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Catch curve stock-reduction analysis: An alternative solution to the catch equations

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ABSTRACT

Legislative changes in the United States and elsewhere now require scientific advice on catch limits for data-poor fisheries. The family of stock reduction analysis (SRA) models is widely used to calculate sustainable harvest levels given a time series of harvest data. SRA works by solving the catch equation given an assumed value for spawning biomass relative to unfished levels in the final (or recent) year, and resulting estimates of recent fishing mortality are biased when this assumed value is mis-specified. We therefore propose to replace this assumption when estimating stock status by using compositional data in recent years to estimate a catch curve and hence estimating fishing mortality in those years. We compare this new "catch-curve stock reduction analysis" (CC-SRA) with an SRA or catch curve using simulated data for slow or fast life histories and various magnitudes of recruitment variability. Results confirm that the SRA yields biased estimates of current fishing mortality given mis-specified information about recent spawning biomass, and that the catch curve is biased due to changes in fishing mortality over time. CC-SRA, by contrast, is approximately unbiased for low or moderate recruitment variability, and less biased than other methods given high recruitment variability. We therefore recommend CC-SRA as a data-poor assessment method that incorporates compositional data collection in recent years, and suggest future management strategy evaluation given a data-poor control rule.

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1. Introduction

Improving the scientific basis for management of "data-poor" fisheries remains a central challenge for fisheries science in the 21st century. Fisheries may have few available data for a variety of reasons, including having low economic value, being in development and/or in the developing world, and having small population size and localized dynamics. In the United States and elsewhere, many such data-poor fisheries have an accurate time series of catch or landings data (Vasconcellos and Cochrane, 2005), though the interpretation of catch data remains an important and highly-contested subject of research (Daan et al., 2011; Pauly et al., 2013).

Since the publication of *Stock reduction analysis, another solution to the catch equations* (Kimura and Tagart, 1982), researchers have commonly combined a time series of catch data with an assumption of final biomass relative to unfished or initial biomass to estimate population productivity and reconstruct historical abundance and exploitation rates. The resulting family of "stock reduction analysis" (Kimura et al., 1984) has since been expanded to incorporate stochastic variability in population dynamics (Walters et al., 2006) and a flexible shape for the production function describing expected changes in population abundance (Dick and MacCall, 2011). Stock reduction analysis can also include age-structured population dynamics (Cope, 2013) and prior information regarding population abundance at the start of the catch time series (Martell and Froese, 2013). Despite these differences, this family of models shares a common dependence upon prior assumptions regarding final depletion, and simulation testing indicates that these methods perform well when assumptions regarding final abundance are met and poorly otherwise (Wetzel and Punt, 2011).

Alternative research has sought to develop rules-of-thumb for population abundance given changes in catch over time (Kleisner et al., 2012). These methods are typically justified by demonstrating that predictions of abundance and/or productivity match stock assessment estimates for assessed species (Froese et al., 2012; Srinivasan et al., 2010), although the degree of match remains contested (Cook, 2013). Alternatively, statistical models may seek to estimate the average relationship between changes in catch and population abundance (Costello et al., 2012; Thorson et al., 2012).

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One possible justification for these statistical methods is that they implicitly reconstruct the coupled dynamics of population abundance and fishing effort (Thorson et al., 2013). However, many species show little predictive relationship between past and future changes in fishing effort (C. Szuwalki, Bren School of Environmental Science and Management, University of California, personal communication 2014), so these effort-based methods of informing population abundance may not be appropriate for many stocks.

Finally, decades of research have developed methods to estimate fishing mortality rates from samples of the age or length composition of the population (Chapman and Robson, 1960). Such estimates can be assessed relative to optimal levels of fishing mortality whenever auxiliary information regarding species' life history is available (Hordyk et al., 2014). Methods using samples of age composition from a fishery are typically called 'catch curves,' and catch curves have been modified since their inception to account for variable recruitment (Schnute and Haigh, 2007) and fishery selectivity (Thorson and Prager, 2011; Wayte and Klaer, 2010). However, catch curves that analyze multiple biological cohorts within a single year (i.e. treating different ages within a year as a "synthetic cohort") must assume that fishing mortality rates are approximately constant over time, and this assumption is rarely met in practice.

In this study, we demonstrate that these disparate research trajectories can be combined to their mutual benefit. Specifically, we repeat the derivation of Kimura and Tagart (1982) that introduced stock-reduction analysis, and show that pre-specifying final depletion is only necessary to obtain a single degree of freedom during parameter estimation. This degree of freedom can also be obtained by estimating fishing mortality in the final year via a catch curve. Therefore, a combined catch curve stock-reduction analysis (CC-SRA) accomplishes the goals of both catch curve and reduction analysis methods, while relaxing problematic assumptions in each method individually. We then use simulation modelling to evaluate the relative performance of catch curves, stock-reduction analysis, and CC-SRA when estimating spawning biomass relative to unfished levels and fishing mortality. We also reposit all code necessary to replicate this analysis or apply CC-SRA to a new data set in the first-author's website (https://sites.google.com/site/thorsonresearch/code/ccsra).

