

FEATURED PAPER

Modeling Growth: Consequences from Selecting Samples by Size

C. Phillip Goodyear*

1214 North Lakeshore Drive, Niceville, Florida 32578, USA

Abstract

Simulated size–age observations were collected from hypothetical populations with known growth to quantify potential bias in estimates of growth and mortality that can result from size-selective sampling. The population lengths at ages were normally distributed around means predicted by published von Bertalanffy (VB) equations for the Striped Marlin *Kajikia audax* or Vermilion Snapper *Rhomboplites aurorubens*. Parameter estimates for the VB equation were accurate when the data were collected with random and age-stratified sampling. Size-stratified sampling caused important bias in estimates of length at age and fitted VB parameters. The bias increased with the coefficient of variation of mean size at age and total mortality. It became more severe when sampling effort was increased to compensate for low sample numbers in bins within the upper tail of the distribution of sizes in the populations. Error occasionally exceeded 100% for asymptotic length L_{∞} and 50% for the Brody growth coefficient K . When a random sample was supplemented with $\leq 10\%$ large fish, the bias was sometimes greater than that observed when a completely size-stratified design was used. Such error could corrupt the reliability of analyses that depend on VB parameters. For Striped Marlins, natural mortality computed with the Pauly (1980) equation using results from length-selective sampling strategies often deviated 50% or more from the values predicted using the “true” growth coefficients. Potential for nonrepresentative sampling of lengths at age should be routinely described when VB models are first published and should be considered whenever the growth estimates are later used for other purposes.

Information on growth and natural mortality is essential for understanding species ecology and for guiding vital aspects of fisheries management. Growth is commonly described by a von Bertalanffy (VB) growth curve fitted to observations of size and age, and the model parameters have wide application for fisheries management (Maunder et al. 2016; Quist and Isermann 2017) and ecological modeling (e.g., Heymans et al. 2016). A recent American Fisheries Society publication describing methods for age and growth of fishes detailed the time-consuming analyses of hard parts (scales, otoliths, and fin rays) needed to age individuals (Quist and Isermann 2017). An earlier, oft-cited paper admonished researchers about overlooking the requirement to verify ages (Beamish and McFarlane 1983), and most authors now

devote significant effort to describe methods and potential errors for ages. In contrast, there is less concern about the accuracy of size observations, which are usually measured with high accuracy and precision. However, the important measure of size is not the size of the individual but how well the mean size at age can be estimated (Chih 2009a; Gwinn et al. 2010). Growth studies sometimes overlook these requirements (e.g., Chen et al. 2012; Dunton et al. 2016).

Satisfying the requirement that mean lengths be accurately estimated with sampling is often a more difficult task than estimating age. The deleterious effects of bias from size-selective sampling and fishery-induced size-selective mortality have been discussed for more than a century (e.g., Lee 1912; Ricker 1969; Gwinn et al. 2010). Bias occurs

*E-mail: phil_goodyear@msn.com

Received November 1, 2018; accepted February 3, 2019

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

when the samples are collected with size-selective gears (Gwinn et al. 2010), when samples are stratified by size (Goodyear 1995; Bettoli and Miranda 2001), or when the data exhibit Lee's phenomenon from a history of population exposure to size-dependent mortality (Ricker 1969). Because growth causes fish to be larger on average and scarcer as they age, investigators sometimes attempt to include presumably older fish by targeting larger individuals for inclusion in the samples or make size stratification part of the experimental design (Potts et al. 1998; Hwang and Kim 2008; O'Malley et al. 2017). Age-length keys (ALKs; Ketchen 1950; Kimura 1977) can be applied proactively to remove stratification biases from size-stratified subsamples (Miranda and Colvin 2017). However, growth studies that employ size stratification in their sampling design often fit the VB equation without correction (e.g., Potts et al. 1998; Hwang and Kim 2008; García-Contreras et al. 2009; Marshall et al. 2009; Siddons et al. 2016; O'Malley et al. 2017).

These factors lead to bias and error in VB parameters and potentially affect every estimate in the published literature to some degree. Assuring that growth data are representative of the distribution about the true mean sizes at each age is often not a simple proposition. It may be effectively impossible if Lee's phenomenon is present since part of the size distribution has not survived to be included in the samples (Ricker 1969); if the sampling gear is size selective; or if the fish themselves are not randomly distributed (e.g., Lee et al. 2017). Nonetheless, even when these caveats apply, VB models are fitted as a matter of routine in studies that collect age-size data. Such considerations become important when the growth estimates are later adopted for another purpose, such as estimating natural mortality (M) when needed values are unknown (e.g., Heymans et al. 2016). A critically important variable for management and other purposes, the M estimate (\hat{M}) is sometimes calculated by substituting fitted VB parameters into a published statistical relation (e.g., Pauly 1980; Griffiths and Harrod 2007; Heymans et al. 2016).

In contrast to studies intended only to estimate growth, the growth model itself is an essential integral feature affecting the accuracy of stock assessments (Maunder and Punt 2013; Maunder et al. 2016). The problems are well known to investigators involved in such research (e.g., Taylor et al. 2005; Francis 2015). Modern statistical approaches allow simultaneous estimation of growth along with other variables that are important to the success of the assessment (e.g., Maunder and Punt 2013; Methot and Wetzel 2013; Maunder et al. 2016; Zhu et al. 2016). In principle, the assessment models can simultaneously estimate time-varying size and age selectivities, growth, recruitment, fishing mortality (F), and M that account for the size-age structure of the population and remove their effects from growth. In practice, the estimate can be confounded by uncertainties in population status as well as any biases in the size-age data (Monnahan et al. 2016; Zhu et al. 2016; Maunder and

Piner 2017). The requirement to disentangle the influences of factors other than growth has invigorated research into methods to quantify and remove errors in growth (e.g., Schueller et al. 2014; Piner et al. 2016, 2018). These methods tend to be developed in association with major marine stocks, where the metric of concern is not necessarily growth but the reliability of management advice because of important economic and conservation consequences (e.g., Crone and Valero 2014; Ono et al. 2015; Zhu et al. 2016). These efforts are also distinguished by extensive time series of ancillary data needed to estimate F and M that are not often available to research programs with more limited resources. Even so, growth often remains ambiguous because of the biases in the information (Francis et al. 2016; Lorenzen 2016; Zhu et al. 2016).

Although critically important for developing management advice, the need to accurately assess growth extends beyond the prevue of stock assessments. Growth models will inevitably be fitted whenever age-size data are collected and must be interpreted in the context of the factors that limit accuracy. Here, I evaluate how sampling strategies affect estimation of mean sizes at age, VB parameters, and values of \hat{M} computed with Pauly's (1980) method. The analyses use simulated growth data from random, stratified, and mixed-mode sampling of hypothetical populations of Vermilion Snapper *Rhomboplites aurorubens* and Striped Marlins *Kajikia audax* in which the population size distribution was affected by the variation of size at age and total mortality. The study also investigated the effects of the total number of specimens collected to fill strata when size or age stratification was part of the design.

METHODS

This study used simulated size-age growth data from hypothetical populations in which mean sizes at age conformed to known growth. The VB model has been the model of choice in fisheries and was adopted here as true for the population simulations and for data analyses. The main features included the population model of the numbers at age and size, simulated sampling of growth data, estimation of parameters of the VB equation from simulated data, and finally an assessment of the reliability of growth estimates and of \hat{M} estimated using Pauly's (1980) method. (Herein, M denotes the true values assumed for the population model, and \hat{M} identifies the values estimated from fitted VB parameters using Pauly's equation.)

Population Model

Size-age samples were drawn from an age-length matrix of population relative abundances ($N_{a,l}$). The population model was adapted from Goodyear (1989, 1995). First, a vector of population numbers N_a at age (a) was created for an assumed constant level of total mortality (Z) as $N_a = 1e^{-aZ}$.

