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Accounting for variable recruitment and fishing mortality in length-based stock assessments for data-limited fisheries

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Abstract

In fisheries with limited capacity for monitoring, it is often easier to collect length measurements from fishery catch than quantify total catch. Conventional stock assessment tools that rely on length measurements without total catch do not directly account for variable fishing mortality and recruitment over time. However, this equilibrium assumption is likely violated in almost every fishery, degrading estimation performance. We developed an extension of length-only approaches to account for time-varying recruitment and fishing mortality. This Length-based Integrated Mixed Effects (LIME) method at a minimum requires a single year of length data and basic biological information, but can fit to multiple years of length data, catch, and an abundance index if available. We use simulation testing to demonstrate that LIME can estimate how much fishing has reduced spawning output in the most recent year across a variety of scenarios for recruitment and fishing mortality. LIME improves data-limited fisheries stock assessments by its flexibility to incorporate additional years or types of data if available, and obviates the need for equilibrium assumptions.

Introduction

Many fisheries worldwide lack the quality and quantity of data used in classical stock assessments, but must deal with limited information to make management decisions (Quinn et al. 2016). Stock assessments can provide a quantitative starting point for developing management strategies and monitoring the impacts of management. For example, the Magnuson-Stevens Fisheries Conservation and Management Act mandates fisheries managers in the United States to set catch limits based on the ‘best available science’, involving advice from stock assessment to inform those limits (Darcy and Matlock 1999; Methot et al. 2014). The Marine Stewardship Council (MSC) similarly requires fisheries seeking certification to go through a stock assessment process to determine their sustainability (Gulbrandsen 2009). In the case of small-scale fisheries in developing nations, it is possible to manage a fishery using only harvest control rules to meet management objectives, without formal stock assessment estimating status relative to reference points (Mahon 1997). However, beyond their use to evaluate management strategies for fishery resources (Carruthers et al. 2014), modeling tools can help with community engagement in the scientific process, such as conflict resolution (Butler et al. 2006) and integration of local knowledge to support cooperation between fishermen and scientists (Neis 1992; Azzurro et al. 2011).

Many stocks worldwide remain unassessed, e.g., the U.N. Food and Agriculture Organization global fishery statistics database includes 19,624 unique combinations of country and taxa (FAO 2016), while the RAM Legacy stock assessment database only includes 1,268 stock assessments (Ricard et al. 2012). The regions of the world with the fewest stock assessments relative to the number of stocks perform worse across fishery management attributes (Melnychuk et al. 2017), indicating the presence of fishery monitoring and assessment may have

some relation with successful management. In the following, we define “data-limited” as any stock with uninformative data (no contrast to provide information on rates of change) or lacking data types typically used in statistical estimates of stock status (e.g. fishery-independent surveys, proportion-at-ages) (Costello et al. 2012; Dowling et al. 2016). Data-limited stock assessment methods are in great demand in both developed and developing nations due to the ubiquity of data-limited fisheries, and the need for science-based management decisions (Wetzel and Punt 2011; Chrysafi and Kuparinen 2016; Dowling et al. 2015).

Length-based assessment methods are a vital component of the data-limited stock assessment toolbox because it is much easier to obtain reliable length measurements of a portion of the fishery catch than to measure total catch or record effort data for many small-scale or non-target species (Harley et al. 2001; Nadon et al. 2015; Prince et al. 2015b; Kokkalis et al. 2015). Similarly, age information and a fishery-independent survey that are representative of total abundance are prohibitively expensive or impossible to collect for most fisheries in the world. Prominent length-based methods for estimating reference points in data-limited fisheries include length-based spawning potential ratio (LB-SPR; Hordyk et al. 2015) and mean-length mortality estimation methods (Nadon et al. 2015). LB-SPR uses length-composition data and assumptions about biological parameters to make a rapid assessment of stock status relative to unfished levels assuming equilibrium conditions (Hordyk et al. 2015; Prince et al. 2015b). While LB-SPR can use multiple years of length data, status determination is based on one year of data at a time (i.e. estimates of status over multiple years are based on that year’s length composition alone). Mean-length mortality estimators (e.g., Gedamke and Hoenig 2006), first developed by Beverton and Holt (1957), assume fishing mortality directly influences mean length of the catch, and have been used for assessments in the U.S. South Atlantic, Pacific islands, and Caribbean (Ehrhardt

and Ault 1992; Ault et al. 2005, 2008; Gedamke and Hoenig 2006; Nadon et al. 2015). As measures of stock status, these length-based methods derive the spawning potential ratio (SPR) reference point, defined as the proportion of unfished reproductive potential at a given level of fishing pressure (Goodyear 1993).

Length-based assessment methods estimating stock status assume that recruitment and fishing mortality arise from deterministic relationships or have not changed over a period significant for management and the life history of the species (termed “equilibrium assumptions”). Equilibrium assumptions are often violated (Gedamke and Hoenig 2006), as recruitment is quite variable for most species and fishing mortality changes with markets and other socioeconomic factors in the fishing community (Thorson et al. 2013, 2014a). Stochastic ocean conditions and productivity regime shifts may cause recruitment to vary erratically, gradually, or periodically at any given time (Vert-pre et al. 2013; Thorson et al. 2014b; Szuwalski et al. 2015). However, the violation of the equilibrium assumption may be difficult to detect. For example, the equilibrium assumption may appear valid when the mean length is constant over time (Gedamke and Hoenig 2006; Nadon et al. 2015). If recruitment is then constant over time, increasing fishing mortality will lead to decreasing mean length as the larger individuals are harvested and only smaller individuals remain in the population. However, constant fishing mortality and a recruitment pulse would also lead to a decrease in mean length, with more young individuals entering the population. Given both variable fishing mortality and recruitment processes occurring on the same population as well as errors when measuring mean length, a mean-length time series may appear constant when time-varying population processes are instead cancelling each other out.

As an alternative to the equilibrium assumptions, a mixed-effects model can be used to deal with important demographic changes by estimating random variation in recruitment, fishing mortality, or other biological processes, as well as the magnitude (variance) of random variation in each process (de Valpine and Hastings 2002; Buckland et al. 2004; Schnute and Haigh 2007; Thorson and Minto 2015). Mixed-effects models can directly account for variation arising from natural processes or measurement processes separately, and therefore improve performance in nonlinear fisheries models (de Valpine and Hastings 2002; Ono et al. 2012; Thorson et al. 2015b). A main criticism of length-based methods with equilibrium assumptions is that with a single year of length-composition data and general understanding of biological parameters, it is impossible to determine whether a larger proportion of small fish in the catch is caused by strong cohort in recent years, or by the removal of larger fish from the system. Accounting for random variation in recruitment, fishing mortality and observation error arising from the process of sampling fish lengths from the population, helps to tease apart each of these processes and better identify the true state of the fish population.

The aim of this study is to introduce a new length-based, integrated, mixed-effects (LIME) model and demonstrate its statistical performance when estimating reference points assuming only length composition and basic biological information are available. This method builds upon the catch-curve stock reduction analysis (CCSRA) model (Thorson and Cope 2014), which includes an estimate of mortality from the age composition and at least one year of total fishery catch to estimate MSY-based reference points without assuming information about final biomass relative to unfished biomass (as generally used in stock reduction analysis). As an extension, LIME uses samples of length in place of the more resource-intensive samples of age, and can estimate the SPR reference point if catch data are unavailable. To demonstrate the LIME

model, we used simulation testing to (i) demonstrate that LIME is unbiased across several life-history types and patterns of fishing mortality and recruitment variability and able to include more years of length measurements and catch and/or abundance index data, (ii) examine the sensitivity of the model to sample size of length measurements and error in input parameters, and (iii) compare LIME against LB-SPR to assess performance under various violations of model assumptions, including the timing of sampling within the year and modeling monthly time steps.