2. Methods

2.1. The original derivation of stock reduction analysis

In its original development (Kimura and Tagart, 1982), stock reduction analysis seeks to calculate a time series of fishing mortality rates F_t for all years t_1 through t_n, as well as the (constant) annual recruitment rate R, given a fixed (assumed known) value for natural mortality M, initial population abundance B_1, and change in abundance ("depletion") between initial and final years D. This therefore involves calculating $N+1$ parameters (one parameter F_t for each of N estimated years, plus one parameter R). Stock reduction analysis gains N degrees of freedom by specifying the Baranov catch equation and using a catch time series C_1 through C_n to solve for F_1 through F_n:

$$C_t = B_t \frac{F_t}{F_t + M}(1 - \exp\{-F_t - M\}) \quad (1)$$

It also uses the following equation for population dynamics:

$$B_t = B_{t-1} \exp\{-F_{t-1} - M\} + R \quad (2)$$

where R here includes both juvenile production and growth, and selectivity is constant among ages. These equations can be solved via forward projection given known values for biomass in the initial year (B_1) and natural mortality (M), except that annual recruitment R is unknown. This latter degree of freedom is gained by the assumption that the total change in abundance is known:

$$D = \frac{B_{n+1}}{B_1} \quad (3)$$

In essence, this approach acknowledges that, given a known value for natural mortality, initial biomass, and catch, there is exactly one possible solution (i.e. one level of annual recruitment) that results in a given change in biomass by the end of the time series. This derivation involves determinstic calculations (for F_1 through F_N, and R) and hence has no way to characterize uncertainty about these calculations, although subsequent developments of stock-reduction analysis have developed formal estimation methods that characterize uncertainty using Bayesian priors or penalties (e.g., on total change in abundance, D, Dick and MacCall, 2011).

2.2. Catch-curve stock reduction analysis

This derivation for stock reduction analysis must be modified in several ways to make it consistent with contemporary assumptions about population dynamics and stock assessment practices. First, many researchers now use age-structured population dynamics and fishery selectivity (Hilborn, 1990). We therefore replace the population dynamics equation (Eq. (2)) with dynamics of abundance at age $N_{a,t}$ for age a and year t:

$$N_{a,t} = \begin{cases} R_t & \text{if } a = 0 \\ N_{a-1,t-1} \exp\{-S_a F_{t-1} - M\} & \text{if } a > 0 \end{cases} \quad (4)$$

where R_t is recruitment in year t and S_a is fishery selectivity at age (which is defined to have a maximum of 1.0). Fishery selection is now assumed to be age-specific, and hence F_t in the age-structured model (Eq. (4)) is the fishing mortality at the age of maximum selectivity, as opposed to the constant selectivity of the original SRA model (Eq. (2)). Spawning biomass SB_t includes the effect of individual weight at age w_a and maturity at age m_a:

$$SB_t = \sum_{a=0}^{a_{\max}} w_a m_a N_{a,t} \quad (5)$$

while fishery catch at age $C_{a,t}$ (in numbers) again uses the Baranov catch equation:

$$C_{a,t} = N_{a,t} \frac{S_a F_t}{S_a F_t + M}(1 - \exp\{-S_a F_t - M\}) \quad (6)$$

and total catch C_t (in weight) in year t is inner product of catch at age and weight at age. Recruitment is a lognormally distributed random variable with mean derived from a parametric stock-recruit relationship. In this case, we use the steepness parameterization of the Beverton–Holt function:

$$\ln(R_t) \sim Normal\left(\ln\left(\frac{4hR_0 SB_t}{SB_0(1-h) + SB_t(5h-1)}\right) - \frac{\sigma_R^2}{2}, \sigma_R^2\right) \quad (7)$$

where steepness h governs the degree of compensation in recruitment. Future research could explore more-flexible stock-recruit curves in CC-SRA (Dick and MacCall, 2011; Mangel et al., 2010), although we do not do so here. We critically assume that abundance at age at the beginning of available catch data is from an approximately unfished state:

$$\ln(N_{a,t_1}) \sim \text{Normal}\left(\ln(R_0 \exp\{-aM\}) - \frac{\sigma_R^2}{2}, \sigma_R^2\right) \quad (8)$$

and the implied link between N_{a,t_1} and R_0 replaces the requirement for assuming a value of B_1 in conventional stock-reduction analysis.

We also assume that age-composition sampling A_t is available for the final year of catches:

$$A_t \sim \text{Multinomial}(C_{a,t}, n_{comp}) \quad (9)$$

where n_{comp} age-composition samples are available, noting that age-composition sampling could just as easily be included for other years instead. This age-composition sampling essentially represents a catch-curve on a synthetic cohort, and hence allows estimation of fishing mortality in the final year. This fishing mortality estimate replaces the requirement of pre-specifying depletion in conventional stock-reduction analysis. We additionally explore an alternative in which age-composition samples are available for the final two years. This represents a scenario in which fisheries managers have more time to plan for an assessment, and therefore there is somewhat more information for estimating biological and fishing parameters.

