



## ARTICLE

# Estimating Total Mortality Rates from Mean Lengths and Catch Rates in Nonequilibrium Situations

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### Abstract

A series of estimates of the total mortality rate ( $Z$ ) can be obtained by using the Beverton–Holt nonequilibrium-based approach of Gedamke and Hoenig (2006) on observations of population mean length over time (ML model). In contrast, only relative mortality rates (not absolute values) can be obtained from a time series of catch rates. We derived the transitional behavior of the catch rate following a change in total mortality in the population. From this derivation, we developed a new method to estimate  $Z$  that utilizes both mean lengths and catch rates (MLCR model). Both the ML model and the MLCR model assume constant recruitment in the population. We used a simulation study to test performance when recruitment is variable. Simulations over various scenarios of  $Z$  and recruitment variability showed that there may be correlated residuals in the mean lengths and catch rates arising from fluctuations in recruitment. However, the root mean square errors of the  $Z$  estimates and the change point (i.e., the year when mortality changed) were smaller in the MLCR model than in the ML model, indicating that the MLCR model can better account for variable recruitment. Both methods were then applied to Mutton Snapper *Lutjanus analis* in Puerto Rico to illustrate their potential application to assess data-limited stocks. The ML model estimated an increase in  $Z$ , but the MLCR model also estimated a subsequent reduction in  $Z$  when the catch rate data were considered.

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Beverton and Holt (1956, 1957) developed an approach to estimating the instantaneous total mortality rate ( $Z$ ; year<sup>-1</sup>) from the mean length in the population and information on growth rates and selectivity. The estimator is based on the

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assumptions that the population is in equilibrium and that recruitment is constant. Despite these stringent assumptions, the estimator has found widespread usage because of its minimal data requirements. Gedamke and Hoenig (2006) derived the transitional behavior of the mean length statistic following stepwise changes in mortality rate over time and developed an estimator for period-specific mortality rates. The required information for applying this extension of the Beverton and Holt equation to nonequilibrium situations includes the von Bertalanffy growth parameters ( $L_\infty$  and  $K$ ), the length of first capture ( $L_c$ ; the smallest size at which animals are fully vulnerable to the fishery and sampling gear), and a time series of mean length ( $\bar{L}$ ) of animals above the  $L_c$ . The methodology and applications to Goosefish *Lophius americanus* and to Barndoor Skate *Dipturus laevis* were described by Gedamke and Hoenig (2006) and Gedamke et al. (2008), respectively.

This approach can be generalized to integrate additional data types when they are available. For example, Gedamke et al. (2008) relaxed the assumption of constant recruitment by incorporating an index of recruitment in the model, and Then (2014) incorporated information on fishing effort. Here, we develop a model to incorporate a time series of catch rates (indices of abundance) into the mean length estimator to better detect changes in mortality and to better estimate  $Z$  compared to using the mean length-only estimator.

In the absence of information on recruitment, the mortality estimators using only mean lengths (ML model) and mean lengths plus catch rates (MLCR model) assume constant recruitment over time. Exploited fish populations can exhibit high interannual variability in recruitment, and while Gedamke and Hoenig (2006) demonstrated the effect of a weak or failed year-class on the mean length statistic over time, the effects of variable recruitment on estimating mortality have not been examined. Here, we evaluate via simulation the effect of variable recruitment on mortality estimation in the two models, which assume constant recruitment. We focus on recruitment because it is often identified as the largest source of variability in fish populations (Thorson et al. 2014).

In this study, we derive the transitional behavior of catch rates expressed in terms of either abundance (number per unit effort [NPUE]) or biomass (weight per unit effort [WPUE]) to develop the MLCR model. Next, we evaluate the effect of variable recruitment on the performance of the ML model and the MLCR model in estimating the parameters of interest:  $Z$  and the years when  $Z$  changed. In addition to standard performance metrics of bias and root mean square error, we examine correlations in paired residuals of mean length and catch rate and runs in the sign (positive or negative) of residuals. Finally, we apply both the ML model and the MLCR model to estimate historical values of  $Z$  for Mutton Snapper *Lutjanus analis* in Puerto Rico.

## METHODS

### Relationship between the Catch Rate and Mortality Rate

Consider what information about  $Z$  can be obtained from catch rates in the simplest scenario when we assume equilibrium conditions, including constant recruitment ( $R$ ) and a constant catchability coefficient ( $q$ ). We assume that the abundance-based catch rate, NPUE, is a function of the probability of an individual being captured by 1 unit of effort ( $q$ ) and the abundance  $N$ :

$$\text{NPUE} = qN. \quad (1)$$

Under equilibrium, abundance will be related to total mortality as follows (Ricker 1975):

$$N = \int_{t_c}^{\infty} R \cdot \exp[-Z(t - t_c)] dt = \frac{R}{Z}, \quad (2)$$

where  $R \cdot \exp[-Z(t - t_c)]$  is the abundance at age  $t$ ; and  $t_c$  is the age at which animals are fully selected by the fishing gear, corresponding to length  $L_c$  via the von Bertalanffy growth equation. With integration, parameter  $t_c$  drops out of the equation and is not used here. We substitute equation (2) into equation (1),

$$\text{NPUE} = \frac{qR}{Z} = \frac{\tilde{q}}{Z}, \quad (3)$$

where  $\tilde{q}$  is a scaling parameter that is the product of  $q$  and  $R$ . Two equilibrium catch rates,  $\text{NPUE}_1$  and  $\text{NPUE}_2$ , corresponding to time periods with mortality rates  $Z_1$  and  $Z_2$ , can provide estimates of the relative change in  $Z$  if  $\tilde{q}$  is assumed to be constant. Thus,

$$\text{NPUE}_1 = \frac{\tilde{q}}{Z_1} \quad (4a)$$

and

$$\text{NPUE}_2 = \frac{\tilde{q}}{Z_2} \quad (4b)$$

imply that the ratio of NPUE is an estimate of the ratio of mortality rates,

$$\frac{\text{NPUE}_1}{\text{NPUE}_2} = \frac{Z_2}{Z_1}. \quad (5)$$

In real-world situations, obtaining reliable estimates of both  $q$  and  $R$  is extremely rare; therefore, it is unlikely that absolute values of  $Z$  can be estimated from catch rates alone. However, there is information on relative mortality rates, and we can incorporate this information into the length-based nonequilibrium mortality estimator of Gedamke and Hoenig (2006).

In a nonequilibrium framework, overall abundance and the corresponding NPUE will not respond instantaneously to changes in  $Z$ . Equation (3) will only reflect the new mortality rate when enough time has passed for the new equilibrium age structure to be established. Assume that  $d$  years have elapsed since a change in mortality from  $Z_1$  to  $Z_2$ . The nonequilibrium NPUE will be equal to

$$\text{NPUE}(Z_1, Z_2, d) = \tilde{q} \cdot \tilde{N}(Z_1, Z_2, d), \quad (6)$$

where the NPUE and  $\tilde{N}$  are now functions of the mortality rates and the time elapsed since the change in mortality. Using the derivations from Gedamke and Hoenig (2006), the relative abundance  $\tilde{N}(Z_1, Z_2, d)$  after dividing out recruitment  $R$  has two components and can be expressed as

$$\begin{aligned} \tilde{N}(Z_1, Z_2, d) = & \int_{t_c}^{t_c+d} \exp[-Z_2(t-t_c)] dt \\ & + \int_{t_c+d}^{\infty} \exp(-Z_2 d) \exp\{-Z_1[t-(t_c+d)]\} dt. \end{aligned} \quad (7)$$

In equation (7), the first integral represents fish recruited after the change in mortality; these animals have only experienced mortality rate  $Z_2$  and are of ages  $t_c$  to  $t_c + d$ . The second integral represents fish that were recruited before the change in mortality; these fish have experienced both the old ( $Z_1$ ) and the new ( $Z_2$ ) mortality rates and are of ages  $t_c + d$  and older. The implications of equation (7) can be envisioned by considering the response of NPUE when  $Z$  hypothetically doubles (Figure 1). The NPUE drops rapidly after the change in mortality rate and then approaches the new asymptotic value, which is half of the starting value.