Methods

LIME is an age-structured population dynamics model with the ability to (1) account for variable fishing mortality and recruitment when only length data are available, and (2) to treat multiple years and types of data in an integrated manner to improve estimates of fishing mortality changes over time. The minimum inputs for the LIME assessment method are data on the length composition of the catch from a single year as well as assumed life history information, including the length-at-age relationship, an assumed natural mortality rate, and length at 50% maturity. LIME estimates annual fishing mortality rates, lengths at 50% and 95% selectivity to the fishing gear, and the Dirichlet-multinomial parameter θ as fixed effects. The effective sample size of length data is linearly related to the input sample size with intercept $(1+\theta)^{-1}$ and slope $\theta(1+\theta)^{-1}$ (Thorson et al. 2017). LIME can be differentiated from other age-structured models (e.g. Stock Synthesis) in that annual recruitments are treated as random effects, where mean and standard deviation of a distribution for recruitment are additionally estimated as fixed effects. Another key difference is that LIME does not require catch data: if no information on the scale of population size is available, recruitment will be estimated relative to average levels for an unfished population. As measures of stock status, we derived the SPR

reference point to compare results with LB-SPR. We also derived the $F_{30\%}$ and $F_{40\%}$ reference points (the fishing mortality rates that would result in SPR of 30% and 40%, respectively; Clark 2002). We derived MSY by finding the fishing mortality rate that results in the highest yield per recruit. When total catch data were available (thereby providing information on scale of the population size), LIME would estimate equilibrium recruitment, which would scale the MSY based on a per-recruit equation to a scale appropriate for the population size.

We developed an operating model to simulate true populations and generate data under a variety of fishing, recruitment, and life history scenarios. We then used this operating model to explore the estimation performance of LIME for different scenarios regarding recruitment, fishing mortality, data-availability, and life history (Figure 1). We conducted all simulation modeling using the open-source statistical software R (R Core Team 2016), and all estimation in the R package *Template Model Builder* (TMB; Kristensen et al. 2015) as implemented in our R package *LIME* (<https://github.com/merrillrudd/LIME>, doi: 10.5281/zenodo.834404, version 1.0.0).

Operating model

We tested LIME for three different life-history types chosen to reflect the types of taxa for which length-based assessments are commonly demanded (Figure 2). These life-history types were: (a) a short-lived fish, mimicking rabbitfish (*Siganus sutor*, L_{∞} =36.2 cm, k =0.87, M =1.49, L_m^{50} =20.2 cm, maximum age =4, Hicks and McClanahan 2012), (b) a medium-lived fish, mimicking spotted rose snapper (*Lutjanus guttatus*, L_{∞} =64.6 cm, k =0.21, M =0.43, L_m^{50} =34.0 cm, maximum age=15, Bystrom 2015), and (c) a longer-lived fish, mimicking red grouper (*Epinephelus morio*, L_{∞} =90.0 cm, k =0.13, M =0.18, L_m^{50} =50.0 cm, maximum age=26, Heemstra

and Randall 1993) (Table 1). Each simulated population began with biomass at a fraction of unfished biomass, drawn from a uniform distribution between 0.05 and 0.95.

For each life history scenario, we tested LIME performance under three scenarios of fishing mortality and recruitment variability (Figure 3). The first is the “equilibrium scenario”, which matches the non-variable fishing mortality and recruitment assumptions of LB-SPR. The equilibrium scenario involved fishing mortality and recruitment constant over a 20-year period, with a standard deviation for fishing mortality and recruitment set to a negligible 0.01. The second scenario, the “two-way base scenario”, involved a linear change from the fishing mortality that would result in the randomly chosen initial depletion to the rate associated with 20% SPR ($F_{20\%}$) over the first seven years of the 20-year time series. This change could be positive or negative depending on the F associated with randomly selected value for initial depletion and $F_{20\%}$. Over the next seven years of the time series, F was constant at $F_{20\%}$, then the fishing rate decreased linearly down to half of $F_{20\%}$ for the last six years of the time series. $F_{20\%}$ was calculated deterministically based on the biological information and selectivity associated with each life-history type. Thus, this value would not vary between different scenarios of variability within a life-history type. The fishing mortality time series in the “two-way base scenario” varied between simulation iterations in a) the randomly chosen initial depletion and b) lognormally distributed deviations around this two-way trip (following the same equation for lognormal recruitment deviates in Table 3, eq. 1 except using the standard deviation for fishing mortality, σ_F , equal to 0.2). While we calculated $F_{20\%}$ for the medium-lived and longer-lived life-history types, we fixed $F_{20\%}$ to 3.0 for the short-lived life-history type. Based on the assumption of instantaneous annual fishing mortality, $F_{20\%}$ for the short-lived fish was calculated to be much greater than could be supported even by very high fishing capacity. Recruitment was variable

and autocorrelated over a 20-year period (Table 3, eq. 2). This scenario included a standard deviation of recruitment residuals σ_R equal to 0.737 and a first-order autoregressive coefficient equal to 0.426, the mean of the predictive distribution from a meta-analysis of recruitment variability in global fish orders (Thorson et al. 2014b). A third scenario, the “one-way base scenario”, involved the same recruitment variability and autocorrelation as the “two-way” scenario, but with fishing mortality changing linearly from the rate that would result in the randomly chosen initial depletion to $F_{20\%}$ over the 20-year period. Thus, this change could be positive or negative depending on the F associated with the randomly chosen initial depletion relative to $F_{20\%}$ for the life-history type. This combination of scenarios tests the ability to track how the population processes are changing over time with variability in the system.

In the operating model, we assumed the natural mortality rate was constant, known, and independent of size or age. We modeled individual growth using a von Bertalanffy growth function (Table 2, eq. 1; Figure 2). We assumed maturity at length m_j was based on a one-parameter logistic function (Table 2, eq. 2; Figure 2). We converted maturity at length to maturity at age using a normal distribution with standard deviation a function of the coefficient of variation of the age-length curve (Table 2, eq. 3). Selectivity-at-length follows a two-parameter logistic model (Table 2, eq. 4; Figure 2), with estimated parameter length at 50% selectivity and a second parameter δ representing the difference between length at 95% and 50% selectivity. We modeled weight at age as an allometric function of individual length at age (Table 2, eq. 5). We calculated annual total biomass as a function of the abundance and weight-at-age (Table 2, eq. 6). Spawning biomass was a function of the total annual biomass and the proportion mature at age (Table 2, eq. 7). These processes contributed to an underlying age-structured model (Table 2, eq. 8). Parameter definitions and input values are listed in Table 1.

Data generation

We generated length data by simulating underlying age-structured dynamics and then sampling length composition from the vulnerable population instantaneously at the beginning of each year. First we calculated the probability of being in a length bin for individuals of each age (Table 3, eq. 3). We then calculated the probability of harvest in each length bin each year as the proportion of the abundance-at-age vulnerable to the fishing gear each year multiplied by the probability of being in a length bin given age (Table 3, eq. 4). We used a multinomial probability distribution to generate the length frequency of samples of the catch in each length bin over time (Table 3, eq. 5).

We assumed a sample size n of 200 individuals were measured annually, and that this was the “true” sample size of the length data. We compared the base case of 200 length measurements annually to model performance under sample sizes of 1,000, 500, 100, 50, and 20. We used the large sample size of 1,000 to confirm the model is unbiased and precise across data availability scenarios under ideal circumstances, and then tested the alternate, lower sample sizes to assess performance under more realistic sample sizes.

We tested seven different scenarios of data availability. Two scenarios included only length data, assuming one or ten years of length data were available (the “one length composition”, “ten length compositions” scenarios). Data from these two scenarios were used to demonstrate the value of additional years of length data for each life-history type. We also explored five scenarios of additional data availability to demonstrate the integrated nature of LIME. The data availability scenarios included (i) a “data-rich” scenario with 20 years of total catch, 20 years of an abundance index, and 20 years of length data, used as proof-of-concept that

LIME works when a high amount of informative data exists; (ii) “index plus 10” with 20 years of an abundance index and 10 years of length data; (iii) “index plus 1” with 20 years of an abundance index and 1 year of length data; (iv) “catch plus 10” with 20 years of total catch data and 10 years of length data; and (v) “catch plus 1” with 20 years of total catch data and 1 year of length data. We assume that catch and abundance indices are lognormally distributed with a log-standard deviation of 0.2 (Table 1). The “catch plus 1” scenario is essentially a stock-reduction analysis while replacing the assumed information regarding final biomass (as used in stock-reduction analysis) with a length-based catch-curve to estimate fishing mortality in the final year, which is analogous to Thorson and Cope (2014), except using length-composition samples. We calculated the expected catch-at-age, using the Baranov catch equation (Table 3, eq. 6), summing to obtain total annual catch (Table 3, eq. 7), based on the true fishing mortality time series and selectivity specified in the operating model. The generated standardized abundance index I_t was proportional to spawning biomass (Table 3, eq. 8).

When not otherwise stated, we generated data on an annual time step, which assumes length-composition data are collected instantaneously at the beginning of the year. In fisheries where only length data and biological information are available (i.e. no catch or abundance index) it is possible length data would be available on less than an annual time step. We tested scenarios where length data were collected on a monthly time step, then either pooled into an annual time step or kept on a monthly time step. The monthly data collection scenario is more representative of fisheries occurring year-round, with no specific season. Furthermore, length data on a monthly time step would be more representative of short-lived fish growth, to account for fish observed between the midpoints of each age class.