Recruitment occurred at age 1. Mortality was constant across all ages and was not size dependent. The numbers at each age were apportioned to length morphs, $N_{a,l}$, by using a normal probability distribution with a specified coefficient of variation (CV) assumed constant for each age. Each morph represented the abundance in a length interval of constant width within a range of ± 4 CVs of the mean at age predicted from the VB equation. The numbers of ages, size intervals, and mortalities evaluated were species specific. Accordingly, the size–age structure was controlled by the assumed growth model, the CV of size about the mean at age, and the level of Z . For simplicity, population numbers at age and size were only evaluated at the age anniversaries. The influences of the CV and Z were examined by varying each parameter. A unique vector of $N_{a,l}$ and an associated discrete cumulative frequency distribution were computed for each parameter combination. All size–age sampling of the simulated population occurred on the anniversary date of the age assignments.

Species Profiles

Two species, the Striped Marlin and Vermilion Snapper, were included to alleviate concerns that sampling-induced biases may be a species-specific phenomenon. The growth parameters used to model growth for each species were selected because they had been used in prior research with important management consequences for each species. They are also used here as reference “true” values to quantify the error in fitted parameters caused by non-representative sampling. However, for reasons underscored by the current research, they may not accurately describe growth for either species. For parsimony, the influence of the CV of size at age was evaluated only with Striped Marlins, and the effects of the explicit number of ages included were evaluated only with Vermilion Snapper.

Striped Marlin.—Growth and mortality data used to populate the age–length matrix for Striped Marlins were taken from a published simulation study investigating the potential benefits of catch and release (Pine et al. 2008). Mean size at age corresponded to a VB model with the following coefficients: asymptotic length $L_\infty = 221$ cm lower jaw-to-fork length (LJFL), Brody growth coefficient $K = 0.23$, theoretical age at zero length $t_0 = -1.6$, and CV of sizes about the mean = 0.1. Pine et al. (2008) used these values and assumed an average environmental temperature of 26°C to compute M from Pauly’s (1980) equation for their simulations. Their result ($M = 0.38$) was also adopted here as the “true” value for the sensitivity study. Total mortality was set either to $Z = 0.38$ for natural mortality alone or to $Z = 0.57$ for total mortality that included F at maximum sustainable yield (MSY; F_{MSY}). The $N_{a,l}$ matrix was evaluated for ages 1–11 at 1-cm intervals of length. Analyses were performed over a range of CVs to study the result of variability of sizes around the means at ages.

Vermilion Snapper.—Growth and mortality for the simulated Vermilion Snapper population were taken from a

recent stock assessment for the species (Lombardi et al. 2015; SEDAR 2016). Mean size at age corresponded to a VB model with the following coefficients: $L_\infty = 344$ mm TL, $K = 0.3254$, $t_0 = -0.7953$, and CV of sizes about the mean = 0.2535. The assessment estimated M as 0.25 and the 1990–1995 average F as 0.16. Total mortality in the simulation was set to $Z = 0.41$. The $N_{a,l}$ matrix was evaluated for age 1 to a maximum of either age 14 or age 26 and at 1-mm intervals of length. By coincidence, the M value estimated using Pauly’s (1980) method based on these growth assumptions and an average temperature of 23.5°C from Manickchand-Heileman and Phillip (1999) was also 0.41. These data were used for the baseline, “true” value to characterize the sensitivity of \hat{M} to error from the sampling protocol used to collect the Vermilion Snapper size–age growth data.

Sampling

Simulated samples were drawn from the hypothetical populations based on their relative position in the discrete cumulative distribution of computed relative abundances of $N_{a,l}$ by inverse transform sampling. First, a unique $N_{a,l}$ was picked from the matrix of the cumulative probability distribution of all values by randomly selecting a and l from uniform distributions between 1 and the age and length maxima. If the value of probability for the selected $N_{a,l}$ was greater than a second uniform random variable, a fish from that $N_{a,l}$ was retained as a sample. This process gives pseudo-random samples with the same distribution as that of the $N_{a,l}$ from which they were drawn. For simplicity, all samples were drawn on age anniversary dates. Computations were performed using Fortran.

This study tested five experimental designs for gathering the age–length samples. The desired sample size for each test was 10,000 observations, but the realized totals were often smaller for stratified designs with finite sampling effort. The sampling strategies included (1) completely random samples, (2) samples stratified by age, and (3) samples stratified by length. The fourth and fifth strategies required at least 90% of the observations to be randomly sampled; these were supplemented with stratified samples of only large fish. Stratification schemes intended to limit the number of specimens that must be aged retain some individuals and discard the remainder because stratum sample goals were satisfied. Here, this was done by placing a quota for the numbers retained in each stratum bin. These quotas were set to divide the total desired sample or subsample equally among the bins. Meeting the quotas for bins in the tails of the distribution required more total sampling effort than meeting the quotas for those nearer the center. The influence of this factor was evaluated by conducting the analyses over a range of effort, measured as the total set of observations from which the growth samples were compiled. When a bin quota was met, additional matching observations were discarded. Simulated

sampling continued until a sampling limit was encountered or the overall sampling goal was achieved.

Random sampling.—The random sampling strategy retained the first 10,000 random size–age observations in each replication.

Age stratified.—Age-stratified sampling was included for contrast because ages would seldom be available to select observations for inclusion in stratified designs in actual studies. Here, each age was a stratum; there were 11 such strata for Striped Marlin and either 14 or 26 strata for Vermilion Snapper for different analyses. Stratum quotas were 909, 714, or 384, respectively, so that the fully populated sampling design would be approximately 10,000 observations.

Length stratified.—For Striped Marlin, size strata were in 5-cm increments and ranged from 75 cm to an arbitrary maximum value that was 4 CVs greater than the mean length at age 11 (290 cm LJFL for $CV = 0.1$; 310 cm LJFL for $CV = 0.2$). The CV-based upper limit allowed the same proportion of the size range to be included in the range of included strata ($\leq 99.5\%$ all sizes). The total sample of 10,000 observations was spread over a larger size range for $CV = 0.2$ such that there were more length strata and fewer samples per stratum. Thus, at $CV = 0.1$, each stratum had a maximum of 233 observations, and at $CV = 0.2$, each stratum had a maximum of 213 observations. For Vermilion Snapper, there were 21 size strata, with bin quotas of 477 observations. These were in 25-mm intervals from 50 to 575 mm TL. Analyses were conducted assuming that all bins were fully sampled and where the stratum totals were limited to those that could be filled within limits of total effort as described below (see *Effective sampling effort*).

Mixed option 1.—Random sampling often leaves older individuals poorly represented in real growth studies. Because these fish also tend to be larger, there is an incentive to disproportionally sample large fish. Two mixed sampling strategies were evaluated to examine the possible impact of this practice. Option 1 started with 9,000 observations (90% of the total desired sample) drawn at random from the population. For the remaining $\leq 10\%$ of the sample, observations were selected by length-stratified sampling of fish between an arbitrary large size and the population maximum used for the length-stratified scheme. These were subjected to sample size limitations, or for some analyses, they were totally populated with observations. For both species, the large fish included individuals equal to or larger than the mean size at age 7. For Striped Marlin, the length-stratified supplement applied to fish 190 cm LJFL and longer. For Vermilion Snapper, the large-fish bins included fish 317 mm TL and longer.

Mixed option 2.—Option 2 examined how small supplemental samples of large fish affected growth parameter estimates. The approach augmented otherwise random

samples with 10 increments of stratified samples amounting to 1–10% of the total overall. Option 2 used the same size stratifications as option 1, but the bins were completely populated with observations for these analyses. At the 10% increment, options 1 and 2 were equivalent if sampling was sufficient to fill all of the length-bins.