As shown by Gedamke and Hoenig (2006: their Appendix 1), after integration and simplification, equation (7) becomes

$$\tilde{N}(Z_1, Z_2, d) = \frac{1 - \exp(-Z_2 d)}{Z_2} + \frac{\exp(-Z_2 d)}{Z_1}. \quad (8)$$

Equations (7) and (8) can then be modified to incorporate any number of changes in mortality (see Gedamke and Hoenig 2006: their equation A.2.2). The corresponding derivation for the behavior of WPUE is provided in the Appendix.

### Integrating Mean Lengths and Catch Rates in a Model

Using the transitional behavior of the mean length and catch rate, we construct a likelihood-based model to estimate  $Z$  and change points (the calendar years when the mortality rate changed) from a time series of mean lengths and catch rates. The assumptions of the MLCR model include those in the ML estimator as described by Gedamke and Hoenig (2006), but

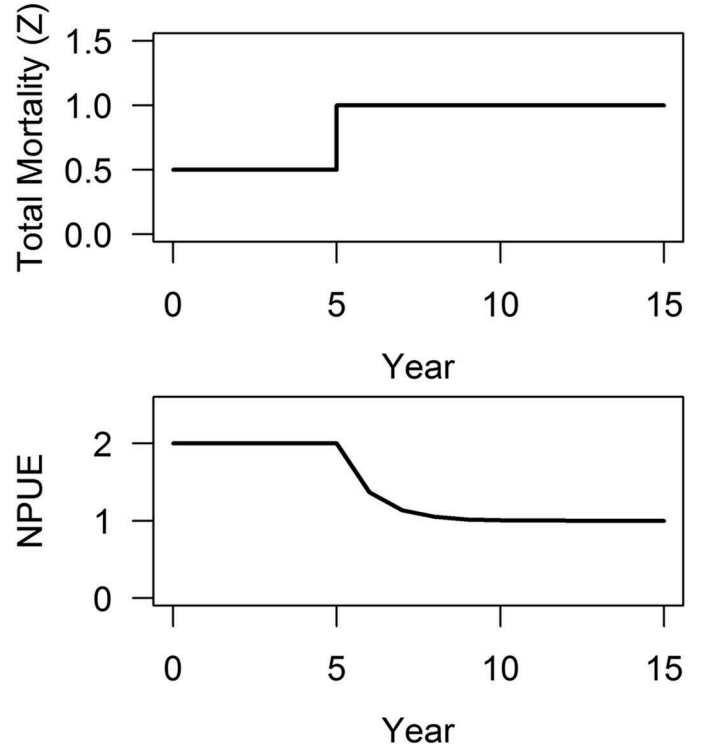


FIGURE 1. Response of a number-per-unit-effort (NPUE) index of abundance (lower panel) to a 100% increase in the total mortality rate ( $Z$ ) from  $0.5 \text{ year}^{-1}$  to  $1.0 \text{ year}^{-1}$  (upper panel). The new asymptotic value of the catch rate will be half of the original equilibrium catch rate. The values of the catch rate are scaled by  $\tilde{q}$ , which is the product of the catchability coefficient  $q$  and recruitment  $R$ .

additionally it is assumed that the NPUE and WPUE are proportional to population abundance and biomass, respectively, by a scaling coefficient  $\tilde{q}$ . Given  $k$  changes in mortality, maximum likelihood estimation is used to estimate the vector of  $k + 1$  total mortality rates (denoted by  $\mathbf{Z} = \{Z_1, Z_2, \dots, Z_{k+1}\}$ ) and the vector of  $k$  change points (denoted by  $\mathbf{D} = \{D_1, D_2, \dots, D_k\}$ ) that best predict the observed data. We construct the joint log-likelihood function,  $\log_e \Lambda(\mathbf{Z}, \mathbf{D})$ , of the MLCR model to be proportional to

$$\log_e \Lambda(\mathbf{Z}, \mathbf{D}) \propto \log_e \lambda_L(\mathbf{Z}, \mathbf{D}) + \log_e \lambda_I(\mathbf{Z}, \mathbf{D}) \quad (9)$$

where  $\log_e \lambda_L(\mathbf{Z}, \mathbf{D})$  and  $\log_e \lambda_I(\mathbf{Z}, \mathbf{D})$  are the log-likelihoods of the mean lengths and catch rates (either in NPUE or WPUE), respectively. Assuming a normal distribution for the annual observed mean lengths (Gedamke and Hoenig 2006), the log-likelihood of the mean lengths is proportional to

$$\log_e \lambda_L \propto -n_L \cdot \log_e \sigma_L - \frac{1}{2\sigma_L^2} \sum_{y=1}^{n_L} m_y (\bar{L}_y - \hat{\bar{L}}_y)^2, \quad (10)$$

where  $y$  indexes year;  $n_L$  is the number of years with mean length observations;  $\bar{L}_y$  and  $\hat{\bar{L}}_y$  are the observed and predicted

mean lengths, respectively, of animals larger than  $L_c$  in year  $y$ ;  $m_y$  is the sample size of observed lengths above  $L_c$  in year  $y$ ; and  $\sigma_L^2$  is the variance of lengths. The log-likelihood of the catch rates, assuming either a normal or lognormal distribution, is proportional to

$$\log_e \lambda_I \propto -n_I \cdot \log_e \sigma_I - \frac{1}{2\sigma_I^2} \sum_{y=1}^{n_I} (I_y - \hat{I}_y)^2, \quad (11a)$$

or

$$\log_e \lambda_I \propto -n_I \cdot \log_e \sigma_I - \frac{1}{2\sigma_I^2} \sum_{y=1}^{n_I} (\log_e I_y - \log_e \hat{I}_y)^2, \quad (11b)$$

respectively, where  $n_I$  is the number of years with catch rate observations;  $I_y$  and  $\hat{I}_y$  are the observed and predicted catch rates, respectively, in year  $y$ ; and  $\sigma_I^2$  is the catch rate variance in either normal (equation 11a) or log-transformed (equation 11b) space.

Equation (9) can be maximized to produce the asymptotically most efficient (maximum likelihood) estimates with SEs and confidence intervals generated for the estimated mortality rates ( $\hat{Z}$ ) and change points ( $\hat{D}$ ), where the circumflex (^) denotes an estimate. A grid search over change points is recommended to identify and avoid local extrema in the log-likelihood function. The required life history information for the MLCR model includes the von Bertalanffy parameters  $L_\infty$  and  $K$  when NPUE is modeled, whereas the allometric exponent  $b$  from the length–weight relationship is also required when WPUE is modeled (Appendix). Compared to the ML model with the same number of change points, two additional parameters are estimated for the MLCR model: the catch rate scaling coefficient ( $\hat{q}$ ) and the catch rate SD ( $\sigma_I$ ). Different numbers of change points can be specified, with model selection procedures used to identify the best-fitting model (Burnham and Anderson 2002). In this study, we use values of Akaike's information criterion with correction for small sample sizes ( $AIC_c$ ) and identify the best-fitting model as the one having the smallest value (i.e., Akaike difference [ $\Delta AIC_c$ ] = 0), with less support for models with larger  $AIC_c$  values.

