable (Figure 2, columns). Simulations with high a_{50} (Figure 2, panels 3, 4, 7, 8, 11, 12, 15, and 16) had relatively few ages that were useable by models with knife-edge selectivity (CC_1 and CC_3), and the age at which they started estimating the catch curve (age at maximum catch) often did not correspond to the age of maximum catch in long-term data. This caused biased estimates of fishing mortality (for example, in panels 3, 7, and 16). By contrast, models that estimated logistic-selectivity parameters (CC_2 and CC_4) estimated maximum catch at an age close to the age of maximum catch in long-term C_a data.

Box plots of $\hat{F} - F_{\text{true}}$ for all four catch-curve methods for each of the 16 simulation modeling configurations (Figure 3) further illustrate the differences in accuracy and precision among methods. As expected, the precision of all models increased (as reflected in shorter whiskers in box plots in Figure 3) if given more data (Figure 3, columns 2 and 4). In general when applied to simulations with gradual selectivity (Figure 3, rows 2 and 4), models that assumed constant selectivity at age (CC_1 and CC_3), were negatively biased, and this bias was largely corrected by models that estimated selectivity at age (CC_2 and CC_4). However, models that estimated selectivity-at-age parameters also were less precise (box plots with larger whiskers, more outliers) than models assuming constant selectivity at age, especially in simulations with knife-edge selectivity (e.g., Figure 3, panels 1 and 5).

In our simulation study, the optimal choice of catch-curve model depended largely upon observable parameters (Table 3). When small sample sizes and juvenile selection were used (configurations 1–4), catch curves that assumed constant selectivity at age were the least biased and had fewest errors, as would be expected, given that they corresponded closely to the simulation models. When larger sample sizes and juvenile selection were used (configurations 5–8), all models had approximately equal levels of error. However, the logistic catch curve (CC_2) was the least biased. When small sample sizes and adult selection were used (configurations 9–12), the logistic catch curve (CC_2) was again the least biased and all models again had similar precision. When larger sample sizes and adult selection were used (configurations 13–16), logistic-selectivity models were the most precise and least biased of the available models.

There were few differences in precision between constant- and Lorenzen-mortality catch curves, either when assuming knife-edge selectivity (CC_1 and CC_2) or estimating logistic selectivity (CC_3 and CC_4). However, constant-mortality catch curves (CC_1 and CC_3) gave estimates of fishing mortality whose median absolute errors were lower than those from Lorenzen-mortality catch curves (CC_2 and CC_4; Figure 3). This pattern was exhibited in all simulation configurations, although it did not consistently cause one set of models to have lower ARUE than another and generally affected only the level of bias that was observed (Table 3).

Application to Atlantic Menhaden

In our comparison of published estimates of F with the estimates from the four catch-curve methods (Figure 4), the latter were generally consistent with those from the latest stock assessment for Atlantic menhaden except during the 1960s, when a large recruitment was working its way through the fishery (D. S. Vaughan, personal communication). The 2010 assessment estimates of asymptotic F range between 1.0 and 4.0 and show cyclic and high interannual variability. Estimates from CC_2 and CC_4 are consistently greater than estimates from CC_1 and CC_3, and this difference generally leads to improved agreement with the stock assessment. All models have comparable levels of error, with CC_4 having the least and CC_1 having the most. The models have wide variability in bias, with logistic-selectivity catch curves (CC_2 and CC_4) having the lowest bias (Table 4).

DISCUSSION

Stock Assessment Implications

Our study demonstrates methods that relax an important assumption of catch-curve methods, namely, that natural and fishing mortality are constant above a certain age. We show that estimating logistic selectivity parameters increases accuracy and eliminates a potential source of bias across a variety of data characteristics. Estimating selectivity-at-age parameters could be easily combined with the other recently developed methods to allow a flexibility that has previously been lacking in standard catch-curve methods. Our code in the R programming language (R Development Core Team 2008) to implement these catch-curve methods or use simulation modeling to test their accuracy is available at the corresponding author's web site (http://filebox.vt.edu/users/thorson/CC/Logistic_catch_curve.r).