261 *Estimation model*

262 The structure of LIME follows the structure of the operating model using equations 1-8 in
263 Table 2 and equations 3-4, and 6-8 in Table 3 to derive the predicted catch, index, and length
264 composition. LIME requires at least one year of length data, but is flexible to include annual
265 fishery catch and/or an abundance index. During our simulation testing, we assumed that LIME
266 had the correct values for the von Bertalanffy length-at-age relationship, including asymptotic
267 length (L_{∞}), growth coefficient (k), and age at length=0 (t_0), length-weight parameters, natural
268 mortality (M), and the one-parameter logistic maturity-at-length schedule. Future studies can
269 obtain these values from local studies, FishBase (Froese 1990), or global meta-analyses of fish
270 life-history parameters (Thorson et al. In press). We tested LIME performance under violations
271 of these assumptions in sensitivity analyses. We also fixed the values for catch and abundance
272 index observation error and coefficient of variation in the process error for the age-length curve.
273 For all data availability scenarios, the model estimates as fixed effects the annual fishing
274 mortality, lengths at 50% and 95% selectivity, the recruitment standard deviation, and the
275 Dirichlet-multinomial parameter θ related to the effective sample size of length measurements in
276 each year. In scenarios when catch data are unavailable, there is no information on the scale of
277 the population. In these scenarios, we fixed mean recruitment to a relative value of 1.0 so that the
278 model does not estimate the scale of the population but only the annual deviations in recruitment,
279 and estimates of relative reference points (e.g. SPR) can be derived but reference points based on
280 the scale of the population (e.g. MSY) are not meaningful. By contrast, when total catch data are
281 available for at least one year, we can estimate mean recruitment and derive spawning biomass.
282 When an index of abundance was available, we estimated the catchability coefficient for that

index as an additional parameter q . A list of parameters estimated and fixed for each scenario is presented in Table 1.

We treated annual recruitment as a random effect in LIME, where recruitment each year is a function of an expected recruitment based on a Beverton-Holt stock recruitment relationship (Table 4, eq. 1), and the estimated recruitment standard deviation (Table 4, eq. 2). For the simulation experiments in this paper, we fixed the steepness parameter h of the Beverton-Holt stock-recruitment function at 1.0, meaning that expected recruitment is constant among years and independent of the spawning stock biomass the previous year. It is possible to fix the steepness parameter at a value less than 1.0, where the mean of the lognormal distribution is the predicted number of recruits from the Beverton-Holt stock-recruitment relationship, as opposed to 1.0 or the equilibrium unfished recruitment. We chose to test LIME with 1.0 for the mean of the lognormal distribution to determine how well the model can estimate annual recruitment with all variation from recruitment deviates. Unfished spawning biomass is calculated using the same equation as fished spawning biomass (Table 2, eq. 7) but without the fishing mortality and selectivity terms (Table 2, eq. 9). Unlike the operating model, we did not account for autocorrelation in recruitment in the LIME estimation model.

We applied a random-walk penalty on annual estimates of fishing mortality, which shrinks the estimate of fishing mortality in year $t + 1$ towards its estimate in year t (Table 4, eq. 3). Drastic changes in fishing mortality between years are unlikely in the real world given costs of entering or leaving a fishery, but the random-walk process accommodates gradual changes in fishing mortality (Nielsen and Berg 2014). However, a fixed value of 0.2 for the standard deviation of the fishing mortality penalty does allow the model to estimate variability in fishing mortality if supported by the data (e.g. exit and entry from the fishery).

We also placed a lognormal penalty on the standard deviation of recruitment deviations, σ_R . Based on the meta-analysis conducted by Thorson et al. (2014), the log of the mean was set to the log of 0.737, with a log standard deviation of 0.353 (Table 4, eq. 4). The prior aids in the convergence of the σ_R parameter estimation, preventing the estimate from going to an unlikely value. There is also an upper bound on σ_R at 2.0.

The joint log-likelihood of the observed data is the sum of the log-likelihoods of the observed length data, log-probability of fishing mortality and recruitment variation, and the log-likelihood of the catch and abundance index, if available. We include bias-correction for recruitment deviations using the TMB bias-correction feature (Thorson and Kristensen 2016). For scenarios that include abundance index and catch data, a lognormal probability distribution was assumed to describe error in both data types (Table 4, eq. 7, eq. 8). The respective observation errors σ_I and σ_C are fixed *a priori* (not estimated as parameters). We assumed the length data arose from a Dirichlet-multinomial probability distribution with estimated parameters θ_c related to the effective sample size of length measurements each year. Many stock assessment methods use a multinomial distribution to fit age or length data, but the effective sample size must be calculated externally (Francis 2014). By contrast, the Dirichlet distribution can represent variability in the proportions in each length bin, but the parameters do not correspond to the easily interpretable effective sample size of length data for which model results are highly sensitive. The Dirichlet-multinomial is an alternative to these two distributions, estimating an additional parameter θ within the integrated model (Thorson et al. 2016). The effective sample size is a nonlinear function of input sample size (Table 4, eq. 6; Thorson et al. 2016). As θ approaches infinity, the effective sample size is equal to the observed sample size, and the multinomial distribution is a special case of the Dirichlet-multinomial distribution.

In model runs, we assessed that the model had converged if the final gradient for all parameters was less than 0.001. If the initial model run did not converge (resulting in NAs or a high final gradient), the model would be run up to ten additional times with starting values equal to the estimates from the non-converged model plus a random number drawn from a normal distribution with mean zero and standard deviation 0.2. For each combination of life-history type, data availability scenario, fishing mortality pattern, and recruitment dynamics, we obtained 100 iterations of generated data and ran the estimation model for each set.

Comparison to LB-SPR

We ran LB-SPR from the R package *LBSPR* (Hordyk et al. 2015) with one year (LBSPR 1) and ten years (LBSPR 10) of length data using the operating model described above. LB-SPR requires as input the length data in each year and the ratio of natural mortality to the von Bertalanffy growth coefficient (M/k), as well as inputs similar to those required for LIME: the von Bertalanffy asymptotic length parameter, coefficient of variation of the asymptotic length, length at 50% and 95% maturity, length-weight parameters, and starting values for the length at 50% and 95% selectivity (Table 1). We assumed the coefficient of variation of the asymptotic length was equivalent to the coefficient of variation of the entire age-length curve. For the base runs, we used the true value for the length at 95% maturity and selectivity from the two-parameter logistic curves used in the operating model. LB-SPR uses these inputs to calculate the abundance at relative age at equilibrium. LB-SPR estimates the ratio of fishing mortality to natural mortality and the lengths at 50% and 95% selectivity to best fit the predicted and observed length composition proportions, and derives SPR, outputting estimates for these four values for each year with length data (Hordyk et al. 2015).

We note that this simulation experiment is comparing performance of LIME and LB-SPR using an operating model that is more similar to LIME. To further compare the strengths and limitations of each method, we used the *LBSPR* package to simulate length data under the LB-SPR equilibrium, length-based structure, so that we could also test LIME and LB-SPR using an operating model that is more similar to LB-SPR.

A major issue in the comparison of models was the time step used. To test model performance, we tested both the LIME and LB-SPR methods using the monthly data generation feature in the operating model, where sampling is spread out over all twelve months instead of collected instantaneously at one point. We then compared LIME and LB-SPR performance pooling the monthly length data into an annual distribution and then running each model on an annual time step. These additional simulation tests were designed to compare these two methods under different data-generating models, with the goal of providing guidance for which methods may be appropriate under a variety of real-world conditions.

Reference points

We calculated SPR (Table 2, eq. 10-12) as a biological reference point, used as a proxy for MSY when information on the scale of population size is not available, and for comparison with LB-SPR. A harvest strategy that targets a fishing mortality rate that is expected to result in 40% of unfished spawning output (termed “40% SPR”), is considered risk averse for many species (Clark 2002). Therefore, we calculated these values as examples of possible fishing mortality reference points that could be used to compare to other length-based assessment methods.

Sensitivity tests

Preliminary exploration suggested that LIME performed poorly for short-lived species when using an annual time step, therefore we explored LIME performance on a monthly time step. We generated monthly length data for the short-lived life-history type and ran LIME on a monthly time step by specifying the number of years as number of months, ages as fractions of a year, and dividing the input natural mortality rate M by twelve so that mortality and growth occurs in each month (Figure A1).