We assume that there exists some prior information regarding the strength of density-dependent recruitment, i.e., a likelihood penalty for steepness h and for natural mortality M. We also assume for simplicity that maturity at age m_a and weight at age w_a are known without error, as well as knowing the true magnitude of variability in recruitment ($\sigma_R{}^2$). In practice, σ_R can be fixed using meta-analysis (Mertz and Myers, 1996; Thorson et al., in press-c), although random-effect estimation methods may also be able to estimate σ_R based on information in the available age-composition data (Thorson et al., in press-b). Finally, we assume that fishery selectivity can be accurately approximated by a logistic function with two parameters: S_{50} representing the age of 50% selection and S_{slope} representing the rate of change in selectivity at age S_{50} (in logit-space). Although recent research has questioned the generality of asymptotic fishery selection (Sampson and Scott, 2012), it is still commonly assumed in data-poor assessments (e.g., Dick and MacCall, 2011) and we do not consider the issue further here (although there are methods for dealing with it generically, e.g., Thorson and Taylor, in press).

In summary, these equations require estimation of unfished recruitment R_0, recruitment compensation h, natural mortality M, fishery selectivity S_{50} and S_{slope}, and annual recruitment R_t. We use maximum penalized likelihood to estimate all parameters, as implemented using ADMB (Fournier et al., 2012). The implementation uses an "explicit-F" parameterization (*sensu* Methot and Wetzel, 2013), i.e., where F_1 through F_n are treated as estimated parameters but where later estimation phases use an increasingly strong penalty on differences between predicted and observed catches to ensure that final estimates of catches match observed catches to a high degree of accuracy. This explicit-F parameterization is a computational approach to solve for the levels of fishing mortality that would generate a given catch time series, which otherwise requires solving a transcendental Baranov catch equation numerically during parameter estimation. The model also estimates initial abundance at age $N_{a,1}$ and recruitment in all years R_1 through R_n while penalizing these values towards their expected values. This is done by running ADMB once to estimate all parameters (including associated standard errors) and using estimated standard errors to adjust bias-correction factors. The model is then run a second time to obtain final estimates of stock status and productivity (following steps detailed in Methot and Taylor, 2011). In this way, the model estimates process errors caused by variable recruitment. Incorporating both process and measurement variability is widely recognized to improve estimation performance and population projections in dynamical models (De Valpine and Hastings, 2002; Holmes, 2001; Ono et al., 2012; Punt, 2003; Schnute, 1991), and the value of the recruitment variability parameter σ_R (which is fixed at its true value) governs the degree of smoothing that occurs when interpreting variation in available data (i.e., compositional data in the final year).

Table 1
Assumptions and estimated parameters for each estimation model.

Model	Assumptions	Estimated parameters
Catch curve	• Fishing mortality is constant for all ages composing the "synthetic cohort" • Fishery selectivity follows a logistic curve • Recruitment is variable around an unknown average value	• Fishing mortality rate F • Selectivity parameters S_{50} and S_{slope} • Annual recruitment R_t given that its average R is fixed at an arbitrary constant value • Natural mortality M (given prior)
Stock reduction analysis (SRA)	• Fishing mortality is variable and follows no specified parametric function • Recruitmenmt follows a determinstic stock-recruit relationship • Fishery selectivity is knife-edge with shape specified a priori	• Annual fishing mortality rates F_1 through F_n • Stock-recruit parameters R_0 and steepness h (given prior on h) • Natural mortality M (given prior)
Catch-curve stock reduction analysis (CC-SRA)	• Fishing mortality is variable and follows no specified parametric function • Recruitment is variable around a stock-recruit relationship • Fishery selectivity follows a logistic curve	• Annual fishing mortality rates F_1 through F_n • Stock-recruit parameters R_0 and steepness h (given prior on h), and annual recruitment R_t • Selectivity parameters S_{50} and S_{slope} • Natural mortality M (given prior)

2.3. Alternative data-poor models for performance comparison

We compare the performance of the CC-SRA with conventional catch curves and stock-reduction analysis, to demonstrate the advantages of combining these two approaches into a single model. Catch curves and stock-reduction analysis were implemented using the same dynamical equations but making different assumptions as explained below. We also summarize the different assumptions of each model (Table 1).

2.3.1. Catch curves

We implement a conventional catch curve while additionally estimating parameters for logistic fishery selectivity (Thorson and Prager, 2011) and stochastic variability in recruitment (Schnute and Haigh, 2007). Specifically, this is implemented by estimating a single constant value for expected recruitment (i.e., by fixing $h = 1$) and a single constant value for fishing mortality (i.e., $F_t = F$ for all years t). We also exclude all catch data such that the model has no information regarding population scale, and hence we fix initial recruitment $R_0 = 1$. We then estimate this model for as many years as there exist ages in the age-composition data to ensure that all cohorts undergo constant fishing mortality rate F for all ages. In summary, the catch curve model estimates selectivity parameters S_{50} and S_{slope}, a single fishing mortality F, and recruitment deviations R_t.