Effective sampling effort.—Where strata were not fully populated by design, the maximum limits for total effort were set as multiples of the intended target of 10,000 observations. The values employed were 1, 2.5, 5, 10, 25, 50, 100, 250, 500, and 1,000 \times . Size or age strata that were too sparse to be fully populated within the maximum limit resulted in total sample sizes for subsequent analyses to be below the intended value of 10,000 observations. Sometimes, the total sample slightly exceeded the target (up to $\approx 0.2\%$) because program conventions required stratum quotas to be integer values. More often, the total sample of length–age observations was less than 10,000 because insufficient numbers of specimens were encountered to completely fill the bin quotas for the rare bins before the limit for the maximum number of (random) samples was encountered.

Analyses

Size frequencies for the simulated observations were compiled, and mean sizes at age were computed for each strategy, each combination of CV and mortality, and at the 10 different levels of sampling effort or augmentation as appropriate. The Striped Marlin model was used to isolate the effects of the CV of mean size at age and mortality on the estimates of mean size at age by sampling strategy. To isolate the effect of the CV, it was varied from 0.05 to 0.30, with mortality at $Z = 1.0$ and the relative effort at 1,000 \times . Similarly, the effects of Z were evaluated between 0.15 and 1.0, with CV at 0.3 and the relative effort at 1,000 \times . Additional evaluations of the influence of the total sampling effort on estimates of mean size at age were performed with $Z = 0.57$ and $CV = 0.3$.

Studies that fitted VB growth equations were partitioned into those that focused on issues related to the population and those that could be further affected by sample design. The first involved Z and the CV of size at age, which influence the relative abundance of $N_{a,l}$. The second varied the total sampling effort, which limits the numbers of observations that can be collected to populate the rarer size- or age-bins. Analyses of factors that affect $N_{a,l}$ were conducted with the Striped Marlin model at $CV = 0.1$ and $CV = 0.2$ and at $Z = 0.38$ and $Z = 0.57$. Sampling for these analyses was assumed sufficient to populate the bin quotas and so emulated the process of targeted sampling from areas and with gears having different selectivities. Both species were used to study the influence of limited total sampling effort with a single representative gear. The Striped Marlin population model assumed $CV = 0.1$ and $Z = 0.38$ for these

analyses. The Vermilion Snapper model with $CV = 0.2535$ and $Z = 0.41$ was used to study the effect of truncating the number of age vectors used to estimate growth at 14 years or extending it to 26 years.

The VB growth equations were fitted with the nonlinear least-squares function “`nls()`” in R (R Core Team 2015) using both means at age and the individual data points. Occasional simulated data sets failed to converge for the Vermilion Snapper model using mean sizes at age and 26 ages; these data sets were replaced. Precision of the fitted equations was not studied. Natural mortality for each fitted VB equation was computed using Pauly’s (1980) method. The fitted parameter estimates were compared with the values assumed to be “true” based on the VB equation used to predict the lengths for the population model. Errors for the growth model parameters were estimated for L_∞ and K as the differences between the estimates and the “true” values. The intercept term for the VB equation, t_0 , was of lesser interest and was not routinely included in further analysis. For natural mortality, error was the difference between \hat{M} computed with the estimated VB parameters and M computed with the “true” VB parameters (used to assign the mean sizes at age in the populations). Pauly’s (1980) method was used for each.

RESULTS

Mean Lengths at Age

Mean sizes at age for the youngest ages were accurately estimated for each parameter combination and sampling treatment explored (Figure 1). Random sampling provided generally accurate estimates of the true mean lengths, but there was a decline in precision of the estimates with increasing age (Figure 1A–C). The trend was greatest at the highest mortality rate, $Z = 1.0$, illustrating the impact of increased sample variability caused by the decreased abundance of the older ages (Figure 1B). This phenomenon also impacted the results in Figure 1A, which assumed $Z = 1.0$, and Figure 1C, which assumed $Z = 0.57$ throughout. The means at age computed from the data collected using the age-stratified strategy overlaid the true values for all of the conditions evaluated (Figure 1D–F). The random and age-stratified strategies evaluated here provided unbiased estimates of mean sizes at age, whereas each of the size-stratified methods favored the overestimation of sizes at age for all but the youngest ages sampled (Figure 1). These effects portend the accuracy of not just the VB model, but any growth model that may be successfully fitted to the data. All of the strategies involving size stratification resulted in upward bias in the mean sizes at age, but the extent and nature of the bias varied in response to population structure and sampling

design (Figure 1G–O). Most of these results show evidence of an asymptotic decline in growth with age that might foster undue confidence in modeling results.

The bias in estimated mean size increased as CV values became larger in trials intended to isolate the effect of variability of growth (Figure 1G, J, M). The CV of size at age governs the overlap of sizes for different ages. With CV at or below 0.05, the stratifications involving size did not appreciably impact mean size compared with larger CVs (Figure 1G, J, M). The effect was more pronounced with age, particularly with the mixed sampling strategies (Figure 1J, M). These results reflect a changing balance between increased relative abundances of large fish at younger ages at higher CVs and the reduced relative abundances of older fish at all sizes due to mortality. Size-stratified sampling with the $CV = 0.3$ and sampling effort at $1,000\times$ resulted in substantial bias at age with each level of mortality investigated. However, the bias increased with Z for intermediate ages (Figure 1H). With this sampling regimen and CV, growth appeared linear at the lower levels of mortality examined (Figure 1H). This pattern was even more apparent in the two mixed strategies, where the large contribution of random observations suppressed the upward bias at lower mortality rates (Figure 1K, N). The effect would reduce K and increase L_∞ in a fitted VB model. Again, mean sizes were all biased upward in trials intended to isolate the effects of maximum sampling effort using size-stratified data with $CV = 0.3$ and $Z = 0.57$ (Figure 1I, L). The main effect of increasing effort in strategies involving stratified sampling was to add observations in progressively rarer size-bins in the upper tails of the distributions. For age-stratified sampling, the additional observations would increase the precision of the estimate of mean size at each age (Figure 1C versus Figure 1F). For size-stratified sampling, this effect increased the bias in the mean size estimates for older ages (Figure 1C versus Figure 1I, L, and O).

Increasing the relative proportions of the total population that came from size-selected observations in the mixed option 2 sampling had the greatest impact on the bias in the older ages (Figure 1O). The mean sizes for older ages were substantially greater than the true values, even when the total sample consisted of 99% random samples augmented with 1% selected to include the largest individuals in the population. This effect results from overrepresentation of exceptionally rare large individuals and might not be of practical concern for a sampling program based on stratifying truly random samples. However, it could be an issue if sampling mixes gears with differing size selectivities.

Observations collected using the random sampling scheme provided samples that were unbiased by age or size. The age-stratified scheme provided unbiased samples of the length frequencies of each age, but the age