We also included sensitivity tests to LIME base models to understand biases associated with imperfect knowledge about species biology, fishery characteristics, and low sample sizes. We assessed the performance of LIME with (a) parameter misspecification of $\pm 25\%$ for each of the life history inputs (M , CV_L , L_∞ , k , and L_m^{50}) and (b) sample sizes of length data of 20, 50, 100, 500, and 1,000 independent samples annually.

Model performance

To assess the ability of the model to accurately and precisely estimate quantities of management interest, we consider bias and precision (Table 4, eq. 9-10) between estimated and true SPR in the last year of data across the 100 iterations of simulated data. We used median relative error (MRE; Table 4, eq. 9) to quantify bias, and median absolute relative error (MARE; Table 4, eq. 10) to quantify precision. To understand the ability of the model to accurately capture uncertainty, we computed the “interval coverage”, the proportion of iterations out of 100 where the true value of a population parameter in the terminal year is within the 50% confidence intervals. A well-performing model would have close to nominal coverage (i.e., a 50% coverage

interval will contain the true value in 50% of simulation replicates). Coverage is presented to illustrate whether confidence intervals accurately capture model uncertainty.

Results

LIME performance across life history, variability, and data scenarios

Based on the Monte Carlo simulations, LIME can estimate unbiased SPR when length data are available and biological characteristics are correctly specified across various scenarios of fishing mortality and recruitment patterns (Figure 4). When tested using the same model structure and assumptions in the operating model, LIME performed best for short-lived fish, with increasing bias and decreasing precision for medium-lived fish, and a further deterioration for longer-lived fish (Table 5). The bias in SPR in the terminal year was 0.002 for short-lived, -0.003 for medium-lived, and 0.016 for longer-lived fish across all data availability and population variability scenarios with 200 length measurements annually. Additional scenarios illustrate further LIME strengths and weaknesses (Table 5). With only one year of length data, LIME estimated SPR with bias of -0.038 for the short-lived life history, -0.186 for medium-lived, and -0.152 for longer-lived across variability scenarios. Integrating ten years of length data improved accuracy in the estimation of SPR in the terminal year on average for each life history type (short-lived from -0.038 to -0.016; medium-lived from -0.186 to -0.048; longer-lived from -0.152 to 0.102). The only exception within variability scenarios was decreased accuracy with ten years of length data for the longer-lived life-history type under the one-way variability scenario (from -0.181 to 0.200). While ten years of length data increased precision of SPR estimates for the short-lived life-history type over one year of length data (from 0.072 to 0.041), the additional

length data decreased precision on average for the medium- and longer-lived life-history types (medium-lived from 0.334 to 0.391; longer-lived from 0.529 to 0.626; Table 5).

LIME provides the added advantage over other length-based assessment methods of including a catch time series and abundance index, if available, which further increases accuracy and precision under most cases. Across all scenarios, including an abundance index decreased bias (from -0.047 to 0.020) compared to when only length data were available. An abundance index particularly improved LIME performance for the short- and medium-lived life-history types. Breaking down by life-history types, bias decreases with an abundance index included for the short-lived life-history type (from -0.026 to 0.005) and medium-lived life-history type (from -0.126 to 0.025), but increases for the longer-lived life-history type (from -0.049 to 0.072) on average. Across all life-history types, including an abundance index increases precision (short-lived from 0.054 to 0.052; medium-lived from 0.346 to 0.190; longer-lived from 0.594 to 0.257).

Adding a catch time series to length data decreased bias minimally on average across all scenarios (from -0.047 to 0.031). The improvement in accuracy is strongest under equilibrium conditions (from -0.036 to -0.007). Given variable fishing mortality and recruitment, including catch data with length composition increased bias (from -0.055 to 0.118). This was mainly due to high bias in the “catch plus one” scenario for short-lived fish (Table 5, Figure 4). Excluding this anomalous scenario, including a catch time series decreased bias for a population with variability (from -0.055 to 0.047). The “catch plus ten” scenario removed the bias from the “catch plus one” scenario for the short-lived life-history type under variability scenarios. However, the “catch plus ten” scenario did not necessarily improve bias nor precision over the “catch plus one” scenario for the medium- and longer-lived life-history types under variability scenarios (Table 5). This indicates that it may be advisable to include a catch time series only when more than one year of

length data are available for a short-lived life-history type, and consider the possibility of over-estimating SPR when fishing mortality is changing over time for medium- and longer-lived life-history types when catch data are included.

LIME converged for 95% of iterations of generated data across life-history types, variability scenarios, data availability scenarios, and sample sizes of length data. LIME converged for 100% of iterations of generated data for the data-rich scenario (Figure 5). With only length data, LIME converged for 95% of iterations across scenarios. The LIME convergence rate was 92% including catch data and 94% including an abundance index. Non-convergence was always due to a high final gradient in parameter estimation, as opposed to any parameter being estimated at the upper or lower bound.

The interval coverage for a 50% confidence interval of LIME was 61% across all scenarios of life history, variability scenarios, data availability, and sample sizes of length data. This indicates confidence interval estimates from LIME are generally informative about model uncertainty, but may be wider (more conservative) on average. LIME estimated confidence intervals that were too narrow or wide for individual life history, variation, and data availability scenarios (Figure 5). The “catch plus one” scenario had the lowest coverage across life-history and variability scenarios (42%), likely because this data availability scenario had the most bias, and thus the true SPR would likely not fall within the confidence intervals at the expected rate. For the short-lived life-history type, LIME interval coverage was only 43%. While the method is expected to be unbiased for this life-history type on average, the confidence intervals are often too tight to include the true SPR within the 50% intervals at a rate of 50%. LIME estimated wider confidence intervals for the medium-lived life-history type, with interval coverage 72%, and longer-lived life-history types, with an interval coverage of 67%.

LIME sensitivity to sample size, input parameters, and selectivity estimation

With one year of length data, LIME estimated SPR with greater precision with more length measurements, but not necessarily with greater accuracy (Table 6). Across all life history types, accuracy and precision improved greatly in the equilibrium scenario between 20 and 1,000 length measurements collected annually. The short-lived life-history type experienced the strongest improvements in accuracy and precision (Table 6). This pattern was strongest with a population in equilibrium, but was generally maintained for scenarios of variability as well. Accuracy generally reached a plateau with greater than 100 samples of length measurements for the short-lived life-history type. Alternatively, accuracy and precision improved for the medium- and longer-lived life-history types with at least 500 samples of length measurements for a population at equilibrium. With variability, there were no clear patterns in accuracy improvement for the medium- and longer-lived life-history types with increasing sample size of length measurements. This indicates accuracy in SPR estimates is more likely to be improved with more data types than increasing sample size, particularly for medium- and longer-lived life histories (Table 5, Table 6).

Like all age or length-based methods, LIME performance is sensitive to the correct specification of life history information (Figure 6). When all biological parameters were correctly specified, LIME estimated unbiased SPR on average with ten years of length data (bias = -0.017). When L_{∞} was misspecified as 25% greater than the truth, bias increased (to -0.554), meaning that on average LIME estimated SPR to be lower than the truth. In this case, we would expect to see larger fish in the observed data. If those fish are not present in the length data, length-based models attribute the difference to a higher fishing mortality, and thus a lower SPR

488 than the truth. On the other hand, when L_{∞} was misspecified as 25% lower than the truth, LIME
489 estimated SPR higher than the truth on average (bias = 0.761). Assuming k was 25% lower than
490 the truth, LIME estimated SPR higher than the truth on average (bias = 0.478). When k was
491 assumed to be 25% higher than the truth, LIME estimated SPR lower than the truth on average,
492 but to a lower degree than the other biases due to life history misspecification (bias = -0.146).
493 However, this lack of severe bias is simply due some model runs resulting in estimates much
494 greater than or lower than the truth, while none are unbiased. When M was fixed 25% higher
495 than the truth, LIME estimated SPR to be higher than the truth (bias = 0.285). A fish that is faster
496 to die can generally sustain a higher fishing pressure, and the interpretation of the higher SPR is
497 that the population has more of its potential spawning biomass than it truly does. When M was
498 assumed to be 25% lower than the truth, LIME estimated SPR lower than the truth (bias = -
499 0.352).

500 Fixing length at 50% maturity at a value 25% higher than the truth resulted in negative
501 bias in SPR (bias = -0.383). In this case the LIME model attributes a lower proportion of the
502 population as being mature, leading the estimated SPR to be lower than the truth. The opposite is
503 true when length at maturity was 25% lower than the truth; estimates of SPR were biased higher
504 than the truth (bias = 0.152). LIME was relatively insensitive to misspecification of CV_L for the
505 age-length curve, but a higher CV_L resulted in a relatively lower estimate of SPR on average
506 (bias = -0.044), and a higher CV_L resulted in a relatively higher estimate of SPR on average (bias
507 = 0.047).