2.3.2. Stock reduction analysis

The age-structured stock reduction analysis includes an addition likelihood component, i.e., a lognormally distributed penalty on final depletion:

$$\ln(D) \sim \text{Normal}(\ln(\mu_D), \sigma_D^2) \quad (10)$$

where $\mu_D = 0.40$ and $\sigma_D = 0.20$, i.e., specifying a priori that final spawning biomass is 40% of average unfished spawning biomass as is currently assumed for depletion-based stock reduction analysis (DB-SRA, Dick and MacCall, 2011) on the U.S. West Coast. The stock reduction analysis has no age-composition information, and hence has no information for estimating fishery selectivity. We therefore fix selectivity to be knife-edge following current practices for DB-SRA (i.e. $S_{slope} = 20$ and S_{50} is fixed at its true value). The model also has no information to estimate recruitment deviations, so we fix initial abundance $N_{a,t=1}$ and recruitment R_t at its expected value (i.e., the limit as σ_R approaches 0). In summary, this general age-structured form of the stock reduction analysis model estimates recruitment compensation h, natural mortality M, and a full time series of fishing mortality from F_1 to F_n (while using the standard deviation of penalties on final depletion, steepness, and natural mortality to inform the standard error of model estimates). We note that all three of these candidate models could conceivably be estimated using integrated assessment software, e.g., Stock Synthesis (Cope, 2013; Methot and Wetzel, 2013).

2.4. Simulation modelling

We compare the performance of these three candidate models when estimating status and productivity using simulated data. To do so, we use an age-structured simulator that generates plausible life history strategies and effort dynamics (Thorson et al., 2013). We specifically simulate data for two life history types (a "fast" or "opportunistic" type, and a "slow" or "periodic" type, see Winemiller, 2005 and Rose et al., 2001), while also testing various different levels of recruitment variability for each. We hypothesize that the "fast" life history type will have degraded performance for catch curve and CC-SRA methods, because the "fast" life history has increased natural mortality resulting in a truncated age-structure, fewer non-zero age-composition bins, and hence less information about mortality rates. We also hypothesize that increased recruitment variability will degrade performance for all methods, due to greater variability in population dynamics.

For simulating life history and population dynamics, we generate two life history types based on life history theory. Both specify that the natural mortality rate $M = 1.84k$, where k is the Brody individual growth coefficient (Charnov et al., 2013). We also specify that weight at age $w_a = (0.01) L_a^{3.04}$ where L_a is length at age, i.e., a close-to-isometric weight-at-age relationship (Froese et al., 2014). Next we specify 50% maturity is achieved at age $a_{mat} = (\ln(3L_\infty - 3L_0) - \ln(L_\infty))/k$ (Williams and Shertzer, 2003), where initial length $L_0 = 1$ cm. and asymptotic maximum length L_∞ varies among life history types, while specifying a logistic maturity ogive with slope $0.25a_{mat}$ in logit-space at age a_{mat}. The first life history type is a "slow" or "periodic" fish, roughly based upon red snapper (*Lutjanus campechanus*), which uses $k = 0.1\ \text{yr}^{-1}$, $L_\infty = 60$ cm, and log-maximum annual spawners per spawner of 1.0 (Myers et al., 1999), corresponding to steepness of $h = 0.65$. The second life history type is a "fast" or "opportunistic" life history, roughly based upon Pacific sardine (*Sardinops sagax*), which uses $k = 0.2\ \text{yr}^{-1}$, $L_\infty = 30$ cm, and log-maximum annual spawners per spawner of 2.0 (Myers et al., 1999), corresponding to a steepness of $h = 0.91$. As theorized by Rose et al. (2001), the opportunistic species has weaker compensation in recruitment than the periodic species. For each life history type, we explore three levels of variability in recruitment, $\sigma_R = \{0.3, 0.6, 0.9\}$, which ranges from low to high variability in Thorson et al. (in press-c). We emphasize recruitment variability during simulation testing because exploratory analysis identified this as an important variable affecting model performance.

To stochastically generate a unique time series of catch data for each simulation replicate, we use the effort-dynamics model from Thorson et al. (2013):

$$\ln(F_t) \sim \text{Normal}\left(\ln\left(F_{t-1}\left(\frac{SB_{t-1}}{\gamma SB_0}\right)^{\lambda}\right) - \frac{\sigma_F^2}{2}, \sigma_F^2\right) \quad (11)$$

while specifying that initial fishing mortality $F_1 = 0.1$, acceleration rate $\lambda = 0.2$, biomass at bioeconomic equilibrium $\gamma = 0.25$, and residual variability $\sigma_F = 0.2$. This effort dynamics is intended to generate many stochastic realizations of fishery development while still providing for a catch time series that increases and sometimes subsequently decreases, and which has an equilibrium value of approximately 25% of unfished biomass. These effort dynamics parameters λ, γ, and σ_F are selected to stochastically generate time series of fishing mortality, and subsequently spawning biomass, and do not appear in the proceeding estimation equations for the catch curve, stock reduction analysis, or CC-SRA. Finally, we specify that fishery selectivity at age has identical parameters (and identical form) to the maturity ogive, and that the catch curve and CC-SRA methods have age-composition sampling data with an effective sample size of 100. We note that exploring the sensitivity of catch curve and CC-SRA results to mis-specifying the effective sample size of these compositional data remains an important research topic, but that this is also an active topic of research in data-rich assessment methods (e.g., Francis, 2011). Methods exist to estimate this effective sample size within a stock assessment model (Hulson et al., 2011; Maunder, 2011), although these estimates may be confounded with estimates of the magnitude of recruitment variability in the CC-SRA (should the latter be estimated in future applications). This confounding of recruitment variability and effective sample size therefore increases the importance of model-based methods for accurately estimating the effective sample size of compositional data (Thorson, 2014).