Our decision analysis demonstrates that logistic-selectivity catch curves can decrease error and bias in the estimation of F compared with conventional catch-curve methods across a variety of data types and quantities. The logistic catch curve relaxes the assumption of knife-edge selectivity, and also eliminates the need to select this age visually from observed catch data (Tuckey et al. 2007). Finally, catch-curve methods that estimate selectivity at age are more efficient in that they use data for catch at younger ages, which would not contribute to conventional catch-curve analysis.

Although life history studies have demonstrated the strong possibility of declining natural mortality with age, few stock assessments currently incorporate age-specific natural mortality as the default assumption. The present study indicates that, in the context of catch-curve analysis, there is little difference in

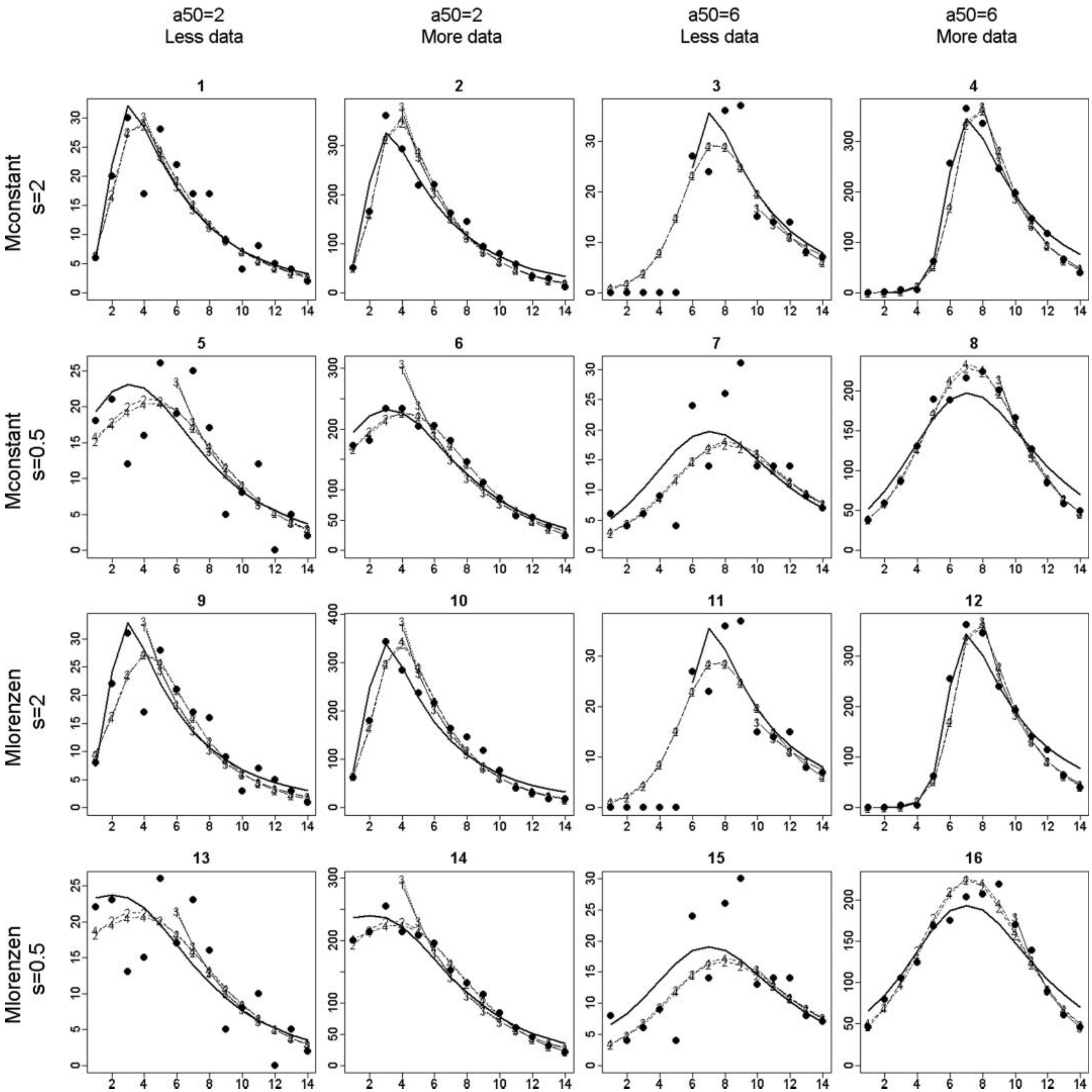

FIGURE 2. Example data sets and results for all observed (columns) and unobserved parameters (rows). Each panel shows the age (*x*-axis) and catch (*y*-axis) for the long-term average catch at age (C_a, i.e., without errors; black line), the observed catch (including recruitment and multinomial sampling variability), and the estimated catch for all catch-curve methods (standard = 1, estimating selectivity = 2, assuming Lorenzen mortality = 3, and employing both methods = 4).

error between assuming constant and Lorenzen M. However, Lorenzen-mortality catch curves generally estimated higher rates of fishing mortality. These differences were small compared with other effects in the study, and could have been an artifact of the assumed values of natural mortality at age for each catch curve within the simulation model.

Our simulation study also illustrated the magnitude of errors that can be expected for conventional and novel catch-curve methods. Average relative unsigned error was nearly 50% given low data availability and adult selection, a degree of error that will cause significant problems for many fishery management strategies. Nonetheless, catch-curve methods will continue to