### Simulation Study of the Mortality Estimators

**Effect of variable recruitment on the mean length and catch rate.**—To illustrate the dynamics of the mean length and catch rate relative to changes in recruitment, consider an age-structured population in which recruitment varies stochastically with a constant mean and variance, while  $Z$  is constant (Figure 2). During periods of poor recruitment relative to the mean, the mean length increases and the catch rate decreases as fewer small animals recruit to the fishery. This pattern produces positive and negative residuals in the mean lengths and catch indices, respectively, from values predicted under constant recruitment. Similarly, the patterns reverse in periods of

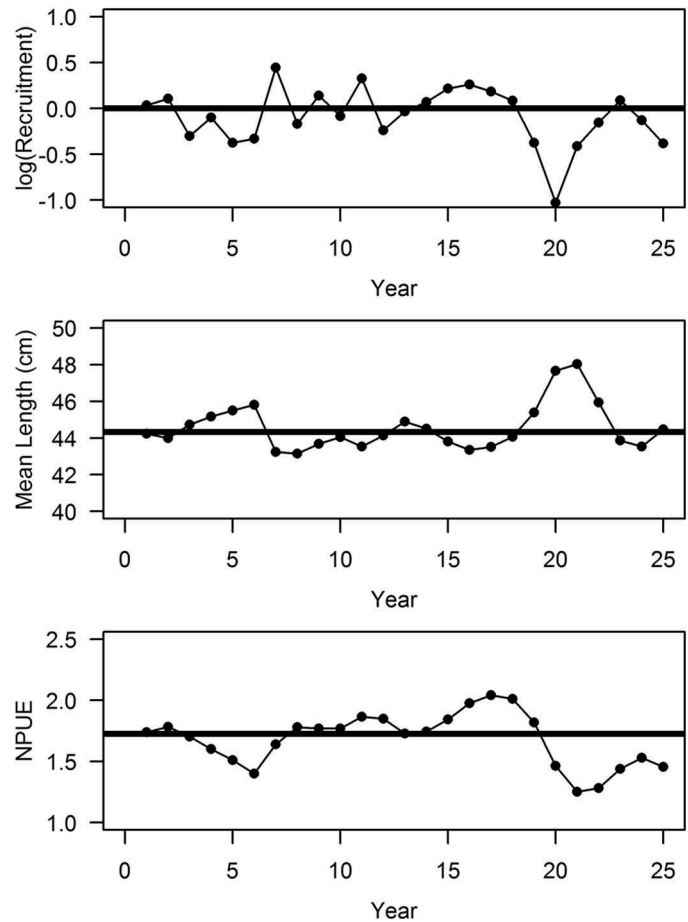


FIGURE 2. Hypothetical time series of stochastic recruitment that is lognormally distributed around a stationary mean (top panel) and the corresponding responses of mean length (middle panel) and catch rate (number per unit effort [NPUE]; bottom panel). Mortality is held constant over time. Solid horizontal lines indicate values that are predicted under constant recruitment. Life history values from Table 1 were used.

relatively good recruitment. We observe two general patterns in the residuals of mean lengths and catch rates. First, variable recruitment produces opposing effects in the residuals of the two data types, creating a negative correlation between the paired residuals. Second, the trends in the residuals can persist as the relative strength of a cohort progresses through the age structure of the population over time.

**Simulation design.**—To examine the implications of using models that assume constant recruitment, we implemented a simulation study with variable recruitment in the population while meeting the other assumptions. The goals of the simulation were to (1) compare the performance of the MLCR mortality estimator relative to that of the ML estimator, (2) compare the performance of both models with variable recruitment in the population, and (3) provide guidance on interpreting the behavior of both models under variable recruitment.

In the simulation model, an age-structured population was constructed,

$$N_{t,y} = \begin{cases} R_y & t = t_c \\ N_{t-1,y-1} \exp(-Z_{y-1}) & t = t_c + 1, \dots, t_{max} \end{cases}, \quad (12)$$

where  $N_{t,y}$  is the abundance at age  $t$  in year  $y$ ;  $R_y$  is the recruitment of animals of age  $t_c$  in year  $y$ ;  $Z_{y-1}$  is the instantaneous total mortality rate in year  $y-1$ ; and  $t_{max}$  is the maximum age. Recruitment followed a lognormal distribution,

$$R_y = \exp(\varepsilon_R - 0.5\sigma_R^2), \quad (13)$$

where  $\varepsilon_R \sim N(0, \sigma_R^2)$  are normally distributed deviations in log space. The expected median recruitment was equal to 1.0 since the magnitude was not relevant in the simulation. To simulate the continuous recruitment assumed in the models, monthly cohorts were created with monthly time steps. Recruitment within each calendar year was held constant.

The population was projected for 20 years. A factorial design for the simulation was created across four values of interannual recruitment variability ( $\sigma_R$ ) and four mortality scenarios (A–D), with a stepwise change in mortality at the beginning of year 11 (Table 1). The mean length ( $\bar{L}_y$ ) and abundance-based catch rate (NPUE<sub>*y*</sub>) in year  $y$  were calculated as

$$\bar{L}_y = \frac{\sum_{t=t_c}^{t_{max}} L_t N_{t,y}}{\sum_{t=t_c}^{t_{max}} N_{t,y}} + \varepsilon_L, \quad (14)$$

TABLE 1. Factorial design and values of parameters used for the simulation study ( $Z$  = total mortality rate).

Variable	Symbol	Values
SD of recruitment	$\sigma_R$	0.0, 0.25, 0.50, 1.0
Mortality scenario	A B C D	$Z_1 = 0.4, Z_2 = 0.8$ $Z_1 = 0.4, Z_2 = 0.6$ $Z_1 = 0.8, Z_2 = 0.6$ $Z_1 = 0.8, Z_2 = 0.4$
Change point	$D$	Year 11
Age of full recruitment	$t_c$	3
Maximum age	$t_{max}$	18
Catch rate scaling coefficient	$\tilde{q}$	1
von Bertalanffy asymptotic length	$L_\infty$	80
von Bertalanffy growth parameter	$K$	0.15
von Bertalanffy location parameter	$t_0$	−1
Observation error SD of mean lengths	$\sigma_L$	1
Observation error SD of NPUE	$\sigma_I$	$0.25\tilde{q}$

$$\text{NPUE}_y = \tilde{q} \sum_{t=t_c}^{t_{max}} N_{t,y} + \varepsilon_I, \quad (15)$$

where  $\varepsilon_L \sim N(0, \sigma_L^2)$  and  $\varepsilon_I \sim N(0, \sigma_I^2)$  are normally distributed deviations in mean length and NPUE, respectively; and  $L_t$  is the length of an animal at age  $t$  following a von Bertalanffy growth function and is calculated as  $L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$ . The mean length and catch rate were observed at the beginning of each year. For each factorial combination, 10,000 stochastic time series of mean lengths and catch rates were generated. The values of the life history parameters, scaling coefficient, and SD parameters for the simulation are defined in Table 1, with growth parameters partly based on a Mutton Snapper stock.

The two mortality rates and single change point were then estimated by using only mean lengths (ML model) or by using both mean lengths and catch rates (MLCR model). In each factorial combination, the percent bias (%Bias) and percent root mean square error (%RMSE) for these parameters were calculated for both models as

$$\% \text{Bias} = \frac{\bar{\hat{X}} - X}{X} \times 100, \quad (16)$$

$$\% \text{RMSE} = \frac{1}{X} \sqrt{\frac{\sum_i (\hat{X}_i - X)^2}{n}} \times 100, \quad (17)$$

where  $X$  is the true value of the parameter of interest,  $\hat{X}_i$  is the estimate in the  $i$ th simulation, and  $\bar{\hat{X}}$  is the mean of the estimates from simulations  $i = 1, 2, \dots, 10,000$ .

Pearson's product-moment correlation of paired mean length and NPUE residuals in the MLCR model was calculated in each factorial combination. Two sets of residuals were examined: (1) the difference between the simulated value and the value expected under constant recruitment with the true mortality rate (true residual); and (2) the difference between the simulated value and the value predicted in the application of the MLCR model (fitted-MLCR residual).