3. Results

We first show examples of the simulated fishing mortality and spawning biomass trajectories (Fig. 1) for each of the three scenarios (recruitment variability being low, medium, or high) for the "periodic" species. In each scenario, spawning biomass starts on average at unfished levels (Fig. 1 right column), although the scenario with high recruitment variability has large variability around this value, with some replicates being <50% or >200% of unfished spawning biomass. Fishing mortality also starts in the initial year at 0.1 in all replicates, but quickly develops different trajectories for each replicate. In particular, fishing mortality often reaches an asymptote or declines somewhat by the end of the simulated time period (i.e., follows a two-way trip).

We first show model estimates from the CC, SRA, and CC-SRA for a single simulation replicate for the "periodic" species. Inspecting estimates of spawning biomass relative to unfished levels for SRA and CC-SRA (Fig. 2 right column) shows that SRA estimates final spawning biomass at 40% of unfished levels because there is essentially no information to update the prior that is used. For this single simulation replicate, this results in biomass estimates that are positively biased in the example for each randomly selected scenario (blue line in right column of Fig. 2). The CC-SRA has wider confidence intervals for estimates of final spawning biomass and, in each of these examples, it more closely matches the true spawning biomass relative to unfished levels. By contrast, inspection of fishing mortality estimates (Fig. 2 left column) shows greater variability in relative performance of methods. The catch-curve estimates a

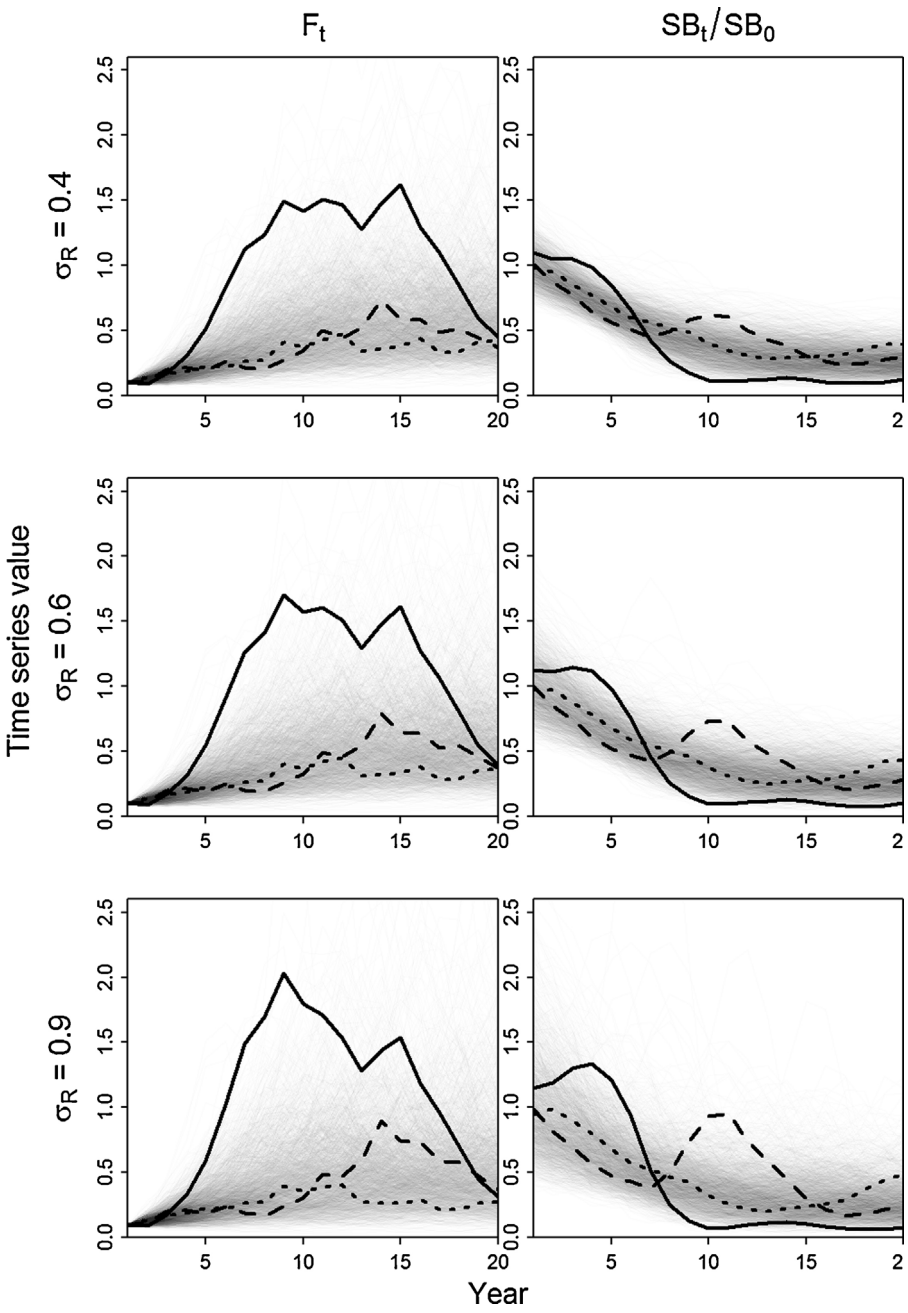

Fig. 1. Simulated values for fishing mortality (F_t: left column) and spawning biomass relative to unfished levels (SB_t/SB_0: right column) for three scenarios representing various levels of recruitment variability (top row: $\sigma_R = 0.4$; middle row: $\sigma_R = 0.6$; bottom row: $\sigma_R = 0.9$) for 2000 replicated data sets in each scenario (light grey lines: all 2000 replicates; solid line: 1st of 2000 replicates; dotted line: 2nd of 2000 replicates; dashed line: 3rd of 2000 replicates) for the "slow" (periodic) life history modelled generally on red snapper.