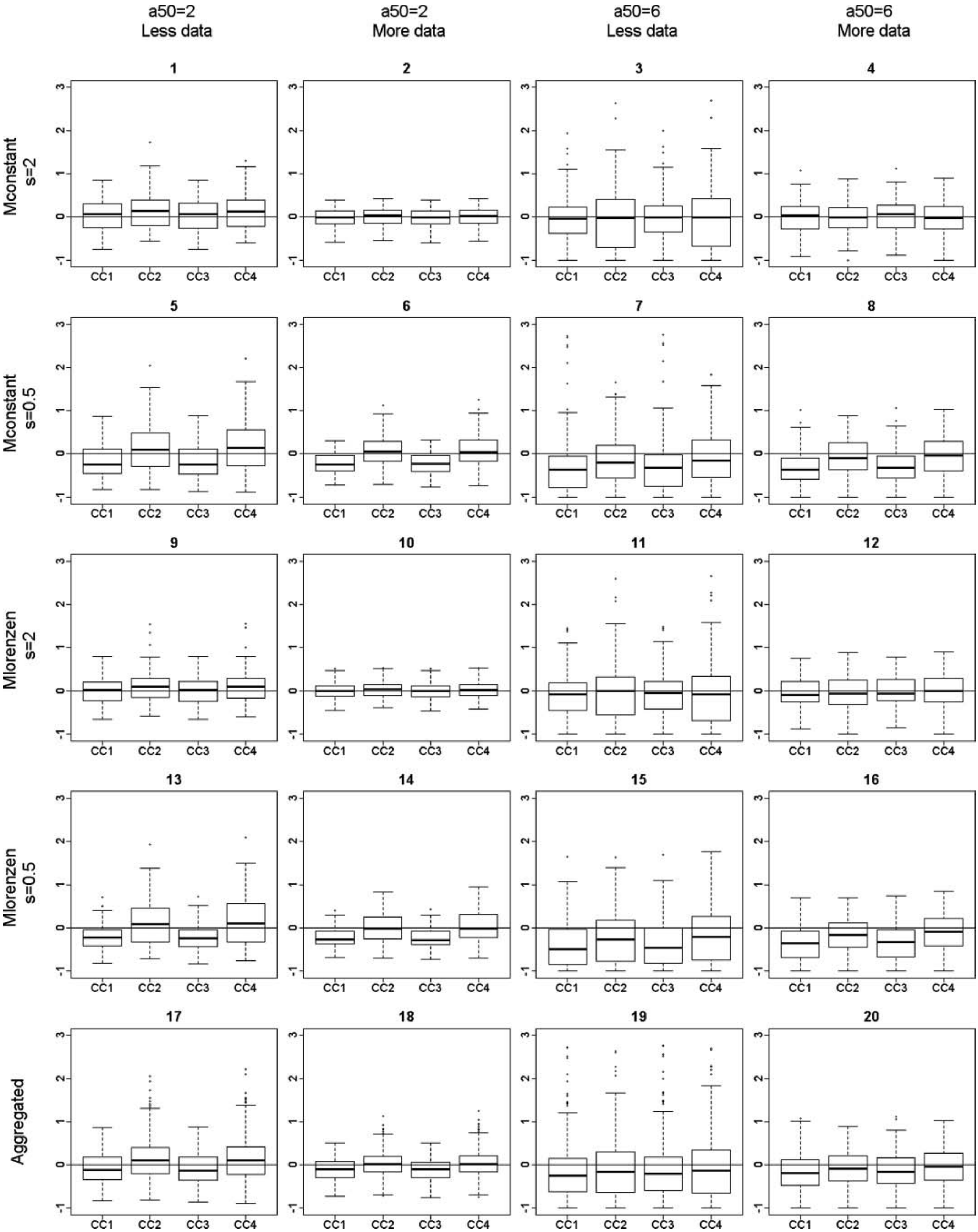

FIGURE 3. The first four rows show the percentage errors in the estimates of F for all catch-curve methods for all observed (columns) and unobserved parameters (rows); the last row shows the percentage errors in all estimates aggregated across unobserved parameters. The black lines within the boxes represent the medians, the box dimensions the interquartile ranges (i.e., the 25th–75th quartiles), and the whiskers three times the interquartile ranges centered at the medians.

TABLE 3. Average relative unsigned error (ARUE, %) and relative bias (RB, % [shown in parentheses]) for all model configurations and 1,000 simulations, with both averaged across four unobservable effects (i.e., true mortality type and slope of steepness curve). The values of ARUE or RB that are best (or within 2.5 percentage points of best) for each block of observable effects are indicated by bold italics.

Configuration	CC_1	CC_2	CC_3	CC_4
Less data, juvenile selection				
1. M_{constant}, $a_{50} = 2$	24.6 (4.6)	29.8 (11.9)	25.2 (7.3)	30.7 (15.3)
2. M_{constant}, $a_{50} = 0.5$	33.4 (–16.6)	42.7 (15.4)	33.6 (–14.5)	45.9 (23.5)
3. M_{Lorenzen}, $a_{50} = 2$	24 (1)	29.1 (8.5)	24.3 (3.6)	29.9 (11.9)
4. M_{Lorenzen}, $a_{50} = 0.5$	34 (–22.2)	40.9 (10.8)	34.5 (–21.1)	44 (19.3)