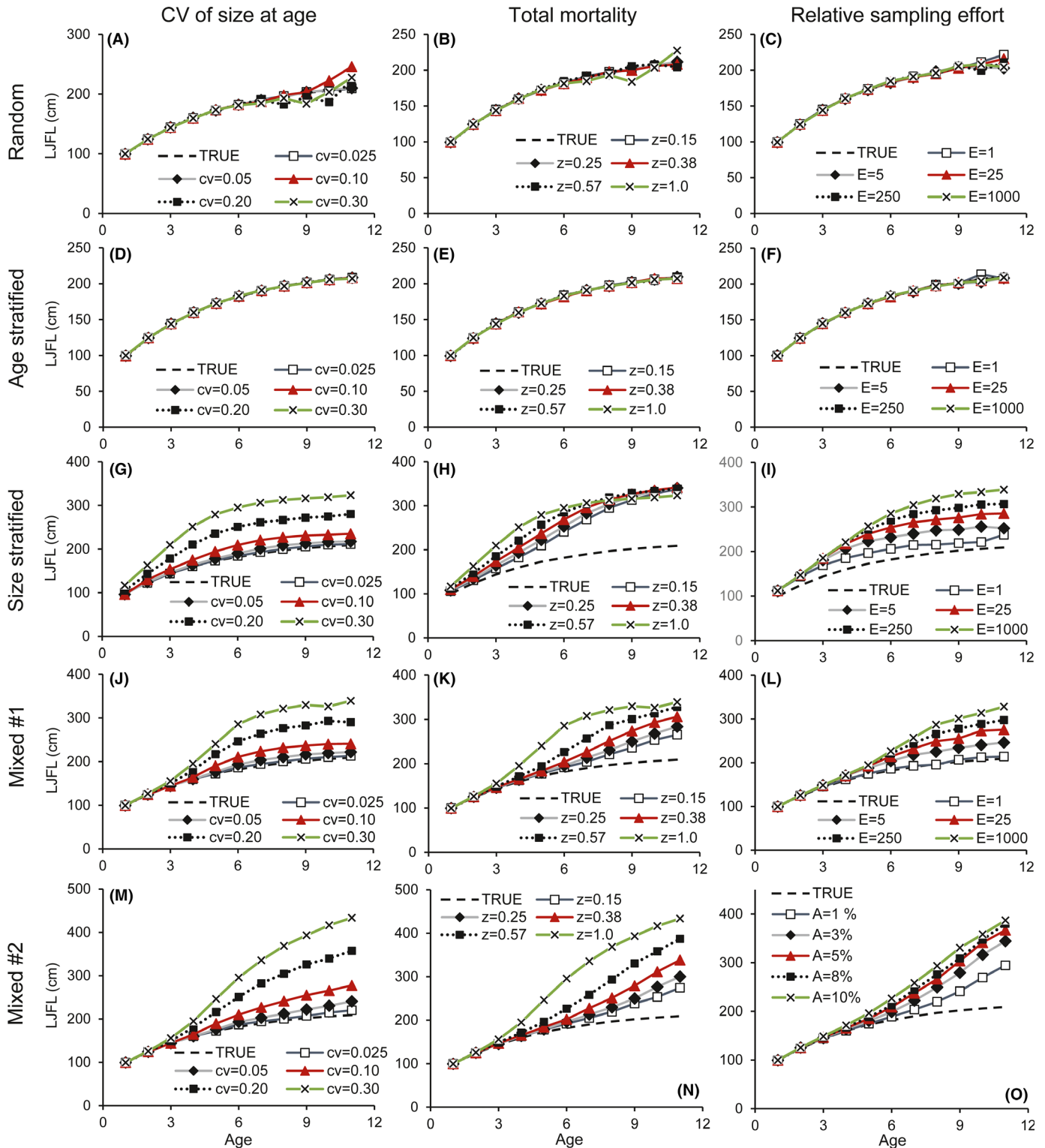


FIGURE 1. Each panel is a scatterplot of mean sizes at age for five treatment levels for a sampling strategy and study variable. The results used the Striped Marlin population model with 11 ages (LJFL = lower jaw-to-fork length). Each point is the mean of 10 replicates. The left column examines the effect of the coefficient of variation (CV) of size at age while holding total mortality (Z) and total sampling effort (E) constant. The center column varies Z while holding the CV and E constant. The right column varies E while holding the CV and Z constant. Panels M and N augment the total sample so that 90% is totally random and 10% is equally divided among size strata larger than the mean at age 7. Panel O uses different levels of the same augmentation scheme (A) with $Z = 0.57$ and $CV = 0.3$.

frequencies at length were biased. The length-stratified sampling scheme provided unbiased samples of the age frequency of each length stratum, but the length frequencies at age were biased, and the samples from mixed options yielded means that were biased in both age and length.

Growth and Mortality Estimates

The accuracy of estimates of growth and derived analyses of M (Figures 2–5; Tables 1–3; Appendix Tables A.1 and A.2) followed patterns expected from the results in Figure 1. Growth estimates were accurate for the random and age-stratified sampling strategies or if the CV of size at age was very low. In contrast, the results from strategies that included size-selected data produced inaccurate estimates of the VB parameters. Estimates of \hat{M} based on Pauly's (1980) method responded accordingly. Although the extent of the bias was influenced by the particular parameters of the assumed VB equation, the bias itself was the result of factors that caused the sizes in samples to differ from the sizes in the population. The results are organized here by factors that affect the distributions of $N_{a,l}$ in the population and factors that affect the differences between the population and sample mean sizes at age.

Factors that influence the abundance of $N_{a,l}$: coefficient of variation and total mortality.—The probability for a discrete $N_{a,l}$ to be sampled was proportional to its abundance. Mortality decreased abundance at successive ages, and the CV controlled the magnitude of survivors among sizes of the same ages. Values of the VB parameters estimated from the simulated data for Striped Marlin by CV and Z are given in Table 1 along with values computed for \hat{M} . Effort was presumed to be sufficient to enable the size strata to be equally populated with observations in these analyses, so

the assumptions for the two mixed options coincided. The data for the mixed option alternative evaluated here included 9,000 random observations plus 1,008 observations stratified by length. The percentage error, measured as differences from the “true” values, is presented in Table 2. For M , the “true” value was the M computed from VB parameters used to create the model size distributions. The random and age-stratified results were much better than the results for the length-stratified or mixed options. Random sampling outperformed the other schemes, but the age-stratified scheme was approximately equivalent, especially for the higher mortality regime when the VB model was fitted to means at age. Neither fitting the VB equation to mean lengths at ages nor fitting the equation to the individual data points was clearly better based on accuracy of parameter estimates. Both strategies that involved size-stratified sampling for Striped Marlin led to overestimates of L_∞ and underestimates of K (Table 2). The results with supplemental size-selective sampling of large fish showed greater divergence from the true values than when all samples were collected via the size stratification. The errors in both cases were substantial. The errors in L_∞ were also greater at the higher CV. For the mixed-sampling model and $Z = 0.57$, the error in L_∞ increased from about 100% at CV = 0.1 to over 200% at CV = 0.2. The numerical values of percent differences between K and its “true” value (K_{true}) were smaller than the errors in L_∞ , but the differences in K/K_{true} ratios of the values in Table 1 were quite large for either scheme employing length stratification. The differences from \hat{M} computed using the “true” VB parameters and those estimated using length-stratified observations commonly exceeded 50% (Table 2). The maximum in these examples included values of computed \hat{M} that varied from 0.025 to 0.419, or a range of about 17-fold, at $Z = 0.57$ and

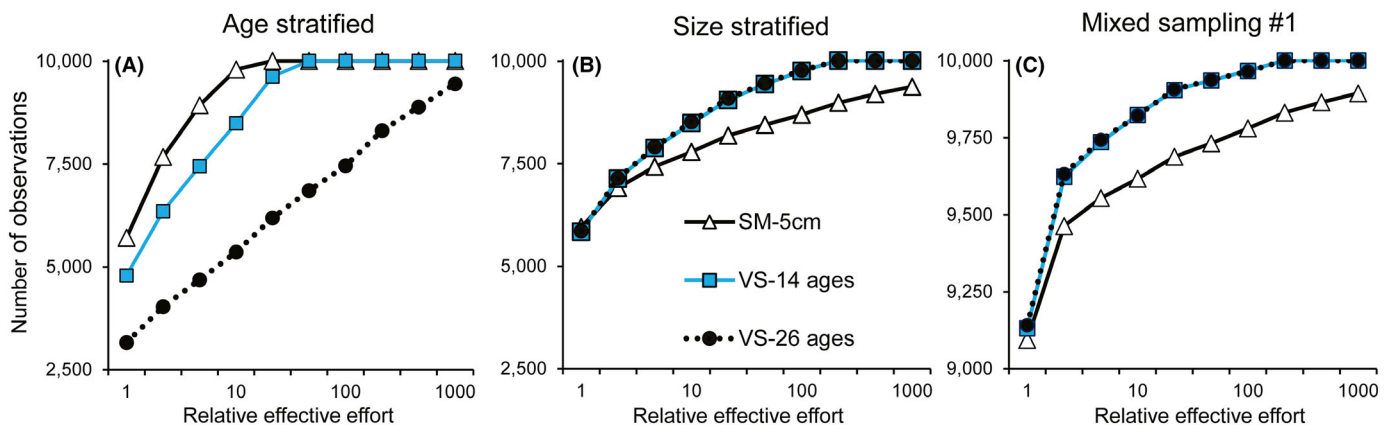


FIGURE 2. Scatterplots of the total number of size–age observations retained for inclusion in model fits at different levels of total sampling effort for three sampling strategies and population models (SM = Striped Marlin model; VS-14 ages and VS-26 ages = Vermilion Snapper models with 14 and 26 age-classes, respectively). Each point is the mean of 10 replicates. Bin quotas were equal. Bins were by year for the (A) age-stratified strategy and by 5-cm (Striped Marlin) or 25-mm (Vermilion Snapper) intervals for the (B) size-stratified strategy and (C) mixed option 1 strategy.