single fishing mortality rate for all years that compose its synthetic cohort, and this fishing mortality estimate is generally similar to the average of the true fishing mortality rate. Similarly, the CC-SRA estimates of fishing mortality rates are less precise given high recruitment variability, when selectivity parameters are harder to estimate. In this single simulation replicate, CC-SRA provides a similar estimate of final fishing mortality to the SRA, and the catch curve provides the most accurate estimate of fishing mortality. However, CC-SRA also provides a measure of stock status, something the catch-curve approach alone does not.

We next summarize results for all simulation replicates of the simulation experiment. Results for the "periodic" species (Fig. 3a) show that the CC-SRA is least biased and has lowest errors given low recruitment variability (see bias and root-mean-squared error values in Fig. 3a, top-left panel). By contrast, the SRA has a positive bias (0.401) in estimates of spawning biomass relative to unfished levels, and a negative bias (−0.460) in final fishing mortality for all scenarios of both "slow" and "fast" life history types (Fig. 3a and b). Despite this bias, the SRA has the lowest error (RMSE = 0.667) in estimates of terminal fishing mortality for the "fast" life history type (Fig. 3b) because the prior constrains the model to be highly precise (little between-replicate variability) around a biased (−0.373) value. Finally, the catch curve has a positive bias in fishing mortality estimates for all scenarios. Model exploration (not shown) confirms that this bias occurs because the catch curve assumes that fishing mortality is (approximately) constant over time, whereas fishing