508

509 *Comparing LIME and LB-SPR*

Simulation testing demonstrated that the LIME and LB-SPR methods perform well under different conditions. LB-SPR is biased when the equilibrium conditions are violated (Table 5). However, testing of LB-SPR against the age-structured LIME operating model with instantaneous sampling at the beginning of each year resulted in poor performance for the short-lived life-history type under equilibrium conditions (Table 5, Table 7, Figure 7). We verified that LB-SPR performs well across life-history types when tested using an operating model that matches its model assumptions. LIME, on the other hand, over-estimated SPR for the short-lived life history type with one year of length data and, similar to the performance under its own operating model, had low precision for the medium- and longer-lived life history types with ten years of length data (Table 7). When length data were collected monthly and pooled into an annual length composition, LB-SPR performance improved over the annual model for the short-lived life history type, but LIME over-estimated SPR (Table 7, Figure 7). Running LIME on a monthly time step with monthly length data decreased bias compared to running on an annual time step (from 0.468 to -0.040 with ten years of monthly length data and 0.484 to 0.034 with one year of monthly length data; Table 7).

Discussion

This study demonstrates that the length-based integrated mixed-effects (LIME) method can be a valuable tool for fisheries stock assessment when at least one year of length data and basic biological information are available for the species (Table 8). LIME estimates reference points more accurately than LB-SPR under many common scenarios. The LIME assessment method has several characteristics that make it particularly useful in situations where an abundance index and/or catch data cannot be collected reliably, as data collection programs

533 improve to include more data types, and when recruitment and fishing mortality are believed to
534 be changing more rapidly than would match the equilibrium assumptions required for existing
535 methods with the same data requirements.

536 The *length-based* aspect of the model setup allows the analyst to fit to length, rather than
537 age, composition data from the catch. The current toolbox of data-limited stock assessment
538 methods includes length-only methods with equilibrium assumptions (Hordyk et al. 2015; Nadon
539 et al. 2015; Kokkalis et al. 2015), *ad hoc* assumptions about changes in mortality (Gedamke and
540 Hoenig 2006), or age-structured models that cannot fit to length-composition data (Martell and
541 Froese 2013; Thorson and Cope 2014). MULTIFAN (Fournier et al. 1990) and Stock Synthesis
542 (Methot and Wetzel 2013) can use length instead of age data to gain information on cohort
543 strength and total mortality, but require a catch time series to estimate stock status. The
544 flexibility of LIME to fit to length composition, as opposed to age-composition, is more realistic
545 for capacity-limited fisheries. LIME can be used in conjunction with other length-based methods
546 as a diagnostic tool to see if variations in recruitment or fishing mortality are being predicted by
547 the model based on the length data, and how the results of the multiple assessment types would
548 vary in light of those possibly violated assumptions.

549 The *integrated* nature of LIME is useful in situations where monitoring programs are
550 continuing to be developed over time, incorporating more years of length data or other data types
551 in the same assessment framework. LB-SPR is a quick way of conducting an assessment with
552 only one year of length data, but as monitoring programs improve, the method must be applied
553 independently over multiple years (Prince et al. 2015a, 2015b). There are also many catch-based
554 methods that assume a catch time series is available, but they are not thoroughly tested in fitting
555 to length, rather than age, composition data (Sabater and Kleiber 2013; Martell and Froese 2013;

Thorson and Cope 2014). LIME allows for these data to be included into the same assessment framework, rather than requiring a switch between assessment models as monitoring programs develop and new data types become available (Maunder and Punt 2013). Also, few existing models can incorporate an abundance index and length data without catch data. LIME can be used in this scenario to estimate a relative SPR reference point with no measure of scale. This scenario is common for small-scale fisheries, bycatch species, or other fisheries where trends in abundance are available but total harvest is not.

Finally, the *mixed effects* aspect of LIME extends length-based methods by estimating changes in recruitment and fishing mortality over time. Estimating random effects has been integrated into existing stock assessment models, such as Stock Synthesis (Thorson et al. 2015a) and the state-space assessment model (SAM) framework (Nielsen and Berg 2014). Many assessments for European stocks now use SAM to separate process and observation errors as an objective method of weighting data in age-structured models (Berg et al. 2014). Computing the marginal likelihood for mixed-effects models was previously too computationally challenging, hindering wide application of mixed-effects models. Now, programs such as TMB can do these computations much faster than previous options (Nielsen and Berg 2014). To illustrate the benefits of LIME, a vignette is available on the repository site that walks the user through a simple example, with tips for model interpretation and convergence. An app using the R package *shiny* (Chang et al. 2017) is also available on the repository site (https://github.com/merrillrudd/LIME_shiny) that allows analysts to run the model in a graphical user interface.

Simulation testing in this study demonstrated the best LIME performance with only length data for the short-lived life-history type, with comparatively lower performance for

579 medium- and longer-lived fish. With only length data, LIME performs well for the shorter-lived
580 fish likely because the model is tracking cohorts through the length data to estimate recruitment
581 deviations. This is likely difficult for the longer-lived life histories due to variation in the age-
582 length relationship (especially for older fish), and because each individual cohort represents a
583 small proportion of total abundance (hence requiring more samples to track each individual
584 cohort). The increasing uncertainty in a longer-lived fish's age with increasing length blurs the
585 cohorts as they age, making it difficult to track recruitment events without a much longer time
586 series of length data. With ten years of length data, accuracy in estimating SPR increases but
587 precision decreases for the medium- and longer-lived life-history types, providing support for the
588 increased ability to track recruitment events but propagating uncertainty in the age-length curve
589 for older individuals. With short-lived fish that only live to four years old, each length more
590 clearly matches up with an age group. Regardless of fish growth, one year of length data holds
591 information on an entire generation for a short-lived fish. Even if recruitment is occurring
592 monthly or seasonally and not annually, a ten-year time series of length data can inform variation
593 in cohort strength across several generations of the short-lived fish.

594 By testing LIME and LB-SPR using multiple operating models, we identified scenarios
595 in which each method excels. LB-SPR performs better than LIME for estimating SPR if the
596 population is at equilibrium and only length data are available. If the population is not in
597 equilibrium, then LIME performs better. If the data are collected continuously throughout the
598 year (e.g. monthly), LIME is expected to estimate higher SPR than the truth for short-lived fish.
599 In this case, analysts should run LIME using monthly (or shorter) time steps to account for fish
600 growth during the year. This bias does not occur for medium- or longer-lived fish, where the
601 growth during the year is less rapid. On the other hand, LB-SPR likely under-estimates SPR for

short-lived fish if data are collected instantaneously, but is unbiased if data are collected continuously.

An important question for management is often how many years or how much data are enough, particularly for fisheries where funding for monitoring is limited. The simulation testing in this study demonstrated that we can get accurate but highly uncertain estimates of SPR, fishing mortality, and recruitment from only one year of length data on average (Figure 8). As expected, collecting more data (ten years of length data instead of one) resulted in greater accuracy and precision in LIME estimates of SPR (Figure 4, Table 5). When using only length data, LIME performance is best with at least 500 independent length measurements per year for medium- and longer-lived life histories, but is expected to perform well with 100 or more length measurements per year for short-lived life-history types (Table 6). However, including an abundance index or catch time series improves bias and precision to a greater extent than collecting more independent length measurements (Table 5, Table 6). Managers must determine how much uncertainty they are comfortable with to set monitoring goals. Collecting more years of length data, taking more independent length measurements during each year of length data collection, conducting surveys, and monitoring catch data hold varying levels of information used to estimate variable fishing mortality and recruitment. Their costs and benefits should be weighed to help managers prioritize data collection.

Including an abundance index or catch time series improves LIME performance in most scenarios. Catch data provides useful information on the scale of the population, which is not possible with length data alone. The abundance index provides useful information to help inform the trajectory of the population from which the length data arose. The abundance index could be more informative on the state of the population than length data alone, as long as the abundance

625 index is proportional to abundance and any significant changes in fishing mortality and
626 recruitment occurred during the surveyed time series. Our simulation study shows that the biases
627 associated with including a time series with one year of length data are often overcome with
628 more years of length data. The exception is for the longer-lived life history type, for which LIME
629 performs worse when including an abundance index with ten years of length composition data
630 than if the abundance index was excluded.