Average	***29 (–8.3)***	35.6 (11.6)	***29.4 (–6.2)***	37.7 (17.5)
More data, juvenile selection				
5. M_{constant}, $a_{50} = 2$	16.7 (–2.2)	17.8 (2.2)	16.6 (0.2)	18.5 (5.8)
6. M_{constant}, $a_{50} = 0.5$	29.4 (–24.4)	28 (7)	28.7 (–22.2)	30.4 (14.4)
7. M_{Lorenzen}, $a_{50} = 2$	17 (–4.8)	17.8 (–1)	16.7 (–2.4)	18.1 (2.5)
8. M_{Lorenzen}, $a_{50} = 0.5$	34.6 (–31.7)	26.7 (–0.8)	34.8 (–31)	28.1 (7.1)
Average	***24.4 (–15.8)***	***22.6 (1.8)***	***24.2*** (–13.9)	***23.8*** (7.4)
Less data, adult selection				
9. M_{constant}, $a_{50} = 2$	36.1 (6.6)	40 (16.7)	37.2 (13.3)	42.1 (23.4)
10. M_{constant}, $a_{50} = 0.5$	50.2 (–24.8)	48.1 (–12.1)	48.1 (–18.6)	48.3 (–3.7)
11. M_{Lorenzen}, $a_{50} = 2$	36.5 (1.3)	40.2 (11.2)	36.7 (8)	41.3 (17.9)
12. M_{Lorenzen}, $a_{50} = 0.5$	53.2 (–29.4)	48.6 (–18.6)	50.8 (–23.1)	47.9 (–9)
Average	44 (–11.6)	***44.2 (–0.7)***	***43.2*** (–5.1)	***44.9*** (7.2)
More data, adult selection				
13. M_{constant}, $a_{50} = 2$	23.7 (–4.4)	25.2 (6.4)	23.5 (2.2)	26.5 (12.6)
14. M_{constant}, $a_{50} = 0.5$	44.3 (–38.6)	33.4 (–10.4)	40.2 (–32.2)	33.6 (–2.8)
15. M_{Lorenzen}, $a_{50} = 2$	25.3 (–10.8)	25.6 (0.9)	23.8 (–4.2)	26.1 (7)
16. M_{Lorenzen}, $a_{50} = 0.5$	48.8 (–44.5)	35.2 (–20)	44.1 (–38.1)	33.2 (–10.6)
Average	35.5 (–24.6)	***29.9*** (–5.8)	32.9 (–18.1)	***29.8 (1.6)***