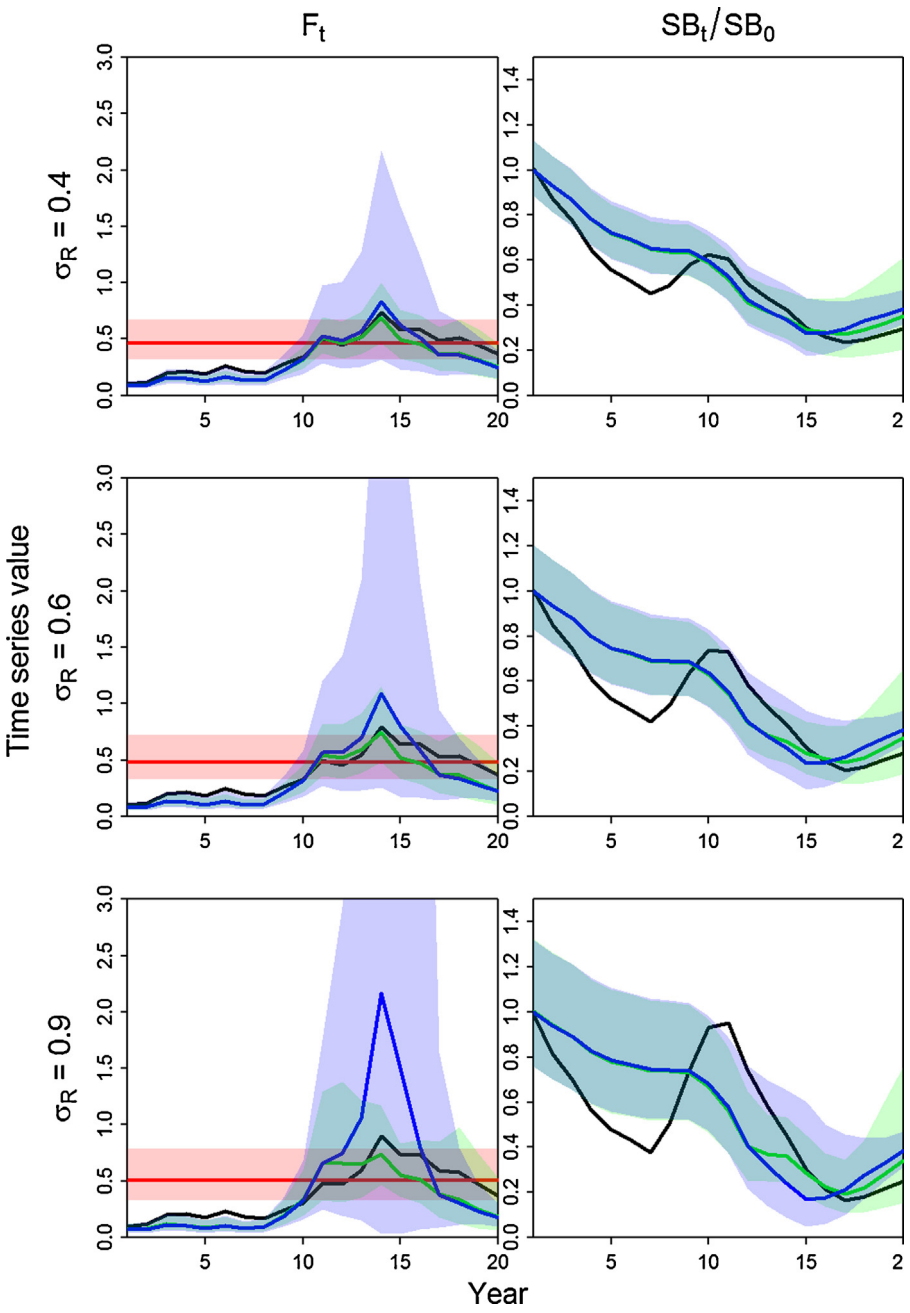

Fig. 2. Illustration of results for a single simulation replicate for the "slow" (periodic) life history modelled generally on red snapper, i.e., true (black line) and estimated (red: catch curve; green: catch-curve stock reduction analysis; blue: stock reduction analysis) fishing mortality (F_t: left column) and spawning biomass relative to unfished levels (SB_t/SB_0: right column) for three scenarios representing various levels of recruitment variability (top row: $\sigma_R = 0.4$; middle row: $\sigma_R = 0.6$; bottom row: $\sigma_R = 0.9$), while also showing estimated 95% asymptotic confidence intervals for each model (shaded regions). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mortality is in fact changing by year. The CC-SRA largely eliminates this bias by using catch data to estimate a time series of fishing mortality that changes over time. As hypothesized, the catch curve and CC-SRA performly significantly worse for the "fast" life history than the "slow" (Fig. 3a and b).

4. Discussion

National regulations have changed across the globe to require scientific advice regarding status and productivity of fishes impacted by human activities (ICES, 2012; Reuter et al., 2010). This has sparked a resurgence of interest in simple methods for estimating productivity and catch limits for fish stocks (Dick and MacCall, 2011; Martell and Froese, 2013; Thorson et al., 2013). In the United States, the vast majority of species have catch limits that are determined using only catch data (Berkson and Thorson, in press), and catch-based methods have therefore taken a particularly central role in recent research. However, methods are also being developed that use compositional data in isolation or in combination with catch data to estimate productivity and status (Brodziak et al., 2012; Gedamke and Hoenig, 2006).

We have shown that disparate methods in the assessment of data-poor fisheries (i.e., catch curves and stock reduction analysis) can be combined in a way that avoids problematic assumptions made by each method individually. The resulting catch-curve stock reduction analysis (CC-SRA) model avoids the assumption