631 However, the simulation study also identified some potential issues with data conflict
632 when an abundance index or catch time series are included with length data. Data conflict can be
633 diagnostic of poor data quality, such as catch misreporting, indices from spatial areas with
634 ontogenetic differences, or length data not representative of the fishery. Data quality is an
635 equally important issue as limited data types and should be considered in LIME applications. In
636 the case of this study, however, poor data quality was not the culprit behind any data conflict
637 because we used the true catch data, abundance index from a single area, and representative
638 length data to test LIME. To avoid data conflict, Maunder and Piner (2015) recommend
639 modeling process error explicitly, most commonly via time-varying recruitment, as a better
640 alternative to down-weighting or eliminating data conflicts. LIME takes this approach, but data
641 conflict may still occur, particularly because recruitment deviations are treated as a random
642 effect even if this is not the correct model process for which the data hold conflicting information
643 (Maunder and Piner 2015). Other options to avoid data conflict are to estimate the variance
644 parameter for observed data outside of the stock assessment model (Lee et al. 2014; Maunder
645 and Piner 2015). Alternatively, an analyst could identify whether data conflict is occurring in the
646 LIME model by likelihood profiling individual data components (Ichinokawa et al. 2014) or

retrospective analysis, which quantifies the impact of additional years of data on the stock assessment output (Hurtado-Ferro et al. 2014).

Like all length-based assessment methods, fixing the biological parameters at their true values is an important first step for estimating unbiased reference points. LB-SPR circumvents this strong assumption by using Beverton-Holt life history invariants to estimate the expected age or length structure, as opposed to assuming known values of natural mortality and growth (Prince et al. 2015a). Sensitivity tests in this study demonstrating the impact of misspecifying biological parameters provide support for local studies of species growth rates for stocks assessed using LIME. Analysts should be aware of how SPR is expected to be biased given their assumptions on fixed values for input parameters or model structure. A next step for LIME is to use Bayesian priors on biological parameters to more thoroughly represent the uncertainty in population parameter estimates relevant to management (e.g., from FishLife; Thorson et al. In press). Sensitivity tests and likelihood profiles should be conducted on different levels of dome-shaped selectivity to understand how SPR is expected to be biased if the model structure is misspecified.

Length-based stock assessments are good starting-points for making management decisions with limited data and monitoring capacity. The shrinkage of poorly estimated parameters towards an estimated distribution (as implemented within mixed effects models) has been shown to increase accuracy and precision in stock assessments (Thorson et al. 2013; Nielsen and Berg 2014), but high uncertainty in estimates of stock status will always result if there are only one or two years of length data. Any stock assessment deals with data limitation and uncertainty, and it is vital to appropriately represent and communicate this uncertainty to managers.

Ideally, conclusions on stock status should be drawn using an ensemble of assessment models with varying structure and assumptions (Stewart and Martell 2015; Anderson et al. 2017). In the data-limited context, existing models represent a relatively small range of alternative model assumptions. We have shown that LIME presents a way to represent both process and observation uncertainty. LIME can complement other length-based (Hordyk et al. 2015; Nadon et al. 2015; Gedamke and Hoenig 2006) and catch-only methods (Rosenberg et al. 2014; Carruthers et al. 2014), with the strength of estimating recruitment variability. More accurate and precise estimates of recruitment variability can help decipher whether decreased mean length is due to fishing pressure or recruitment variability, and understanding the range of possible levels of recruitment into the future. We therefore conclude that LIME is a step forward in dealing with uncertainty in decision-making for fisheries where length data are collected.

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Table 1. Parameter definitions, including parameter input values for the base scenario for each of the three life history types, and whether the parameter is fixed (“Fixed”) or estimated (“Est.”) depending on the data availability scenario, or if the parameter is used in data generation only (“Sim.”). Values separated by commas indicate alternate values for sensitivity analysis. Note that scenarios including “LC” are each divided into two scenarios with either one or ten years of length data. Parameter input values are based on short-lived *Siganus sutor* (Hicks and McClanahan 2012), medium-lived *Lutjanus guttatus* (Bystrom 2015), and longer-lived *Epinephelus morio* (Heemstra and Randall 1993).

Symbol	Description	Input value			Data Scenario			
		Life history type			Rich	Index + LC	Catch + LC	LC only
Biological		Short	Medium	Longer				
L_{∞}	Asymptotic length	36.2cm	64.6cm	90.0cm	Fixed	Fixed	Fixed	Fixed
k	Brody growth coefficient	0.87	0.21	0.13	Fixed	Fixed	Fixed	Fixed
t_0	Age at length=0	-0.01	-0.01	-0.01	Fixed	Fixed	Fixed	Fixed
L_m^{50}	Length at 50% maturity	20.2cm	34.0cm	50.0cm	Fixed	Fixed	Fixed	Fixed
α	Length-weight scalar	0.0597	0.0245	0.0264	Fixed	Fixed	Fixed	Fixed
β	Length-weight allometric	2.75	2.79	2.96	Fixed	Fixed	Fixed	Fixed
A	Maximum age	4	18	26	Fixed	Fixed	Fixed	Fixed
M	Natural mortality	1.49	0.43	0.18	Fixed	Fixed	Fixed	Fixed
h	Steepness parameter	1	1	1	Fixed	Fixed	Fixed	Fixed
CV_L	Coefficient of variation for the length-age curve	0.1	0.1	0.1	Fixed	Fixed	Fixed	Fixed
J	Maximum length bin	54cm	97cm	135cm	Fixed	Fixed	Fixed	Fixed
R_0	Equilibrium recruitment	1	1	1	Est.	Fixed	Est.	Fixed
σ_R	Recruitment standard deviation	0.737	0.737	0.737	Est.	Est.	Est.	Est.
ρ	Recruitment autocorrelation	0.426	0.426	0.426	Sim.	Sim.	Sim.	Sim.
Non-biological								
L_s^{50}	Length at 50% selectivity	11.3cm	20.0cm	25.0cm	Est.	Est.	Est.	Est.
δ	Difference $L_s^{95} - L_s^{50}$ (expressed here as ratio L_s^{95} / L_s^{50} to compare across life histories)	1.3	1.3	1.3	Est.	Est.	Est.	Est.
q	Catchability coefficient	1e-5	1e-5	1e-5	Est.	Est.	Fixed	Fixed
σ_F	Fishing mortality penalty standard deviation	0.2	0.2	0.2	Fixed	Fixed	Fixed	Fixed
σ_c	Standard deviation for observed catch	0.2	0.2	0.2	Fixed	Fixed	Fixed	Fixed
σ_I	Standard deviation for observed abundance index	0.2	0.2	0.2	Fixed	Fixed	Fixed	Fixed
θ	Dirichlet-multinomial parameter related to effective sample size	10	10	10	Est.	Est.	Est.	Est.
n	Sample size of length measurements	200	200	200	Fixed	Fixed	Fixed	Fixed
ϕ	Cumulative normal probability distribution							

887 Table 2. Population dynamic equations used in the operating model and LIME estimation model.

Equation		Description
1	$L_a = L_{\infty}(1 - \exp(-k(a - t_0)))$	Von Bertalanffy length-at-age a
2	$m_j = 1/(1 + \exp(L_m^{50} - j))$	Maturity-at-length
3	$m_a = \sum_{j=1}^J m_j \left(\frac{1}{L_a CV_L \sqrt{2\pi}} \right) \exp\left(-\frac{(j - L_a)^2}{2L_a CV_L^2}\right)$	Maturity-at-age
4	$S_j = 1/(1 + \exp\left(-\frac{\ln(19)(j - L_s^{50})}{L_s^{95} - L_s^{50}}\right))$	Logistic selectivity-at-length
5	$w_a = \alpha L_a^{\beta}$	Weight-at-age
6	$B_t = \sum_{a=1}^A N_{a,t} w_a$	Annual total population biomass
7	$SB_t = \sum_{a=0}^A N_{a,t} w_a m_a$	Annual spawning biomass
8	$N_{a,t} = \begin{cases} R_t, & a = 0 \\ N_{a-1,t} \exp(-M - F_t S_{a-1}), & 0 < a < A \text{ and } t=1 \\ \frac{N_{a-1,t} \exp(-M - F_t S_{a-1})}{1 - \exp(-M - F_t S_{a-1})}, & a = A \text{ and } t=1 \\ N_{a-1,t-1} \exp(-M - F_{t-1} S_{a-1}), & 0 < a < A \text{ and } t > 1 \\ (N_{a-1,t-1} + N_{a,t-1}) \exp(-M - F_{t-1} S_{a-1}), & a = A \text{ and } t > 1 \end{cases}$	Abundance at age over time
9	$SB_0 = \sum_{a=0}^A R_0 \exp(-aM) w_a m_a$	Unfished spawning biomass
10	$E_0 = \sum_{a=0}^A \exp(-aM) w_a m_a$	Expected lifetime egg production (unfished)
11	$E_f = \sum_{a=0}^A \exp(-a(M + F S_a)) w_a m_a$	Expected lifetime egg production (fished)
12	$SPR = \frac{E_f}{E_0}$	Spawning potential ratio

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890 Table 3. Functions for generating data in the operating model. All except Equations 2 and 5 are
 891 also used in the LIME estimation model to predict values for the observed data.