To analyze the trends in residuals, we calculated the mean of the longest run of positive and negative residuals of the mean lengths and catch rates from the 10,000 time series in each factorial combination. For both data types, we calculated the true residual and the fitted-MLCR residual. For the mean lengths, we also calculated a third type of residual from the difference between observed values and the values predicted by the ML model (fitted-ML residual).



## Application to the Mutton Snapper Pot Fishery in Puerto Rico

The Mutton Snapper is one of the more important commercially caught fishes in Puerto Rico, yet it is a data-limited stock with unknown stock status (SEDAR 2007). Annual mean lengths (1983–2006) of Mutton Snapper larger than 30 cm (i.e., the assumed length of full vulnerability,  $L_c$ ) were calculated. Standardized WPUEs (1990–2006) were obtained from Cummings (2007) and were used to index biomass trends (SEDAR 2007). Mortality rates were estimated using the ML and MLCR models implemented in AD Model Builder (Fournier et al. 2012). Life history values for the analyses were obtained from Burton (2002):  $L_\infty$  was 86.9 cm,  $K$  was 0.16 year<sup>-1</sup>, and  $b$  was 3.05.

Sensitivity of the MLCR model to growth parameters was evaluated by refitting the model with alternative values of  $L_\infty$ ,  $K$ , and  $b$ . The parameters were sampled 100 times from a multivariate normal distribution with the means from the base analysis. The covariance matrix was created, assuming coefficients of variation (CVs) of 0.15, 0.04, and 0.0098, respectively, based on the estimated SEs reported by Burton (2002). The von Bertalanffy parameters  $L_\infty$  and  $K$  were sampled assuming a correlation of  $-0.90$ , while both were independent of  $b$ .

## RESULTS

### Simulation Study of the Mortality Estimators

The bias in estimates of  $Z$  and the change point was generally small for both the ML model and the MLCR model in all factorial combinations. The %Bias metric was less than 10% in almost all cases, although it increased with increasing recruitment variability (Figure 3). For most factorial combinations in the simulation, both the ML model and the MLCR model produced a positive bias in the mortality estimates. This result was consistent with the findings in previous simulation studies of the Beverton–Holt equation (Then et al. 2015), although the positive bias was less likely to occur when recruitment variability was highest ( $\sigma_R = 1.0$ ).

Compared to the ML model, the MLCR model generally produced less-biased estimates of the higher mortality rate (i.e.,  $Z_1$  when mortality decreased or  $Z_2$  when mortality increased). The %Bias in the estimate of the change point and the difference in bias between the ML model and MLCR model were small (all  $< 2.0\%$ ). The estimates from the MLCR model also had a %RMSE that was equal to or lower than those from the ML model for all parameters in all factorial combinations, indicating higher precision when using the MLCR model (Figure 4).

When the MLCR model was used to estimate  $Z$ , the correlation between paired residuals of mean length and NPUE was negative (Figure 5). The true residuals were uncorrelated when there was no recruitment variability ( $\sigma_R = 0.0$ ). However, the fitted-MLCR residuals showed a slight negative correlation

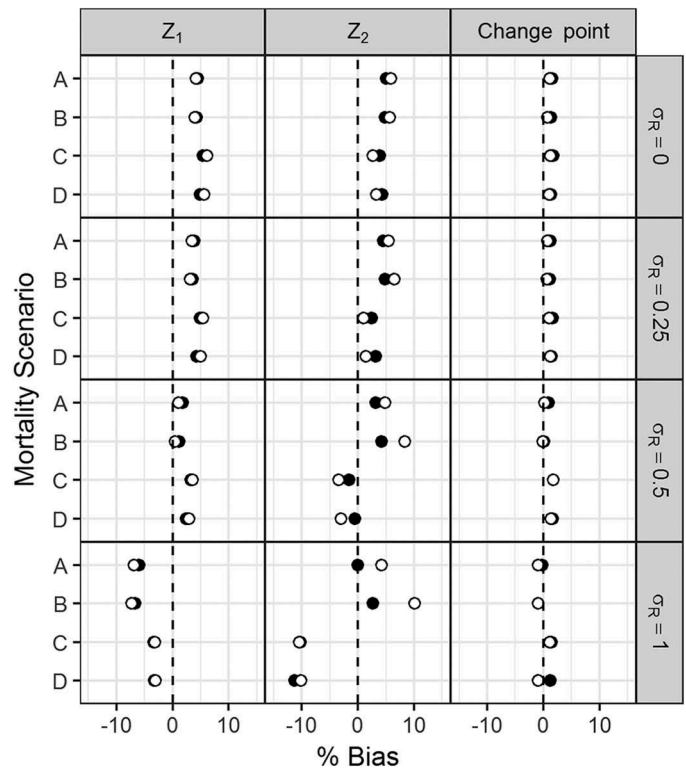


FIGURE 3. Percent bias (%Bias) of estimated total mortality rates  $Z_1$  and  $Z_2$  and the change point based on mean lengths only (ML; open circles) or based on mean lengths and catch rates (MLCR; filled circles) from the simulation. The four mortality scenarios (A–D) and four values of recruitment variability ( $\sigma_R$ ) from the simulation are described in Table 1. Dashed vertical lines indicate a %Bias value of zero. In some cases, open circles directly overlap the filled circles.

coefficient of approximately  $-0.05$  even when there was no recruitment variability. With increasing recruitment variability, the correlation coefficient of fitted-MLCR residuals ranged from  $-0.2$  to  $-0.6$ , with the most extreme correlation value observed when recruitment variability was highest. In all cases, the fitted-MLCR residuals had stronger correlations than the true residuals.

The magnitude of the largest run of positive or negative residuals in the mean lengths and catch rates increased as recruitment variability increased (Figure 6). When there was no recruitment variability ( $\sigma_R = 0.0$ ), the mean largest run in the true residual for mean lengths and NPUE was approximately 4.6. The mean largest run in the true residual increased to as much as 6.0 for mean length and as high as 8.9 for NPUE with high recruitment variability. In all recruitment and mortality scenarios, residuals from the both the ML model and the MLCR model showed shorter runs than the true residuals. For the fitted-MLCR residuals, the mean largest run was as high as 5.2 in mean length and 6.2 in NPUE with high recruitment variability. For the mean length, the fitted-ML residual had shorter runs than the fitted-MLCR residual of the corresponding scenarios.

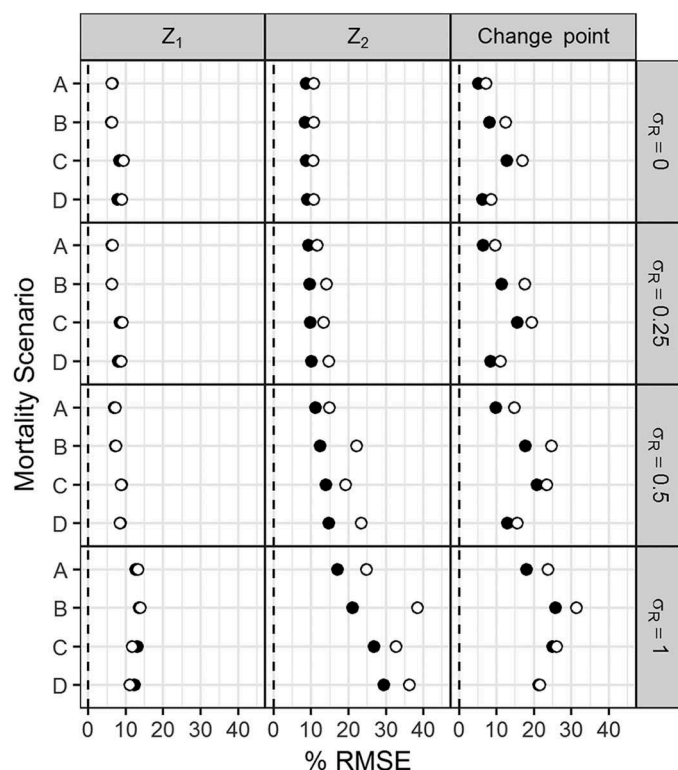


FIGURE 4. Percent root mean square error (%RMSE) of estimated total mortality rates  $Z_1$  and  $Z_2$  and the change point based on mean lengths only (ML; open circles) or based on mean lengths and catch rates (MLCR; filled circles). The four mortality scenarios (A–D) and four values of recruitment variability ( $\sigma_R$ ) from the simulation are described in Table 1. Dashed vertical lines indicate a %RMSE value of zero. In some cases, open circles directly overlap the filled circles.