be important in fisheries with limited data, and novel catch-curve methods do appear to decrease errors in many cases. Perhaps more importantly, the conventional catch-curve methods strongly underestimated fishing mortality in many circumstances (particularly when logistic selectivity was gradual). In this study, that bias was largely eliminated by using methods that estimate selectivity-at-age parameters.

Finally, we explored a variety of sensitivity analyses in our simulation modeling. One such sensitivity modified the procedure for identifying at which age to start using age composition in the conventional catch-curve analysis. Specifically, the modified procedure used the age immediately older than the age of maximum catch, as recommended by Pauly (1984). This procedure improved the accuracy of the nonlogistic methods (CC_1 and CC_3) such that they were more competitive with logistic methods (CC_2 and CC_4), but did not improve the bias arising from nonlogistic methods. Other sensitivities included increasing the autocorrelation or increasing the variability in recruitment for simulated data. Both of these latter modifications made the catch composition data less informative and had an effect similar to decreasing the sample sizes of available data.

In the application to real-world data for Atlantic menhaden, estimates from catch curves with logistic selectivity had less bias and slightly less error than the conventional method when compared with assessment estimates. This result agrees with the general conclusion of our simulation model, but should be confirmed by a comparison with published stock-assessment estimates of fishing mortality for other stocks before general conclusions are drawn. The large errors and biases that remain in this application, even for logistic-selectivity catch curves, serve as a reminder that catch curves are not as reliable at estimating annual mortality rates as methods that integrate a variety of data inputs.

Study Limitations

Although our results were robust to a variety of sensitivity analyses only briefly described here, we were not able to test all biological scenarios that might occur in real-world applications of catch-curve methods. Other configurations might include dome-shaped (e.g., double normal or gamma curve) selectivity. Nonasymptotic selectivity at age would violate the assumptions of conventional catch-curve methods and would also not fit the assumption of logistic-selectivity methods. By contrast, our results were robust to autocorrelated variation in recruitment, as well as to changes in maximum age, changes in