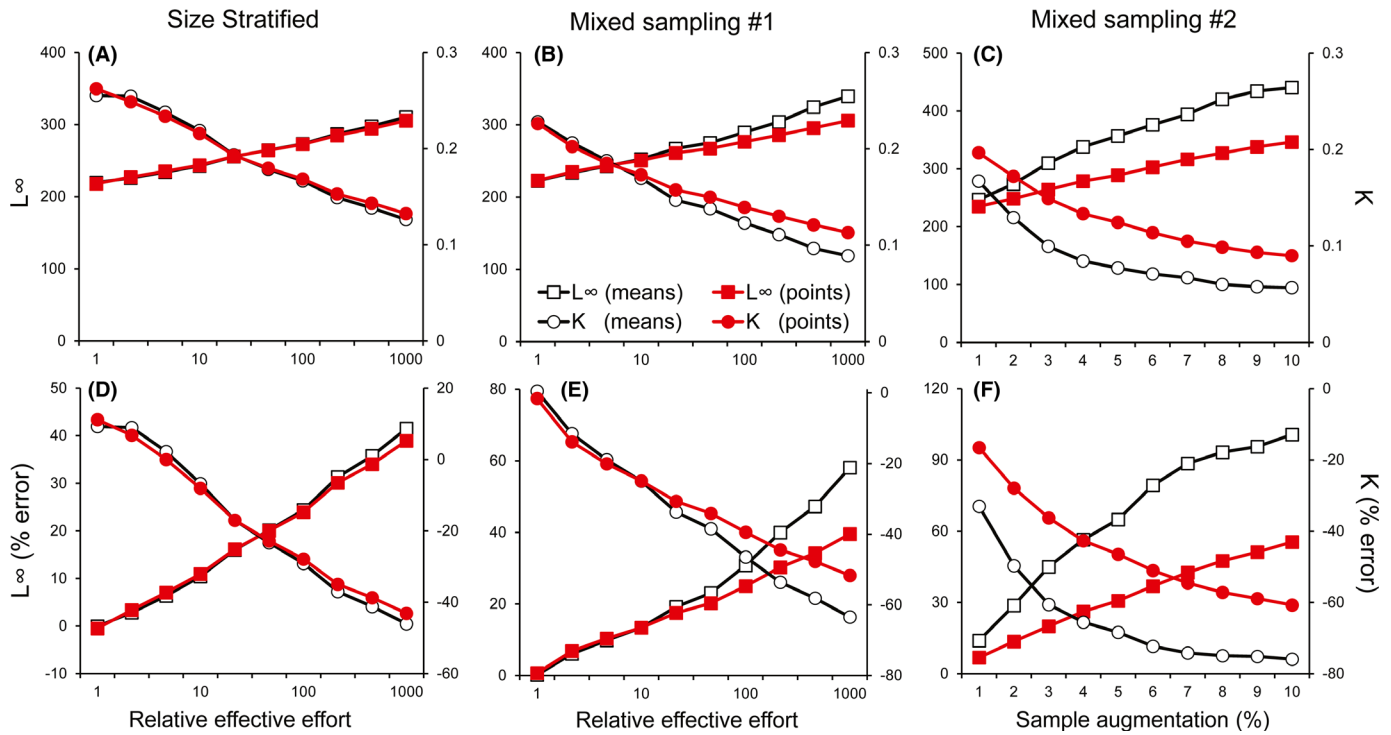


FIGURE 3. Estimates of (A)–(C) von Bertalanffy parameters (asymptotic length L_{∞} [cm lower jaw-to-fork length] and Brody growth coefficient K) and (D)–(F) percent error for various 5-cm, length-stratified treatments of simulated size–age data for Striped Marlin. Estimates from fitting mean sizes at age are identified as $L_{\infty}(\text{means})$ and $K(\text{means})$; those resulting from fitting the individual data points are identified as $L_{\infty}(\text{points})$ and $K(\text{points})$. In panels A and D (size-stratified strategy), the entire sample is stratified. In panels B and E (mixed option 1 strategy), a random sample of 9,000 observations is supplemented by 5-cm, length-stratified bins larger than the mean at age 7 and collected from an increasingly large total set of random observations. In panels C and F (mixed option 2 strategy), a total sample of about 10,000 observations is split into a random component supplemented with a fixed percentage of 5-cm, length-stratified observations of large fish.

CV = 0.2. Most of this variability was a consequence of the sampling strategy (Tables 1 and 2).

Impact of total number of fish collected by a non-selective gear and the number of observations retained for analyses.—The influence of total effective sampling was investigated with Striped Marlin at $Z = 0.38$, CV = 0.1, and a maximum of 11 ages. The analyses were repeated with Vermilion Snapper at $Z = 0.41$ and CV = 0.2535 assuming the experiment anticipated a maximum of either 14 or 26 ages. The values of L_{∞} , K , computed \hat{M} , error, and CV for each factor are presented in Table 3 for Striped Marlin and in Tables A.1 and A.2 for Vermilion Snapper. The table rows present results in the order of increasing effort as described in the Methods (*Effective sampling effort*). However, for the random scheme, the baseline effort was sufficient to satisfy sampling targets in each of the three population-parameter combinations evaluated. Consequently, only three rows are included for each random strategy, and they are duplicative. For the stratified strategies that replaced discarded observations until a ceiling was obtained, the size of the sample used to fit the growth equation depended on both the

characteristics of the population and the total number of individuals inspected. The resulting average numbers of observations for each level of total effort are presented in Figure 2 for the strategies affected. The results contrast the effects of resource allocations caused by study design. For example, retained observations approached the 10,000-observation study goal more quickly with the sample goal for Vermilion Snapper partitioned into 14 ages rather than 26 (Figure 2A). This was a consequence of a higher bin quota when the design anticipated fewer ages: 715 (10,000/14 ages) compared to 385 (10,000/26 ages). However, when the partitions were based on the same expected size distribution, the numbers of retained samples for each level of total sampling effort were nearly identical (Figure 2B).