### Application to the Mutton Snapper Pot Fishery in Puerto Rico

Time-specific  $Z$  was estimated from mean lengths by using the ML model (Figure 7). With one change point in the mortality rate over time, mortality was estimated to have increased from  $\hat{Z}_1 = 0.51 \text{ year}^{-1}$  to  $\hat{Z}_2 = 1.00 \text{ year}^{-1}$ , with the change point  $\hat{D}_1$  at 1992.7 (change points are estimated in continuous time, with the decimal representing tenths of a year). With two change points, mortality increased from  $\hat{Z}_1 = 0.51 \text{ year}^{-1}$  to  $\hat{Z}_2 = 1.25 \text{ year}^{-1}$  and subsequently decreased to  $\hat{Z}_3 = 0.79 \text{ year}^{-1}$ , with change points of  $\hat{D}_1 = 1993.3$  and  $\hat{D}_2 = 1998.9$ , respectively. There was strong support for the one-change model over the two-change model, as the  $AIC_c$  value increased by 2.3 units for the latter model with the additional change point (Table 2).

Next, the MLCR model was used to estimate  $Z$  from mean lengths and WPUEs (Figure 8). Assuming one change in mortality,  $Z$  was estimated to have increased from  $\hat{Z}_1 = 0.51 \text{ year}^{-1}$  to  $\hat{Z}_2 = 0.81 \text{ year}^{-1}$  in 1987 (Table 3). An examination

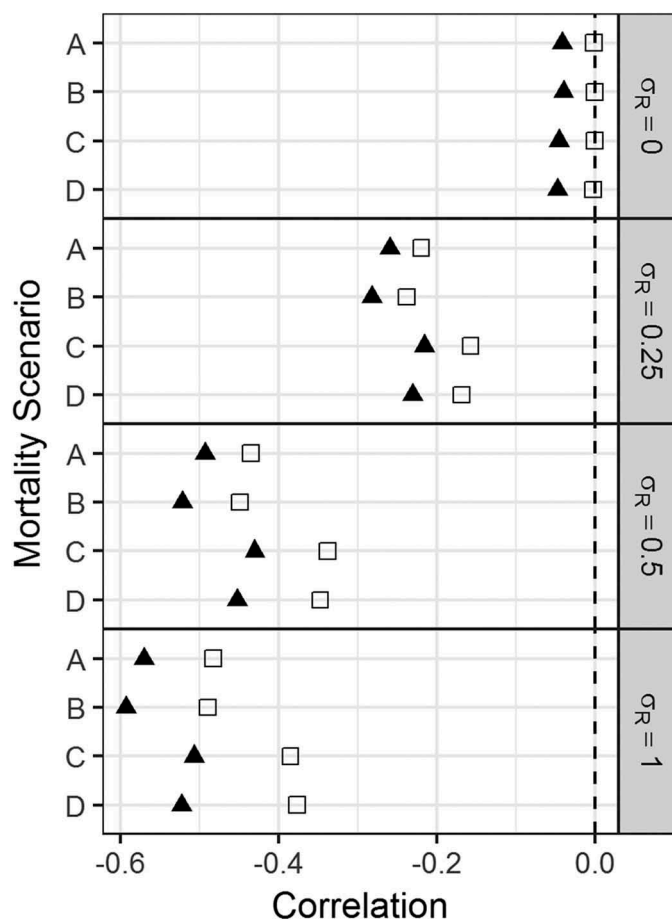


FIGURE 5. Pearson's product-moment correlation coefficients between paired residuals of mean length and catch rate (open squares = true residuals; filled triangles = fitted-MLCR residuals [i.e., mean length–catch rate model]) from the simulation. The four mortality scenarios (A–D) and four levels of recruitment variability ( $\sigma_R$ ) are described in Table 1. The dashed vertical line indicates a correlation coefficient of zero.

of the predicted and observed WPUE values showed a clear pattern to the residuals, suggesting that the one-change model did not fit the data well (Figure 8). The model was reformulated to include a second change in mortality. In the two-change model, mortality was estimated to have increased from  $\hat{Z}_1 = 0.51 \text{ year}^{-1}$  to  $\hat{Z}_2 = 1.19 \text{ year}^{-1}$  with  $\hat{D}_1 = 1987.3$ , followed by a reduction to  $\hat{Z}_3 = 0.61 \text{ year}^{-1}$  with  $\hat{D}_2 = 1997$ . The two-change model was the better fit to the mean lengths and catch rates, with the  $AIC_c$  value reduced by 22.8 units despite the need to estimate an additional mortality rate and change point.

The sensitivity analysis of growth parameters was performed for the MLCR model with two change points. Model estimates were all highly correlated with  $L_\infty$  (positively) and  $K$  (negatively). The magnitude of the correlation between  $L_\infty$  and model estimates was greater than 0.85 in all cases,

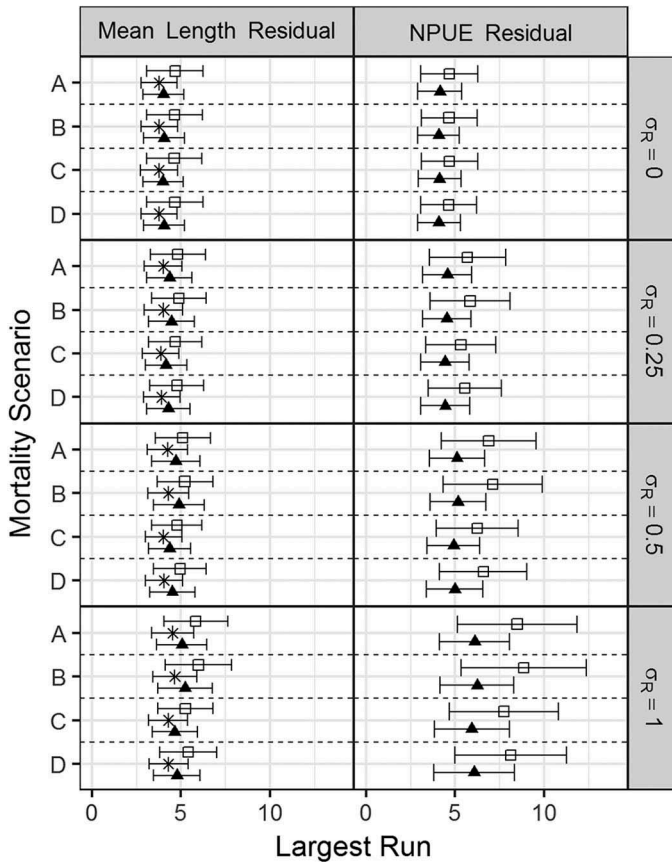


FIGURE 6. Mean ( $\pm$ SD;  $n = 10,000$ ) of the largest run for sequences of positive and negative residuals of the mean length and catch rate (number per unit effort [NPUE]); open squares = true residuals; asterisks = fitted-ML residuals [i.e., mean length-only model]; filled triangles = fitted-MLCR residuals [i.e., mean length–catch rate model] in a 20-year time series. The four mortality scenarios (A–D) and four levels of recruitment variability ( $\sigma_R$ ) from the simulation are described in Table 1.

whereas there was little correlation (magnitude all less than 0.05) between  $b$  and the model estimates. The CV of the most recent mortality rate ( $Z_3$ ) was 0.27 (Figure 9).