Equation		Description
1	$\varepsilon_t \sim \text{Lognormal}(0, \sigma_R)$	Non-autocorrelated recruitment deviations
2	$\tau_t = \varepsilon_t \quad t = 1$ $\tau_t = \varepsilon_t \tau_{t-1} \rho \sqrt{1 - \rho^2} \quad t > 1$	Autocorrelated recruitment deviations
3	$p_{j,a} = \begin{cases} \phi\left(\frac{j - L_a}{L_a CV_L}\right), & j = 1 \\ \phi\left(\frac{j - L_a}{L_a CV_L}\right) - \phi\left(\frac{j - 1 - L_a}{L_a CV_L}\right), & 1 < j < J \\ 1 - \phi\left(\frac{j - 1 - L_a}{L_a CV_L}\right), & j = J \end{cases}$	Probability of being in a length bin given age
4	$\pi_j = p_{j,a} \frac{\sum_{a=0}^A N_{a,t} S_a}{N_t}$	Predicted probability of harvest by length bin
5	$\tilde{\pi}_j \sim \text{Multinomial}(n, \pi_j)$	Generated probability of harvest by length bin
6	$C_{a,t} = \frac{F_t S_a}{M + F_t S_a} N_{a,t} (1 - \exp(-M - F_t S_a))$	Annual catch at age
7	$C_t = \sum_{a=0}^A C_{a,t}$	Annual catch
8	$I_t = q B_t$	Abundance index

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Table 4. Components of the joint likelihood function in the LIME model, as well as performance metrics across iterations of generated data.

Equation	Description
1 $\mu_{Rt} = \frac{4hR_0SB_{t-1}}{SB_0(1-h) + SB_{t-1}(5h-h-h)}$	Expected annual recruitment based on Beverton-Holt stock-recruit relationship
2 $R_t \sim \text{Lognormal}(\mu_{Rt}, \sigma_R^2)$	Annual recruitment R_t arising from a lognormal distribution
3 $F_t \sim \text{Normal}(F_{t-1}, \sigma_F^2)$	Penalty on annual fishing mortality F_t
4 $\sigma_R \sim \text{Lognormal}(0.7, 0.2^2)$	Recruitment standard deviation penalty
5 $\log L(\pi_j, \theta \tilde{\pi}_j, n) = \log \Gamma(n+1) - \sum (\log \Gamma(n\tilde{\pi}_j + 1)) + \log \Gamma(\theta n) - \log \Gamma(n + \theta n) + \sum (\log \Gamma(n\tilde{\pi}_j + \theta n\pi_j) - \log \Gamma(\theta n\pi_j))$	Dirichlet-multinomial log-likelihood
6 $n_{eff} = (1 + \theta n) / (1 + \theta)$	Effective sample size
7 $C_t^{obs} \sim \text{Lognormal}(\sum_{a=0}^A C_t, \sigma_C^2)$	Lognormal likelihood (catch)
8 $I_t^{obs} \sim \text{Lognormal}(qB_t, \sigma_I^2)$	Lognormal likelihood (abundance index)
9 $MRE = \text{median} \left(\frac{x_{estimated} - x_{true}}{x_{true}} \right)$	Median relative error to quantify bias
10 $MARE = \text{median} \left(\left \frac{x_{estimated} - x_{true}}{x_{true}} \right \right)$	Median absolute relative error to quantify precision

Table 5. LIME performance in estimation of SPR in the terminal year across life-history types, scenarios of data availability, and patterns in fishing mortality and recruitment variability, compared with LB-SPR. Bias (top) is measured as median relative error and precision (bottom) is measured as median absolute relative error from 100 iterations of generated data using the LIME age-structured operating model assuming instantaneous sampling with 200 length measurements annually. Dark green indicates bias/precision less than 5%, light green indicates bias/precision less than 10%, yellow indicates bias/precision less than 20%, light blue indicates bias/precision less than 30%, and dark blue indicates bias/precision greater than 30%.

Data availability scenario	Short			Medium			Longer		
	Equilibrium	Variability, two-way F	Variability, one-way F	Equilibrium	Variability, two-way F	Variability, one-way F	Equilibrium	Variability, two-way F	Variability, one-way F
<i>Bias (MRE)</i>									
Rich	-0.019	-0.017	0.023	-0.004	0.005	0.034	0.001	0.012	0.023
Index+LC10	-0.014	-0.039	0.023	-0.049	-0.001	0.094	0.125	0.173	0.076
Index+LC1	0.012	-0.006	0.033	-0.003	0.060	0.065	0.040	-0.061	0.029
Catch+LC10	-0.018	-0.045	0.018	-0.021	0.150	0.165	-0.002	0.124	0.280
Catch+LC1	0.029	0.796	0.972	-0.056	0.119	0.193	0.010	-0.146	0.236
LC10	-0.022	-0.056	0.016	-0.086	-0.137	0.072	0.104	-0.006	0.200
LC1	-0.045	-0.082	-0.025	-0.140	-0.355	-0.154	0.166	-0.468	-0.181
LBSPR10	-0.570	-0.676	-0.708	0.006	-0.405	0.196	0.062	-0.359	0.452
LBSPR1	-0.603	-0.698	-0.738	-0.030	-0.372	-0.181	0.059	-0.403	0.296
<i>Precision (MARE)</i>									
Rich	0.027	0.069	0.028	0.038	0.044	0.101	0.038	0.042	0.089
Index+LC10	0.039	0.051	0.038	0.185	0.176	0.295	0.244	0.449	0.352
Index+LC1	0.046	0.079	0.062	0.105	0.207	0.235	0.180	0.223	0.223
Catch+LC10	0.025	0.055	0.035	0.080	0.382	0.476	0.077	0.423	0.630
Catch+LC1	0.060	0.796	0.972	0.129	0.429	0.496	0.161	0.313	0.714
LC10	0.028	0.063	0.031	0.246	0.499	0.470	0.498	0.743	0.702
LC1	0.072	0.126	0.039	0.216	0.437	0.362	0.301	0.705	0.549
LBSPR10	0.570	0.676	0.708	0.066	0.412	0.404	0.078	0.367	0.486
LBSPR1	0.603	0.698	0.738	0.113	0.478	0.432	0.120	0.501	0.536

Table 6. LIME bias and precision in estimating SPR in the terminal year for a variety of sample size of independent length measurements. In all cases one year of length data are provided to the model. Bias (top) is measured as median relative error and precision (bottom) is measured as median absolute relative error from 100 iterations of generated data using the LIME age-structured operating model assuming instantaneous sampling. Dark green indicates bias/precision less than 5%, light green indicates bias/precision less than 10%, yellow indicates bias/precision less than 20%, light blue indicates bias/precision less than 30%, and dark blue indicates bias/precision greater than 30%.

Sample size	Short			Medium			Longer		
		Variability, two-way F	Variability, one-way F		Variability, two-way F	Variability, one-way F		Variability, two-way F	Variability, one-way F
<i>Bias (MRE)</i>	Equilibrium			Equilibrium			Equilibrium		
1000	-0.033	-0.070	-0.029	0.034	-0.369	-0.201	-0.061	-0.449	-0.201
500	-0.028	-0.117	-0.041	-0.001	-0.505	-0.157	-0.031	-0.621	-0.145
200	-0.045	-0.082	-0.025	-0.140	-0.355	-0.154	0.166	-0.468	-0.181
100	-0.027	-0.070	-0.028	-0.055	-0.370	-0.201	-0.127	-0.480	-0.206
50	-0.082	-0.124	-0.041	-0.182	-0.499	-0.163	-0.141	-0.621	-0.107
20	-0.171	-0.153	-0.043	-0.295	-0.431	-0.214	-0.465	-0.751	-0.451
<i>Precision (MARE)</i>									
1000	0.070	0.148	0.048	0.110	0.443	0.422	0.240	0.648	0.474
500	0.053	0.172	0.047	0.125	0.514	0.423	0.245	0.663	0.519
200	0.072	0.126	0.039	0.216	0.437	0.362	0.301	0.705	0.549
100	0.087	0.147	0.046	0.217	0.453	0.429	0.397	0.665	0.503
50	0.108	0.178	0.046	0.343	0.510	0.455	0.421	0.665	0.506
20	0.228	0.168	0.045	0.374	0.469	0.610	0.547	0.754	0.615

Table 7. Comparison of LIME and LB-SPR performance in estimation of SPR in the terminal year between equilibrium scenarios with length data collected annually and using an annual model, length data collected monthly but pooled annually for an annual model, and using the LB-SPR operating model. We also compared the annual model runs with monthly length data run on a monthly time step for the short-lived life-history type. Bias (top) is measured as median relative error and precision (bottom) is measured as median absolute relative error from 100 iterations of generated data. Dark green indicates bias/precision less than 5%, light green indicates bias/precision less than 10%, yellow indicates bias/precision less than 20%, light blue indicates bias/precision less than 30%, and dark blue indicates bias/precision greater than 30%.