Accuracy decline with increasing effort.—Fits using data from the random and age-stratified strategies provided accurate estimates of the VB parameters for Striped Marlin (Table 3). Mean errors were a few tenths of a percent for both L_{∞} and K . The CVs were also about 1% or below for estimates of L_{∞} and were a little more than 2% for K (Table 3). No important effect from total sampling

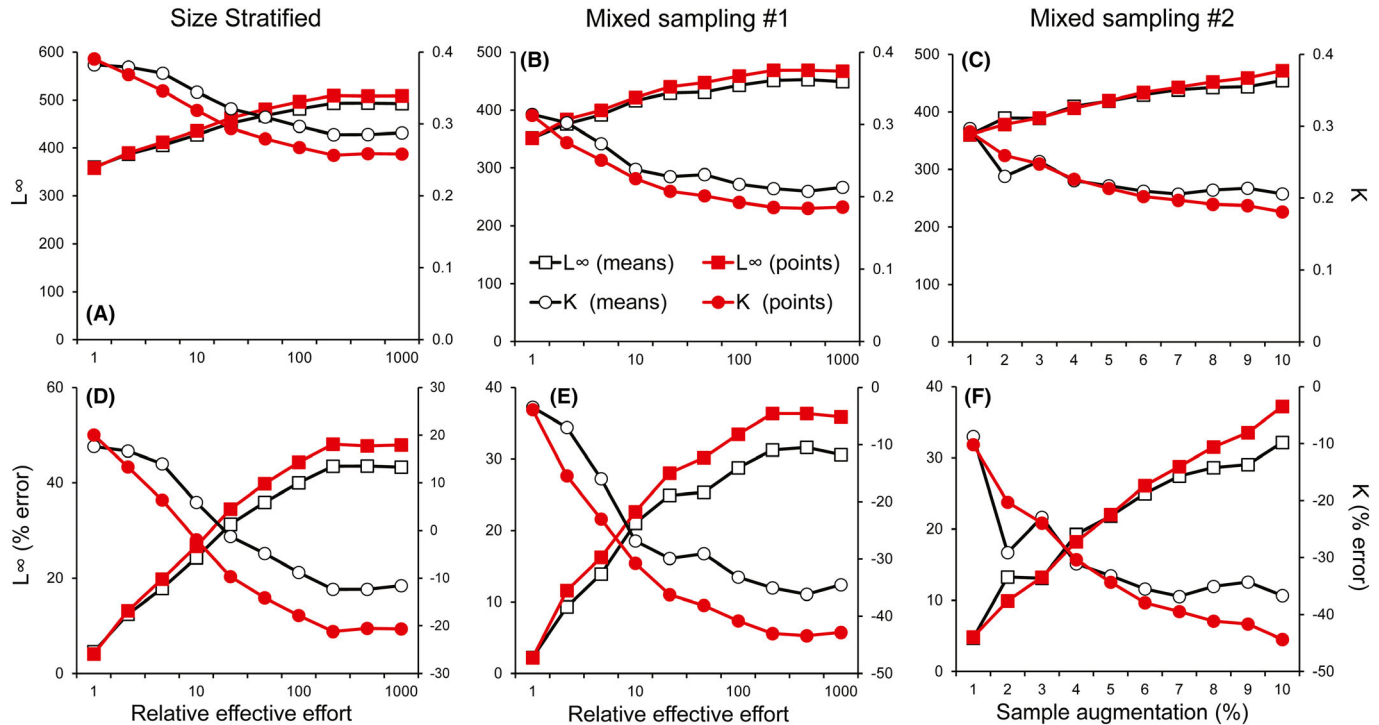


FIGURE 4. Estimates of (A)–(C) von Bertalanffy parameters (asymptotic length L_{∞} [mm TL] and Brody growth coefficient K) and (D)–(F) percent error for various 25-mm, length-stratified treatments of simulated size–age data for Vermilion Snapper with the age structure truncated to 14 years. Estimates from fitting mean sizes at age are identified as $L_{\infty}(\text{means})$ and $K(\text{means})$; those resulting from fitting the individual data points are identified as $L_{\infty}(\text{points})$ and $K(\text{points})$. In panels A and D (size-stratified strategy), the entire sample is stratified. In panels B and E (mixed option 1 strategy), a random sample of 9,000 observations is supplemented by 25-mm, length-stratified bins larger than the mean at age 7 and collected from an increasingly large total set of random observations. In panels C and F (mixed option 2 strategy), a total sample of about 10,000 observations is split into a random component supplemented with a fixed percentage in 25-mm bins of fish larger than the mean at age 7.

effort was apparent in the results for the age-stratified sampling. The Pauly (1980) estimates of \hat{M} were also very nearly the same as the “true” value for the random and age-stratified strategies. In contrast, results for strategies involving size selection for the Striped Marlin data strongly responded to the total effort expended to sample large individuals (Table 3). For the length-stratified strategy, the estimated value of L_{∞} from fits to the mean size at age increased from about 220 cm LJFL to 310 cm LJFL for the range of total effort examined (Figure 3). Corresponding values of K declined from 0.26 to 0.13 over the same range of total sampling effort, and the value of \hat{M} computed from these data decreased from 0.41 to 0.24. Results from fitting the VB equation to the individual data points provided similar results (Table 3). The CV for each of the tabulated values was about 2% or less. The results for the two strategies that supplemented random samples with a subsample of individuals larger than the mean at age 7 showed the same patterns of increasing error (Figure 3; Table 3). However, the error in estimates of L_{∞} , K , and \hat{M} were larger and increased more rapidly with increasing effort. There also was more divergence between

the results of fits to mean sizes at age versus the individual data points, particularly for mixed option 2.

Effect of increasing the number of ages in the analyses.—The same analyses using the two maximum age assumptions with the Vermilion Snapper growth model are presented in Tables A.1 and A.2. The results were qualitatively similar to the Striped Marlin findings. Random and age-stratified sampling produced accurate estimates. For the three strategies with size strata, L_{∞} was biased high, and it increased with increasing total samples. Biases in K showed the opposite trend and declined as total effort was increased. For the fully size-stratified strategy, the bias changed from positive to negative for both maximum age assumptions. Furthermore, L_{∞} and K estimated using the individual observations were more strongly biased than when mean sizes at age were used (Figures 4, 5). The values of \hat{M} computed from these data followed the same patterns (Tables 3, A.1, and A.2). The most important effect from inclusion of more ages in the design for Vermilion Snapper was that the analyses based on mean sizes at age were much more variable. The increased numbers of strata reduced the sample size in