## DISCUSSION

### Simulation Study of the Mortality Estimators

In the simulation, the %RMSE for  $Z_1$  was similar between the ML model and the MLCR model. The data (mean lengths and catch rates) available to estimate  $Z_1$  were in equilibrium in our simulation, and the model did not need to account for the transitory behavior of the data that would occur after a change in mortality. This is apparent because the %RMSE was larger for estimating the mortality rate that followed the change point (i.e.,  $Z_2$ ). For the change point, the %RMSE was larger when the magnitude of the change in mortality was small (mortality scenarios B and C). In such situations, the changes in mean lengths and catch rates were relatively small and more difficult to detect. As a result, having two data types in the MLCR

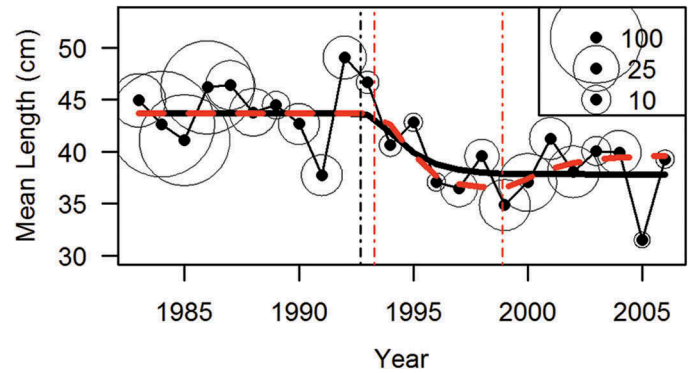


FIGURE 7. Observed mean lengths (points) and predicted mean lengths assuming one change in mortality (solid black line) or two changes in mortality (dashed red line) for Mutton Snapper based on the mean length-only model. Dot-dashed vertical lines indicate the estimated change points for the respective models (black = one change; red = two changes). Concentric circles around mean lengths indicate the annual sample size of observations used in the likelihood function (with legend provided); the area of the circle is proportional to the sample size.

model noticeably reduced the %RMSE in estimating  $Z_2$  and the change point.

Generally, when using either mean length or catch rate alone, there is no ability to distinguish between a change in mortality and a change or variability in recruitment. However, the two data types together can be used to estimate stepwise changes in mortality when recruitment is variable. The MLCR model essentially splits the difference in the information between the two data types. Both ML and MLCR fit the model to produce shorter-than-expected residual runs, but in doing so the MLCR model produced correlations that were more negative than expected in paired residuals (Figures 5, 6). The runs of mean length in the ML model were shorter than those in the MLCR model, but this resulted in less precision in mortality estimation for the former model. From our simulations, the estimates of mortality and inference on the mortality history using both data types were better (by reducing the %RMSE) despite correlations in residuals and residual patterns, both of which should be

TABLE 2. Estimates of total mortality ( $Z$ ) and change points ( $D$ ) for Mutton Snapper from the mean length-only model ( $\Delta AIC_c$  = difference in Akaike's information criterion with correction for small sample sizes). Coefficients of variation (CVs) for the parameter estimates are shown in parentheses; in CV calculations for the change points, the number of years elapsed since the first year of the model (i.e., 1983) was used in the denominator.

Parameter	One change point ( $\Delta AIC_c = 0.0$ )	Two change points ( $\Delta AIC_c = 2.3$ )
$Z_1$	0.51 (0.06)	0.51 (0.06)
$D_1$	1992.70 (0.14)	1993.30 (0.23)
$Z_2$	1.00 (0.14)	1.25 (0.02)
$D_2$		1998.90 (0.06)
$Z_3$		0.79 (0.03)



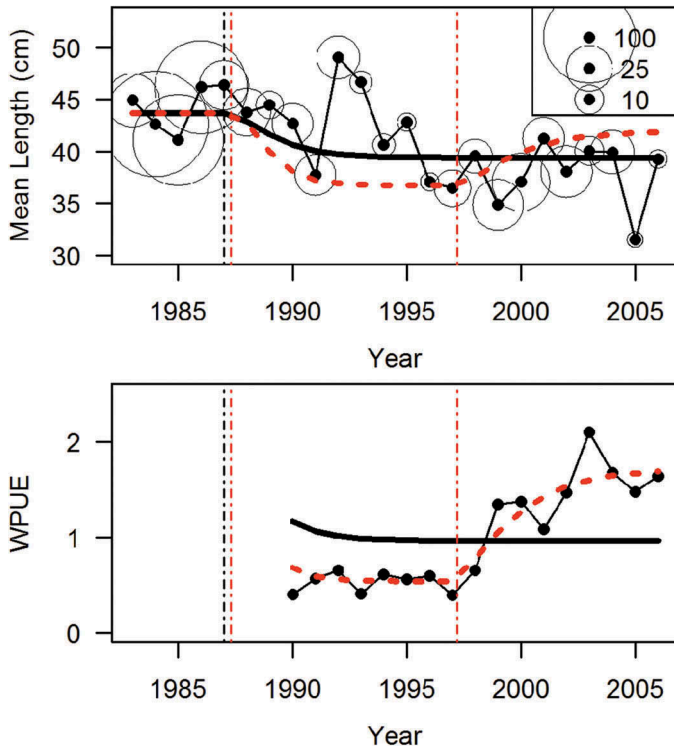


FIGURE 8. Observed (points) and predicted mean lengths (upper panel) and weight per unit effort (WPUE; lower panel) assuming one change in mortality (solid black line) or two changes in mortality (dashed red line) for Mutton Snapper based on the mean length–catch rate model. Dot-dashed vertical lines indicate the estimated change points for the respective models (black = one change; red = two changes). Concentric circles around mean lengths indicate the annual sample size of observations used in the likelihood function (with legend provided); the area of the circle is proportional to the sample size.

expected given the variability of recruitment in fish populations.

The values of  $\sigma_R$  used in the simulation encompassed the range of recruitment variability likely to be encountered in marine fish stocks (Thorson et al. 2014). Our simulation generated data by only including two sources of error: recruitment variability and observation error. Increased or decreased random observation error in the data will decrease or increase, respectively, correlations and runs in residuals. Other nonrandom sources of error, such as the extent to which the catch rate is representative of stock abundance and the length composition data of the population size structure, also need to be evaluated for each application of the MLCR model. These factors make it unlikely to be able to estimate recruitment variability based on residual behavior in the data-limited model.

The behavior of residuals arises from the constant recruitment assumption in the model. Recruitment could be explicitly modeled in a mortality estimation procedure, but this would require a different derivation of the mean length and catch rate than the one presented in the current study.

TABLE 3. Estimates of total mortality ( $Z$ ) and change points ( $D$ ) for Mutton Snapper from the mean length–catch rate model ( $\Delta AIC_c$  = difference in Akaike's information criterion with correction for small sample sizes). Coefficients of variation (CVs) for the parameter estimates are shown in parentheses; in CV calculations for the change points, the number of years elapsed since the first year of the model (i.e., 1983) was used in the denominator.