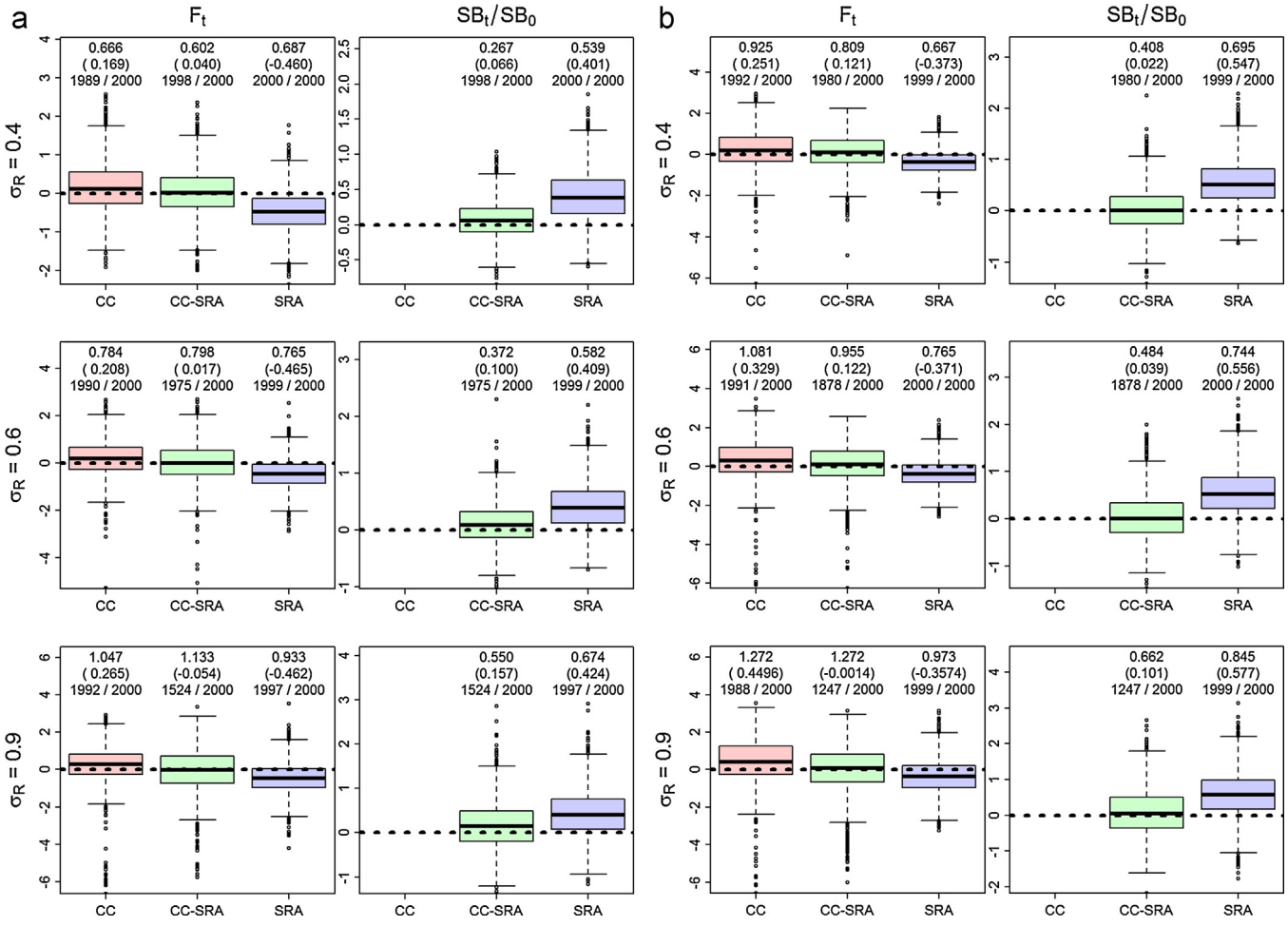

Fig. 3. Boxplots (box: interquartile range (IQR); whiskers: furthest observation from the median that is less than 1.5×IQR from the median; circles: observations outside the whiskers) summarizing estimation errors (ln(estimated value) − ln(true value)) across all replicates of our simulation experiment, involving three estimation methods (CC: catch curve; CC-SRA: catch-curve stock reduction analysis; SRA: stock reduction analysis) when estimating fishing mortality (F_t: left column) and spawning biomass relative to unfished levels (SB_t/SB_0: right column) in the final year for three scenarios representing various levels of recruitment variability (top row: $\sigma_R = 0.4$; middle row: $\sigma_R = 0.6$; bottom row: $\sigma_R = 0.9$). Numbers above each boxplot indicate: (Top number) the root-mean-squared error (a measure of total error); (Middle number) the bias (a measure of directional errors); and (Bottom number) the number of model runs that converged as a fraction of the 2000 simulation replicates for each model. Panel A shows results for the "slow" (periodic) life history modelled generally on red snapper while Panel B shows results for the "fast" (opportunistic) life history modelled generally on Pacific sardine. The catch-curve does not estimate spawning biomass and hence the box-and-whisker is missing for *CC* in the right column.

of constant fishing mortality, as required by conventional catch curves, by using available catch data to inform estimates of changes in fishing mortality over time. Given prior information about natural mortality rates, the catch curve provides an estimate of fishing mortality that can replace the assumption of a known change in spawning biomass as required by conventional stock reduction analysis (Kimura and Tagart, 1982). The model also uses age-structured equations for population dynamics, and can therefore easily use information about recruitment compensation (Myers et al., 1999) and recruitment variability (Mertz and Myers, 1996; Thorson et al., in press-c) from other stocks via meta-analysis (Thorson et al., in press-a).

These methods could also be combined with other recently-developed assessment methods for data-poor fisheries. In particular, fishing mortality rates do not change randomly from year to year, but reflect changes in fishing effort and efficiency. Therefore, future research might constrain changes in fishing mortality, using either meta-analytic information regarding regional fishing effort in multispecies fisheries (MacCall, in preparation) or effort-dynamics models in directed single-species fisheries (Thorson et al., 2013). Future research could also improve priors on final spawning biomass by using expert opinion and information regarding species vulnerability (Patrick et al., 2010). CC-SRA could be combined with auxiliary information, i.e., museum and historical records of maximum sizes (Dayton and MacCall, 1992), and this could be informative about the natural mortality rate or used to relax the assumption that the population is in unfished equilibrium in the initial year. Finally, we have not implemented the CC-SRA using Bayesian estimation, although there is no reason this could not be done in the future, and Bayesian estimation would more-appropriately propagate information about certainty (i.e., integrating over the variance of Bayesian priors on life history parameters).

Despite these benefits, CC-SRA and other data-poor methods require additional testing prior to use for management of data-poor fisheries. Of particular importance to test is their performance in closed-loop simulation. However, management strategy evaluation first requires the development of management strategies (i.e. harvest control rules, or other pre-determined management procedures) and these have not generally been developed for catch-based data-poor methods (although see Wiedenmann et al., 2013 and Carruthers et al., 2014). Nevertheless, management strategy evaluation generally favours models that have little bias in their estimates of stock status, because imprecision can be rectified by sequentially re-assessing a population every several years

whereas bias cannot easily be identified during subsequent assessment. Previous research shows that stock-reduction analysis will be biased when priors on final depletion are mis-specified (Wetzel and Punt, 2011), and our results also show bias in SRA because our effort-dynamics model generates a distribution of final depletion that differs from the assumed prior of final biomass being 40% of unfished levels. For this reason, we hypothesize that methods such as CC-SRA that avoid a prior on depletion in a particular year will have better performance than SRA in management strategy evaluation. However, this remains an important topic for future research in this and other data-poor assessment methods. Finally, we note that CC-SRA is dependent upon model assumptions. In particular, (1) fishery selection being non-asymptotic, (2) natural mortality being age-specific, or (3) life history parameters having mis-specified priors will likely degrade model performance. However, this caveat also applies to data-rich assesssment methods, and data-poor methods such as presented here should not be held to a higher standard than their richer cousins.

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