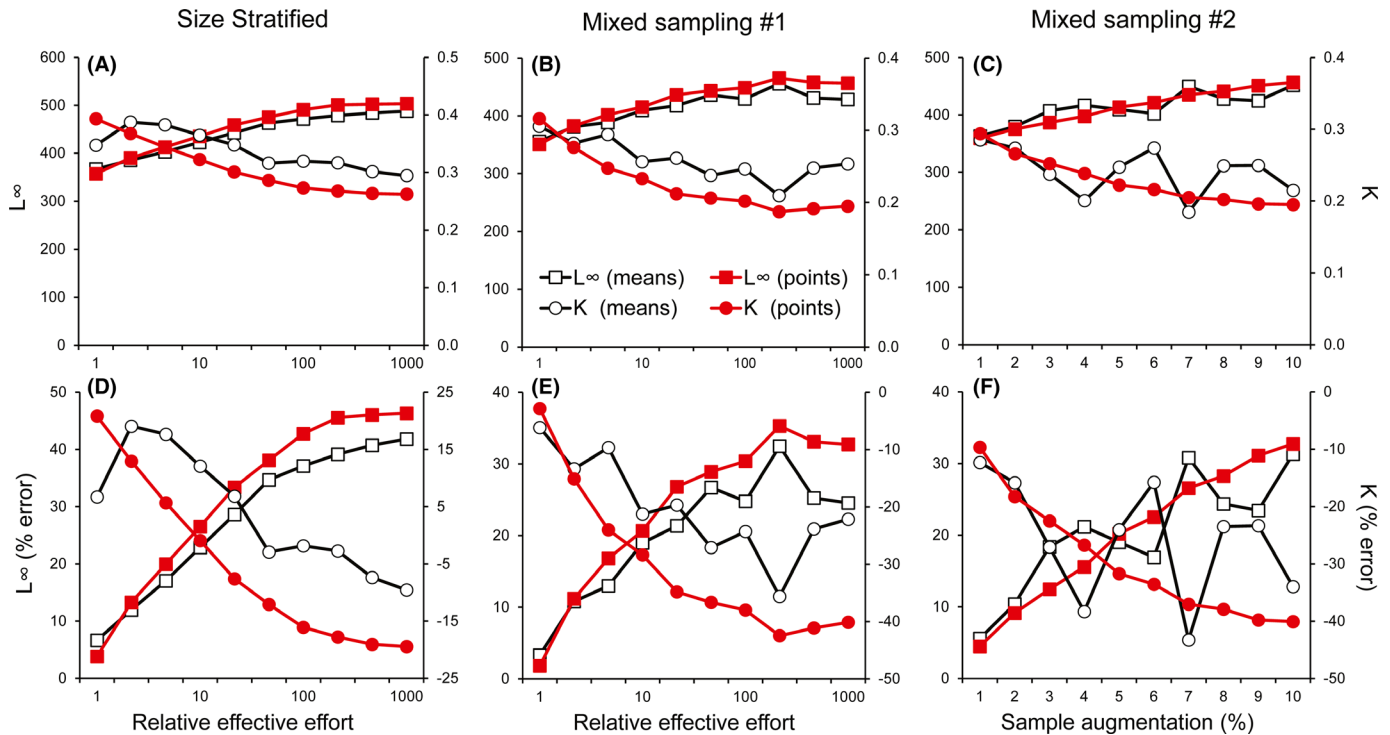


FIGURE 5. Estimates of (A)–(C) von Bertalanffy parameters (asymptotic length L_{∞} [mm TL] and Brody growth coefficient K) and (D)–(F) percent error for various 25-mm, length-stratified treatments of simulated size–age data for Vermilion Snapper with the age structure extending to 26 ages. Estimates from fitting mean sizes at age are identified as L_{∞} (means) and K (means); those resulting from fitting the individual data points are identified as L_{∞} (points) and K (points). In panels A and D (size-stratified strategy), the entire sample is stratified. In panels B and E (mixed option 1 strategy), a random sample of 9,000 observations is supplemented by 25-mm, length-stratified bins larger than the mean at age 7 and collected from an increasingly large total set of random observations. In panels C and F (mixed option 2 strategy), a total sample of about 10,000 observations is split into a random component supplemented with a fixed percentage in 25-mm bins of fish larger than the mean at age 7.

each stratum, which reduced the accuracy of the means for size at age to which the VB equation was fitted. In addition, the increased number of age strata enhanced the inclusion of data points where estimated mean sizes of older, rare ages were based on very few observations. The effect partially obscured the trends from increasing levels of total effort for both of the mixed sampling schemes (Figure 5E, F).

DISCUSSION

Growth Data: Age and Size of Individual Fish

In a classic paper, Beamish and McFarlane (1983) called attention to the requirement that age assignments be validated to avoid major errors in the understanding of population dynamics. Age validation is now an expected component of age and growth studies. The attributes of the size part of the growth data often receive less attention. Unlike age, the difference between a fish's measured size and its true size is not usually informative about error. The growth model predicts population mean sizes,

not the sizes of the individuals. The important “error” in size is not the deviation of measured size from the true size of the fish but rather how the aggregate mean at age deviates from the population's unfettered true mean for that age. The influences of size bias were studied here by manipulating sampling designs, but many other factors could be involved in field studies. Examples include spatial heterogeneity in habitat utilization, size-selective sampling gears, and/or historical exposure to size-selective mortality. For the growth models used in this study, a sampling-induced error with a magnitude of 10% of the mean length at age 11 was equivalent to misreading age by more than 4 years for Striped Marlin and by more than 5 years for Vermilion Snapper. Biases of this magnitude are well within the ranges observed here when sampled growth data were selected by size from a larger unbiased sample of the population.

Fully Size-Stratified Sampling

Size-selective sampling, whether by the gear or design, biases the sampled means (Goodyear 1995; Gwinn et al. 2010). In the case of length stratification, the sampled

in order of increased level of augmentation.

Strategy	N	Means only						All points											
		L_{∞}			\hat{M}			L_{∞}			\hat{M}								
		Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%						
Random	10,000	223.2	1.1	1.0	0.22	3.5	-3.4	0.37	2.6	-2.5	222.0	0.7	0.4	0.23	2.1	-1.3	0.38	1.6	-1.0
Age stratified	10,000	221.3	1.1	0.1	0.23	3.6	0.0	0.38	2.7	0.0	221.4	0.8	0.2	0.23	2.2	-0.3	0.38	1.7	-0.3
	10,000	221.1	0.9	0.0	0.23	3.3	0.1	0.38	2.4	0.1	221.5	0.7	0.2	0.23	2.4	-0.6	0.38	1.8	-0.4
	5,711	220.9	0.9	0.0	0.23	3.3	0.0	0.38	2.4	0.0	220.7	0.4	-0.2	0.23	1.6	0.4	0.38	1.1	0.3
	7,674	221.2	0.6	0.1	0.23	2.3	0.1	0.38	1.7	0.0	221.2	0.6	0.1	0.23	2.3	0.1	0.38	1.6	0.1
	8,934	221.6	0.4	0.3	0.23	2.0	-1.4	0.38	1.4	-1.0	221.5	0.5	0.2	0.23	2.1	-1.3	0.38	1.5	-0.9
	9,806	221.5	0.6	0.2	0.23	2.5	-0.9	0.38	1.8	-0.7	221.4	0.6	0.2	0.23	2.3	-0.9	0.38	1.7	-0.6
	10,010	221.4	0.3	0.2	0.23	1.3	-0.7	0.38	0.9	-0.5	221.4	0.3	0.2	0.23	1.3	-0.7	0.38	0.9	-0.5
	10,010	220.9	0.4	0.0	0.23	1.7	0.6	0.39	1.2	0.4	220.9	0.4	0.0	0.23	1.7	0.6	0.39	1.2	0.4
	10,010	221.1	0.4	0.0	0.23	1.9	0.0	0.38	1.4	0.0	221.1	0.4	0.0	0.23	1.9	0.0	0.38	1.4	0.0
	10,010	220.7	0.4	-0.2	0.23	2.0	0.3	0.38	1.4	0.3	220.7	0.4	-0.2	0.23	2.0	0.3	0.38	1.4	0.3
Size stratified	10,010	221.1	0.4	0.1	0.23	1.4	-0.4	0.38	1.0	-0.3	221.1	0.4	0.1	0.23	1.4	-0.4	0.38	1.0	-0.3
	10,010	221.3	0.3	0.1	0.23	1.2	-0.8	0.38	0.9	-0.6	221.3	0.3	0.1	0.23	1.2	-0.8	0.38	0.9	-0.6
	5,955	219.5	1.1	-0.7	0.26	3.7	11.0	0.41	2.7	7.3	218.0	0.6	-1.4	0.26	2.0	14.1	0.42	1.5	9.4
	6,921	225.8	0.8	2.2	0.25	2.9	10.7	0.41	2.2	6.2	227.1	0.6	2.8	0.25	2.0	8.2	0.40	1.5	4.5
	7,433	234.0	0.5	5.9	0.24	2.0	3.4	0.39	1.4	0.6	235.2	0.4	6.4	0.23	1.2	1.6	0.38	0.9	-0.7
	7,791	242.6	0.4	9.8	0.22	1.4	-4.9	0.36	1.0	-5.7	243.6	0.4	10.2	0.22	1.2	-6.2	0.36	0.9	-6.7
	8,194	255.5	0.7	15.6	0.19	2.2	-15.9	0.33	1.6	-14.2	255.9	0.7	15.8	0.19	2.0	-16.1	0.33	1.5	-14.4
	8,454	264.4	0.6	19.6	0.18	1.8	-22.4	0.31	1.4	-19.4	264.1	0.5	19.5	0.18	1.3	-21.9	0.31	1.0	-19.1
	8,701	273.3	0.6	23.7	0.17	1.9	-27.6	0.29	1.4	-23.7	272.6	0.5	23.3	0.17	1.6	-26.8	0.30	1.2	-23.1
	8,991	287.0	0.6	29.8	0.15	2.1	-35.2	0.27	1.6	-30.0	284.8	0.5	28.9	0.15	1.7	-33.5	0.27	1.3	-28.7
Mixed option 1	9,201	297.8	0.6	34.7	0.14	1.3	-39.9	0.25	1.0	-34.0	294.4	0.6	33.2	0.14	1.3	-37.7	0.26	1.0	-32.3
	9,383	310.4	0.4	40.5	0.13	1.1	-45.1	0.24	0.8	-38.6	305.4	0.4	38.2	0.13	1.0	-42.4	0.24	0.7	-36.3
	9,094	222.4	1.7	0.6	0.23	5.9	-0.7	0.38	4.3	-0.7	222.8	0.6	0.8	0.23	1.9	-1.6	0.38	1.4	-1.3
	9,464	233.7	0.9	5.7	0.21	3.4	-10.3	0.35	2.5	-8.3	234.8	0.5	6.2	0.20	1.5	-11.9	0.35	1.1	-9.5
	9,555	242.7	1.2	9.8	0.19	3.6	-18.4	0.33	2.7	-14.7	243.6	0.9	10.2	0.19	2.4	-19.5	0.32	1.8	-15.6
	9,617	252.3	1.1	14.2	0.17	3.5	-26.3	0.30	2.6	-21.1	250.7	0.7	13.4	0.17	1.9	-24.8	0.31	1.4	-19.9
	9,689	267.3	0.9	20.9	0.15	2.5	-36.2	0.27	1.9	-29.3	261.0	0.4	18.1	0.16	1.0	-31.5	0.29	0.8	-25.5
	9,732	275.1	1.3	24.5	0.14	3.6	-40.0	0.26	2.7	-32.7	267.1	0.7	20.9	0.15	1.7	-34.7	0.28	1.3	-28.3
	9,781	289.5	1.3	31.0	0.12	2.9	-46.5	0.24	2.3	-38.4	276.5	0.9	25.1	0.14	2.2	-39.4	0.26	1.7	-32.3
	9,831	304.1	2.3	37.6	0.11	4.8	-51.7	0.22	3.7	-43.2	285.7	1.5	29.3	0.13	3.2	-43.4	0.25	2.6	-35.9
9,865	324.6	2.8	46.9	0.10	5.2	-57.9	0.20	4.2	-49.0	295.6	1.8	33.7	0.12	3.8	-47.3	0.23	3.0	-39.3	
9,895	339.7	2.7	53.7	0.09	5.6	-61.3	0.18	4.4	-52.3	305.7	1.6	38.3	0.11	3.4	-50.8	0.22	2.7	-42.6	