Parameter	One change point ( $\Delta AIC_c = 22.8$ )	Two change points ( $\Delta AIC_c = 0.0$ )
$Z_1$	0.51 (0.08)	0.51 (0.08)
$D_1$	1987.00 (0.24)	1987.30 (0.20)
$Z_2$	0.81 (0.12)	1.19 (0.27)
$D_2$		1997.20 (0.04)
$Z_3$		0.61 (0.16)

The log-likelihood function (equation 9) assumes that observation errors for length and catch rate are uncorrelated because the length and catch rate data are sampled independently from each other. If a stock exhibits characteristics that would cause correlated observation errors—for example, if schooling behavior occurs in certain size-classes, resulting in concurrent high catch rates, and the data are sampled as paired observations (e.g., within individual fishing trips or gear hauls)—then

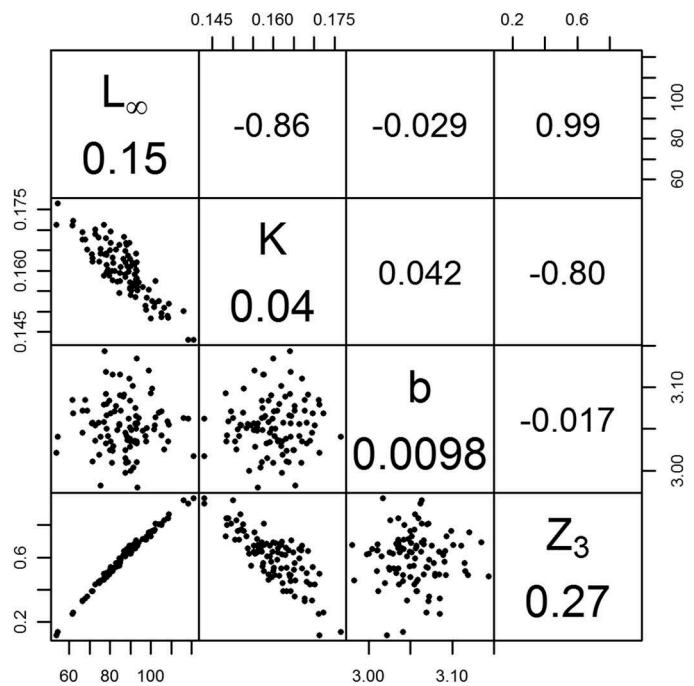


FIGURE 9. Scatterplots (lower triangle), correlation coefficients (upper triangle), and coefficients of variation (diagonal) for life history parameters sampled from a multivariate normal distribution ( $L_\infty$ ,  $K$ , and  $b$ ; symbols defined in Table 1 and the mean values for the sensitivity analysis are defined by Burton [2002]) and the resulting total mortality estimate ( $Z_3$ ) in the terminal year of the time series for Mutton Snapper based on the mean length–catch rate model with two change points.

correlations in observation error can occur. The log-likelihood can be modified on a case-by-case basis to account for such situations.

### Application to the Mutton Snapper Pot Fishery in Puerto Rico

In application of the MLCR model to the Mutton Snapper data specifying two change points, there was some disagreement in the signals from the mean length and WPUE data, as was apparent from examination of the residuals (Figure 8). For the mean lengths, there was a run of five positive residuals in 1992–1996 and four negative residuals in 2002–2006, which were within the range of the mean largest runs observed in the simulation. On the other hand, there did not appear to be a pattern in the residuals of the catch rates. The correlation of the 17 paired residuals was  $-0.07$  but was not statistically significant ( $t = -0.27$ ,  $df = 15$ ,  $P = 0.79$ ). These diagnostics could suggest relatively low recruitment variability in Mutton Snapper. Low sample sizes of lengths during some years may also contribute to large residuals, but this aspect was not evaluated in the simulation.

Recruitment variability has been found to be higher when oceanographic conditions are less stable (Myers and Pepin 1994; Myers 2001). Thus, the tropical distribution of Mutton Snapper suggests that recruitment variability of the stock is likely to be lower than those of higher-latitude species. Stock assessments of several lutjanid species based on age-structured models have also suggested low values of recruitment variability, with  $\sigma_R$  no greater than 0.3 (SEDAR 2003, 2015, 2016), although a formal meta-analysis has not been performed for lutjanids. In the context of the ML and MLCR models and the simulation study, recruitment refers to the cohort entering the fishery at age  $t_c$ , at which time cohort strength can be dampened by density-dependent processes. In contrast, recruits can also be defined at age 0 when individuals reach the settlement phase immediately after the larval stage of the life cycle. High interannual variability in these postsettlement recruits of tropical coral reef fish species has been observed (Shulman 1985; Rankin and Sponaugle 2014).

According to the transitional behavior of the mean length and catch rate presented by Gedamke and Hoenig (2006) and in the present study, respectively, the mean length data suggested an initial change in mortality during 1992–1993 (Figure 7; Table 3), whereas the stability of WPUE during 1990–1997 suggested that a mortality change occurred prior to 1990 (Figure 8). When both types of data were used in the MLCR model, the WPUE data apparently received more weight given the current log-likelihood equation, resulting in the early estimates of the first change point in the two-change-point model.

Additional modifications are also possible to balance the contribution of the length and catch rate log-likelihoods in the MLCR model. Weight coefficients can be assigned to each log-likelihood component in equation (9); as more weight is given to the length data, the results will approach those in the

ML model at the expense of model fit to the catch rates. When there is high interannual variability in the precision of the catch rate, annual estimates of the catch rate SD (often obtained via standardization techniques; Maunder and Punt 2004) can serve as input into the log-likelihood to weight each annual value accordingly.

Results from the ML model and MLCR model illustrate that different models can produce different interpretations about the pattern of mortality experienced by the Mutton Snapper stock. All four models presented here (ML and MLCR models, each with one or two change points) predicted the same initial increase in  $Z$  around 1989–1993 because only length data were available prior to 1990. There appeared to be an increase in the mean length data in the early 2000s, which would suggest a second change in  $Z$  (Figures 7, 8). However, this trend alone did not provide sufficiently strong evidence of a reduction in mortality using the ML model until the concurrent increase in the catch rate was also considered in the MLCR model.

The predicted catch rates in the MLCR model specifying two changes in mortality tracked the observed values very well, but the high variability of the mean length data still resulted in some uncertainty surrounding the estimates of  $Z$  since 1990 (i.e.,  $\hat{Z}_2$  and  $\hat{Z}_3$ ; Table 3). This is expected when we consider that the clear trend in the catch rates will only provide information on the relative change in mortality; information from the mean lengths is still required to estimate the absolute mortality rates.

The four models agreed on the initial  $Z$  before 1988, but the mortality rates estimated after that year were extremely variable. Variability of the mean length data in this time period was partly attributable to low sample sizes in some years. Since the likelihood function for the mean lengths weights the time series by annual sample size, years with few length observations may produce large outliers and large residuals, as was seen in this application. Additionally, the WPUE time series does not provide information for estimating the ratio of the first change in mortality since data prior to 1990 were not available.

All four models indicated that since 1998, mortality has either (1) decreased if mortality had been very high (ML and MLCR models with two change points) or (2) held constant at a more moderate value (ML and MLCR models with one change point). Reliable estimates of  $Z$  over time will require a more intensive, standardized fishery sampling program or alternatively a standardized survey index of Mutton Snapper relative abundance through time. Utilizing the best-fit model that considers all available data (i.e., MLCR with two changes in mortality) implies that the  $Z$  in the terminal year of the time series was markedly smaller than values from the other models (Tables 2, 3).

Estimates of mortality are also conditional on the values of life history parameters used in the model. In the MLCR model, mortality estimation is partly based on the magnitude

of mean lengths relative to  $L_{\infty}$ . Larger values of  $L_{\infty}$  imply a larger mortality rate, which is why we observed a strong correlation between the two in the sensitivity analysis. Larger uncertainty in  $L_{\infty}$  would result in a proportionate increase in the uncertainty of mortality estimates. This behavior is consistent with what has been observed in the ML model (Gedamke and Hoenig 2006). In contrast, there is generally less uncertainty in the allometric exponent  $b$  relative to von Bertalanffy parameters.