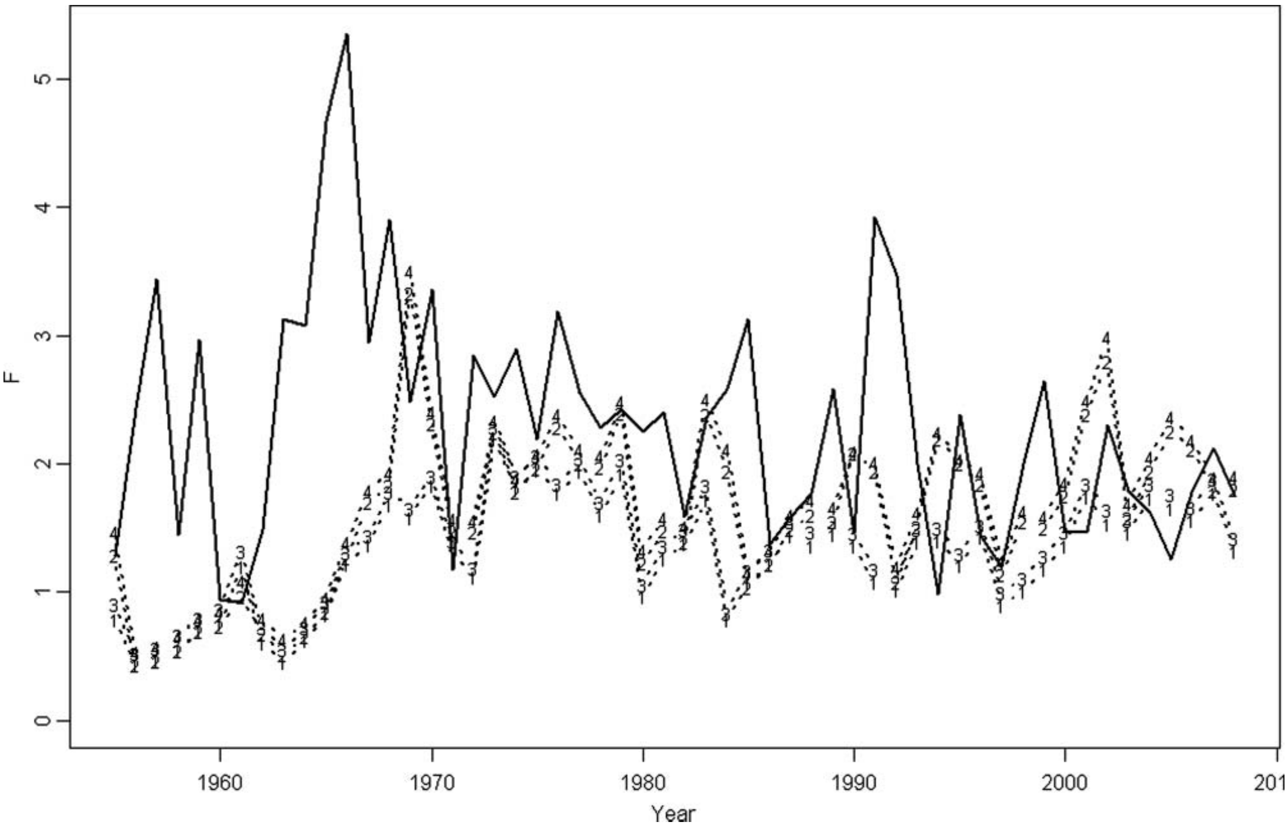

FIGURE 4. Published stock assessment (solid line) and catch-curve estimates of fishing mortality using four methods (1–4; see Figure 2) for all years for which catch-at-age data are available (1955–2008) for Atlantic menhaden in the U.S. South Atlantic fisheries management region.

magnitude of recruitment, magnitude of observation errors, and changes in the magnitude of fishing mortality.

In our simulation study, we evaluated both the precision and bias of model estimates of fishing mortality. However, we did not distinguish between positive and negative bias. Scientists or managers might prefer to overestimate rather than underestimate fishing mortality if they are risk averse. By contrast, our decision analysis weighting of bias was risk-neutral, as is frequently recommended for stock assessment methods (FAO 2009; PFMC 2009).

Our simulation study also did not account for many of the interacting errors that typically exist in real-world data. Such errors include aging errors in the C_a data, fluctuations or trends in F due to time-varying catchability (Wilberg et al. 2010), time-varying M, errors in growth parameters, and similar effects. However, such errors (and others) were presumably present in the Atlantic menhaden data and, in this application, catch curves captured the general magnitude of fishing mortality—but often failed to capture interannual variability. This example shows that catch-curve methodologies, like all simple models, can exhibit significant estimation error when applied to limited data sets, and that management actions based on limited data should be designed to be robust to such errors.