Data availability scenario	Short				Medium			Longer		
	Annual data and model	Monthly data, annual model	Monthly data, monthly model	LB-SPR	Annual data and model	Monthly data, annual model	LB-SPR	Annual data and model	Monthly data, annual model	LB-SPR
<i>Bias (MRE)</i>										
LC10	-0.022	0.468	-0.040	0.068	-0.086	0.072	-0.133	0.104	0.184	-0.112
LC1	-0.045	0.484	0.034	0.195	-0.140	-0.104	-0.097	0.166	0.168	-0.113
LBSPR10	-0.570	0.136	NA	-0.005	0.006	0.090	0.002	0.062	0.117	0.010
LBSPR1	-0.603	0.111	NA	0.021	-0.030	0.056	-0.003	0.059	0.114	-0.030
<i>Precision (MARE)</i>										
LC10	0.028	0.468	0.102	0.140	0.246	0.272	0.260	0.498	0.442	0.429
LC1	0.072	0.484	0.130	0.233	0.216	0.209	0.133	0.301	0.311	0.167
LBSPR10	0.570	0.138	NA	0.050	0.066	0.094	0.048	0.078	0.117	0.050
LBSPR1	0.603	0.154	NA	0.152	0.113	0.139	0.138	0.120	0.157	0.149

Table 8. Summary table of key questions and conclusions.

Objective	Conclusion
1. <i>Is LIME unbiased:</i>	
a. Across life-history types?	Yes, if the assumption of instantaneous length sampling is met, and growth parameters are known with no error. Performance is best for life histories with longevity less than 20 years under this assumption.
b. With population variability?	Yes. It is recommended to use more than one year of length data for short- and medium-lived life-history types, and include catch or an abundance index if longer-lived.
c. With inclusion of catch and/or an abundance index?	Yes, with more than one year of length data for short-lived species. May over-estimate SPR for medium and longer-lived species if the population is not in equilibrium.
2. <i>Is LIME sensitive to:</i>	
a. Sample size of length measurements?	Yes, accuracy and precision generally improve with higher annual sample size. There is a performance plateau for 100 samples for short-lived fish and 500 samples for medium- or longer-lived fish.
b. Error in input parameters?	Relatively insensitive to error in the CV of the age-length curve. If asymptotic length, von Bertalanffy growth coefficient, or length at 50% maturity are input lower than the truth, or natural mortality input higher than the truth, SPR will be estimated higher than the truth (and vice versa).
3. <i>Comparison of LIME and LB-SPR under equilibrium conditions</i>	
a. Instantaneous annual sampling from age-structured model	LIME unbiased across life-history types; LB-SPR estimates lower SPR for short-lived life history.
b. Continuous sampling (monthly) from age-structured model	LIME should use monthly time steps for short-lived species, but can use annual time steps for medium and longer-lived species.
c. Length-structured operating model	LIME over-estimates SPR for short-lived and under-estimates SPR for medium- and longer-lived. LB-SPR unbiased across life-history types.

Figure 1. Diagram of the simulation study. “LC” stands for length data, numbers indicate number of years in the 20-year time-period modeled. In the case of the instantaneous, annual length measurement scenario, we compared multiple sample sizes of length measurements annually (1,000, 500, 200, 100, 50, and 20). For the other scenarios, we assumed the base case of 200 length measurements annually.

Figure 2. Selectivity, maturity, and length at age curves for the three life-history types tested in the simulation study, mimicking: (a) rabbitfish (*Siganus sutor*), a short-lived fish ($L_{\infty}=36.2$ cm, $k=0.87$, $M=1.49$, $a_m^{50}=1$ year, maximum age $A=4$ years, Hicks and McClanahan 2012), (b) spotted rose snapper (*Lutjanus guttatus*), a medium-lived fish (asymptotic length $L_{\infty}=64.6$ cm, von Bertalanffy $k=0.21$, natural mortality $M=0.43$, length at 50% maturity $a_m^{50}=4$ years, maximum age $A=15$ years; Bystrom 2015), and (c) red grouper (*Epinephelus morio*), a longer-lived fish ($L_{\infty}=90$ cm, $k=0.13$, $M=0.18$, $a_m^{50}=7$ years, maximum age $A=26$ years; Heemstra and Randall 1993).

Figure 3. Scenarios of fishing mortality and recruitment under equilibrium and variable conditions for the three life-history types, with corresponding trajectories of relative spawning biomass. Shaded regions represent the area between the 5th and 95th percentile of generated data, and the lines show three randomly chosen iterations out of 100, as examples. Scenarios labeled “equilibrium” demonstrate that the initial depletion may start between 0.05 and 0.95, but fishing mortality remains constant to produce that level of depletion, and recruitment is constant at 1.0 over time. Scenarios labeled “two-way” demonstrate fishing mortality that increases to a fishing mortality rate $F_{20\%}$ that results in 20% SPR over the first seven years, stays at $F_{20\%}$ for seven years, and then drops to half of $F_{20\%}$ for the last six years. Scenarios labeled “one-way” demonstrate a change from equilibrium fishing mortality resulting in an initial depletion between 0.05 to 0.95 to the fishing mortality $F_{20\%}$ over the 20-year period.

Figure 4. Distribution of relative error ($(estimated - true) / true$) for spawning potential ratio (SPR) in the current year for 100 iterations of simulated populations across the LIME and LB-SPR data availability scenarios for the three life-history types and scenarios of equilibrium and variable fishing mortality and recruitment with 200 samples of length measurements annually. The gray bean represents the “data-rich” scenario, which verifies LIME is unbiased and most precise when an unrealistically high amount of data are available. Darker colors represent data availability scenarios with 10 years of length data, and lighter colors represent the scenario with one year of length data available. Each life-history type has a different y-range.

Figure 5. Proportion of iterations out of 100 where the true value of the spawning potential ratio (SPR) lies within the 50% confidence intervals for each life-history type across various patterns of fishing mortality and recruitment (gray circles) compared to the convergence rates for the same scenario (pink triangles).

Figure 6. Comparison of the distribution of estimation error for spawning potential ratio (SPR) in the terminal year with the life history parameters fixed at +/- 25% of their true value from 100 iterations of generated data across the various life history scenarios for the equilibrium (blue) and the two-way fishing mortality scenario with variable and autocorrelated recruitment (red), with other biological parameters fixed at their true values, including 10 years of length data with 200 length measurements annually. Life history parameters include natural mortality, asymptotic length, von Bertalanffy growth coefficient, length at 50% maturity, and the coefficient of variation for the age-length curve.

Figure 7. Comparison of the LIME and LB-SPR methods in the equilibrium state via the distribution of relative error ($\text{estimated-true}/\text{true}$) for spawning potential ratio (SPR) in the current year for 100 iterations of simulated populations from the LIME age-structured operating model using annual length composition collected instantaneously in the year (a-c), monthly length data collection pooled into annual length compositions (d-f), and the LB-SPR operating model based on relative ages. The methods are compared across life-history types. Darker colors represent data availability scenarios with 10 years of length data, and lighter colors represent the scenario with one year of length data available. Each scenario has a different y-range.

Figure 8. Example of model estimates (color lines) with 95% confidence intervals (shaded areas) and the true simulated population dynamics (black dotted line) for each of the data availability scenarios for one iteration of a simulated population with medium-lived life history, 200 length measurements annually in the length data, for the base variation scenario.

Appendix A.

Figure A1. Size at age for the yearly (blue) vs. monthly (white-orange) time steps for the short-lived life-history type. White lines (monthly) overlapping blue lines (yearly) demonstrate that size-at-age is identical at the start to each year, and orange lines increasing in density indicate the size-at-age distributions during the following months within each year.