The estimates of  $Z$  from these models could be used to obtain fishing mortality if an external estimate of natural mortality is available. Biological reference points from spawning potential ratio or yield-per-recruit analyses can then be used to evaluate stock status. We did not do so here because the Mutton Snapper application was an illustration of the methods and not intended to be an assessment of the stock.

## Conclusions

In this study, we derived the transitional behavior of the catch rate following a change in  $Z$ . Since catch rates can provide additional information on mortality trends over time, we developed a mortality estimator that uses both mean length and catch rate data. Simulations showed that when the assumption of constant recruitment was violated, patterns in the residuals were generated. Despite this, the %Bias values for the  $Z$ -estimates and change point were relatively low when  $\sigma_R$  was less than 1.0, and the %RMSE was reduced in all situations with the inclusion of catch rates compared to when mean lengths were used alone. Thus, residual patterns arising from nonconstant recruitment are unlikely to substantially bias the estimates of  $Z$ . The application to Mutton Snapper highlights the value of considering the catch rates together with the mean lengths; an additional change in mortality was estimated when both mean length and catch rate data were used in one model.

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### Appendix: Derivation of the Transitional Behavior of Weight per Unit Effort

The catch rate in weight per unit effort (WPUE) is

$$\text{WPUE} = qB, \quad (\text{A.1})$$

where  $q$  is the catchability coefficient and  $B$  is the biomass. In equilibrium, the biomass is modeled as

$$B = \int_{t_c}^{\infty} N_t W_t dt, \quad (\text{A.2})$$

where  $N_t$  is the abundance at age  $t$  and is calculated as  $N_t = R \cdot \exp[-Z(t - t_c)]$ ;  $t_c$  is the age of full selectivity; and  $W_t$  is the weight of individual animals at age  $t$  and is calculated as  $W_t = W_{\infty} \{1 - \exp[-K(t - t_0)]\}^b$ . The weight at age is a composite of the allometric weight-length equation,  $W_t = aL_t^b$ , with the von Bertalanffy equation for length at age,  $L_t = L_{\infty} \{1 - \exp[-K(t - t_0)]\}$ , where  $W_{\infty} = aL_{\infty}^b$ . After substitution, equation (A.2) becomes

$$B = RW_{\infty} \int_{t_c}^{\infty} \exp[-Z(t - t_c)] \{1 - \exp[-K(t - t_0)]\}^b dt, \quad (\text{A.3})$$

where  $R$  is the recruitment at age  $t_c$ ;  $Z$  is the instantaneous total mortality rate; and  $W_{\infty}$ ,  $K$ , and  $t_0$  are growth parameters. To evaluate equation A.3, the substitution  $u = 1 - \exp[-K(t - t_0)]$  is made, which implies

$$t = t_0 - \frac{1}{K} \log_e(1 - u) \quad (\text{A.4})$$

and

$$dt = \frac{1}{K(1 - u)} du. \quad (\text{A.5})$$

After substitution, equation (A.3) simplifies to

$$B = \frac{RW_{\infty}}{K} \left(1 - \frac{L_c}{L_{\infty}}\right)^{-Z/K} \left[1 - \text{Beta}\left(\frac{L_c}{L_{\infty}}; b + 1, \frac{Z}{K}\right)\right], \quad (\text{A.6})$$

where  $L_c$  is the length at age  $t_c$ ; and  $\text{Beta}(x; \alpha, \beta) = \int_0^x u^{\alpha-1} (1 - u)^{\beta-1} du$  is the incomplete beta function to be evaluated numerically.

Assuming one change in mortality, the biomass is a function of the time elapsed,  $d$  years, since the change in mortality from  $Z_1$  to  $Z_2$ ,

$$\begin{aligned} B(Z_1, Z_2, d) &= RW_{\infty} \left[ \int_{t_c}^{t_c+d} \exp[-Z_2(t - t_c)] \{1 - \exp[-K(t - t_0)]\}^b dt + \int_{t_c+d}^{\infty} \exp(-Z_2 d) \exp\{-Z_1[t - (t_c + d)]\} \{1 - \exp[-K(t - t_0)]\}^b dt \right] \\ &= \frac{RW_{\infty}}{K} \left[ \left(1 - \frac{L_c}{L_{\infty}}\right)^{-\frac{Z_2}{K}} \left[ \text{Beta}\left(\lambda; b + 1, \frac{Z_2}{K}\right) - \text{Beta}\left(\frac{L_c}{L_{\infty}}; b + 1, \frac{Z_2}{K}\right) \right] + \exp[-(Z_2 - Z_1)d] \left(1 - \frac{L_c}{L_{\infty}}\right)^{-\frac{Z_1}{K}} \left[1 - \text{Beta}\left(\lambda; b + 1, \frac{Z_1}{K}\right)\right] \right] \end{aligned} \quad (\text{A.7})$$

where  $\lambda = 1 - (1 - L_c/L_{\infty}) \exp(-Kd)$ . The first term represents the biomass of animals recruited after the change in mortality, and the second term represents the biomass of those recruited before the change.

Assume that there have been  $k$  changes in mortality. Let  $\theta = \{Z_1, Z_2, \dots, Z_{k+1}, d_1, d_2, \dots, d_k\}$ , where  $Z_1, Z_2, \dots, Z_{k+1}$  is the vector of total mortality rates that the population has sequentially experienced over time; and  $d_i$  is the elapsed duration of mortality rate  $Z_{i+1}$ . The general solution for the biomass is

$$\begin{aligned} B(\theta) &= \frac{RW_{\infty}}{K} \sum_{i=1}^{k+1} \left\{ a_i w_i \left(1 - \frac{L_c}{L_{\infty}}\right)^{-\frac{Z_{k+2-i}}{K}} \left[ \text{Beta}\left(\gamma_i; b + 1, \frac{Z_{k+2-i}}{K}\right) - \text{Beta}\left(\lambda_i; b + 1, \frac{Z_{k+2-i}}{K}\right) \right] \right\}, \end{aligned} \quad (\text{A.8})$$

where

$$\begin{aligned} a_i &= \begin{cases} 1 & i = 1 \\ \exp\left(-\sum_{j=1}^{i-1} Z_{k+2-j} d_{k+1-j}\right) & i = 2, \dots, k + 1 \end{cases} \\ w_i &= \begin{cases} 1 & i = 1 \\ \exp\left(Z_{k+2-i} \sum_{j=1}^{i-1} d_{k+1-j}\right) & i = 2, \dots, k + 1 \end{cases} \end{aligned}$$



$$\gamma_i = \begin{cases} 1 - \left(1 - \frac{L_c}{L_\infty}\right) \exp\left(-K \sum_{j=1}^i d_{k+1-j}\right) & i = 1, \dots, k \\ 1 & i = k + 1 \end{cases}$$

$$\lambda_i = \begin{cases} \frac{L_c}{L_\infty} & i = 1 \\ 1 - \left(1 - \frac{L_c}{L_\infty}\right) \exp\left(-K \sum_{j=1}^{i-1} d_{k+2-j}\right) & i = 2, \dots, k + 1 \end{cases}$$

WPUE( $\theta$ ) =  $q \cdot B(\theta) = \tilde{q} \cdot \tilde{B}(\theta)$ , (A.9)

where  $\tilde{q} = \frac{qRW_\infty}{K}$  is a scaling parameter for the WPUE; and  $\tilde{B}(\theta)$  is the biomass excluding  $K$ ,  $R$ , and  $W_\infty$ , with  $\tilde{B}(\theta) = \frac{K}{RW_\infty} B(\theta)$ . In this way, trends in biomass can be modeled without  $W_\infty$ . Compared to the model of NPUE, the only additional information required to model WPUE is the allometric growth exponent  $b$ .

The corresponding WPUE after  $k$  changes in mortality is