Future Directions

Catch-curve analysis is frequently applied to data-poor fisheries, where a variety of disparate information sources (each of low quality for stock assessment) may be available. Future work could formalize a process by which catch curves are combined with expert opinion (i.e., interviews with fishers) and other data-poor analyses (e.g., changes in mean length) into a quantitative estimate of stock status. We believe that methodologies for integrating types of data that provide limited information will become increasingly important in data-poor fisheries management regions as U.S. federal regulations are tightened. Just as integrated methods have become important to assessment of data-rich stocks (Methot 2005), we believe that different integrated methods may become important to assessments of data-poor stocks.

TABLE 4. Average relative unsigned error (ARUE, %) and relative bias (RB, %) for each of the four catch-curve methods when applied to catch-at-age data for Atlantic menhaden.

Statistic	CC_1	CC_2	CC_3	CC_4
ARUE	40	37	37	36
Bias	−35	−19	−30	−14

We expect and hope that future research will continue to develop methods for estimating management benchmarks for data-poor stocks. Such benchmarks are frequently used to interpret estimates from methods such as catch-curve analysis and are central to the Magnuson–Stevens Reauthorization Act (MSRA 2006). Although analytical and meta-analytical methods have been used to estimate and define status benchmarks in data-poor stocks (Dorn 2002; MacCall 2009; Brooks et al. 2010), less progress has been made in developing analytical overfishing benchmarks for data-poor stocks in the absence of meta-analysis results for a region. Research on such methods would complement the use of novel catch-curve methods in benchmark status evaluation as required by U.S. federal law.

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APPENDIX: MODEL EQUATIONS AND PARAMETERS

TABLE A.1. Equations used either in the simulation model (S) or the estimation models (E).

Equation	Number	Use
$L(F, a_{50}, s, \sigma \mid C) = \pi(a_{50}, s) \prod_{a=r}^{A} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{[\log_e(C_a)-\log_e(\hat{C}_a)]^2}{2\sigma^2}\right]$	A1.1	E
$\pi(a_{50}, s) = \exp\{1,000[\text{argmin}(S_A, 0.99) - 0.99]^2\}$	A1.2	E
where		
argmin $(S_A, 0.99)$ returns the minimum between S_A and 0.99		
$\hat{N}_a = K \prod_{i=1}^{A} \exp(-S_i F - M_i)$	A1.3	E
$K = \exp\left[\sum_{a=r}^{A} \log_e(C_a) - \sum_{a=r}^{A} \log_e(\hat{C}_a)\right]$	A1.4	E
$\hat{C}_a = \frac{S_a F}{S_a F + M_a} \hat{N}_a[1 - \exp(-S_a F - M_a)]$	A1.5	E, S
$S_a = \frac{1}{1+\exp[-s(a-a_{50})]}$	A1.6	E, S
where		
a_{50} is the age of 50% selectivity		
s is the rate of increase in selectivity at a_{50}		
$M_{\text{Lorenzen}} = M_0 A(L_\infty\{1 - \exp[-k(a - t_0)]\})^{-\xi,B}$	A1.7	E, S
where		
k, t_0, and L_∞ are von Bertalanffy growth parameters		
A and B are allometric growth parameters		
ξ is the Lorenzen parameter		

TABLE A.2. Parameters for operating model and data analysis. NA = data not available.

Parameter	Symbol	Simulation model (red snapper)	Real-world application (menhaden)
Maximum observed age	$t_{\max}$	57 years	10.2 years
von Bertalanffy growth	K	0.2/year	0.382/year
von Bertalanffy age at length 0	t_0	−0.53 year	−0.412 year
von Bertalanffy maximum length	L_∞	93.8 cm	33.69 cm
Allometric weight at age	A	0.0169g/cm^3	0.0099g/cm^3
Allometric weight at age	B	2.99	3.216
Constant natural mortality	M	0.0822/year	0.456/year
Lorenzen mortality at age 0	M_0	1.153/year	2.299/year
Lorenzen parameter	ξ	−0.305	−0.305
Fishing mortality	F	0.164/year	NA
Autocorrelation in recruitment	P	0.5	NA
Coefficient of variation in recruitment	CV_r	0.46	NA
Coefficient of variation in F	CV_F	0.10	NA