TABLE 3. Continued.

Strategy	N	Means only									All points								
		L_∞			K			\hat{M}			L_∞			K			\hat{M}		
		Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%
Mixed option 2	10,005	246.8	2.3	11.7	0.17	6.2	-27.3	0.30	4.7	-21.3	234.8	0.8	6.3	0.20	2.1	-14.5	0.34	1.6	-11.2
	10,010	273.5	1.7	23.8	0.13	3.9	-43.7	0.25	3.0	-35.3	248.5	1.0	12.4	0.17	2.4	-25.1	0.31	1.8	-19.9
	10,015	309.5	4.5	40.1	0.10	9.6	-56.7	0.20	7.5	-47.4	264.1	1.4	19.5	0.15	3.3	-35.2	0.27	2.6	-28.3
	10,020	338.1	4.0	53.0	0.08	7.8	-63.3	0.18	6.2	-53.9	278.5	1.2	26.0	0.13	2.9	-42.0	0.25	2.2	-34.3
	10,003	356.9	2.7	61.5	0.08	4.8	-66.5	0.16	3.9	-57.2	288.8	0.9	30.7	0.12	2.0	-45.9	0.24	1.5	-37.9
	10,009	376.1	3.2	70.2	0.07	5.8	-69.1	0.15	4.7	-60.0	302.7	1.7	37.0	0.11	3.3	-50.6	0.22	2.6	-42.2
	10,013	394.1	6.1	78.3	0.07	10.3	-70.8	0.15	8.4	-62.0	316.4	1.8	43.2	0.10	3.6	-54.4	0.21	2.9	-45.8
	10,019	420.3	4.0	90.2	0.06	7.1	-73.9	0.13	5.8	-65.2	327.3	1.6	48.1	0.10	2.9	-57.1	0.20	2.3	-48.5
	10,002	434.6	5.6	96.6	0.06	9.3	-74.9	0.13	7.6	-66.5	338.1	1.6	53.0	0.09	3.2	-59.4	0.19	2.6	-50.8
	10,000	440.5	5.6	99.3	0.06	9.7	-75.3	0.13	7.9	-66.9	346.2	2.4	56.7	0.09	4.9	-60.9	0.18	3.9	-52.3

age frequency in a size-bin is governed by the abundance of different ages at that length. Thus, if the total number of observations at that length is capped by a bin quota, the sampled lengths of each age are influenced by the abundances of the other ages in the bin. Here, the quotas for each bin were set equal to facilitate analyses, but the principle applies to other schemes that (1) discard potential observations that would otherwise be included because the sizes were already sufficiently sampled and/or (2) include specimens because of their size. Factors that influence the relative abundances of different ages in a length-bin will affect the accuracy of the overall sample. The CV of size at ages affects the overlaps of the size distributions in the different ages. The influence of this factor is reflected by the trends in the left column of Figure 1. Mortality affects the relative abundances of the ages and hence the proportions of ages in each length stratum. The effect is evident in the center column of Figure 1. Though not studied here, variations in year-class strength would also have the same kind of effect.

In order for the sample in a size stratum to exert any influence on the sampled length frequencies for ages, the bin quota must have been exceeded. Otherwise, the samples collected within that particular bin are random samples from the sampled population. In a typical study, the observation totals would be a mix of (1) biased data from bins for the most abundant sizes where quotas had been met and (2) random observations in the tails where bin quotas had not been reached. Additionally, in this study the bias increased when more observations were discarded. That feature would be increased by increasing the total number of specimens inspected during the study until all of the bin quotas were filled. The combined effect is apparent in the right-hand column of Figure 1 and in the fitted VB parameters presented in Figures 3–5; Tables 3, A.1, and A.2, which all become increasingly biased at higher effective sampling effort. In a length-stratified design, the harder one tries to meet sampling quotas for incomplete bins, the more biased is the final result.

That general rule probably applies equally to mixing samples from different size-selective gears and habitats. The scale for relative sampling effort in the size-stratified analyses here ranged to a maximum of 1,000. At 1,000 \times , 1,000 “specimens” were inspected for every single specimen at the base level in an attempt to meet bin quotas with individuals sampled at random. That seemingly impossible real-world goal might sometimes be easily accomplished by mixing samples from different gears or habitats that have much higher probabilities of including the rarer size-classes. In practice, the actual magnitude of bias will be governed by the extent to which the final sampling of large fish is actually size-selected.

Supplemental Sampling to Include Large Individuals—Mixed Strategies

The magnitude of effects from supplementing random samples with large fish to increase the numbers of older individuals is difficult to anticipate. The large specimens may be collected from the same gear or from different gears with different selectivities. The latter option could greatly reduce the number of specimens that must be examined. The problem was investigated here using two arbitrary sampling schemes (mixed options 1 and 2). In one case, 9,000 observations were random, and the rest were from length-stratified sampling between the mean size at age 7 and the largest in the population. The actual number of observations in each bin was limited by the number of fish encountered in the random samples. The second scheme added observations in the strata of large fish without regard for sampling effort, but the additional large fish were a specific small percentage of the total. Both schemes resulted in important bias that increased with the number of large fish in the final sample (Figures 3–5; Tables 3, A.1, and A.2). These supplemental samples had a disproportionate effect compared to the length-stratified scheme. Inspection of the data in Figure 1J–L reveals that the mean sizes at age for the younger ages were less affected than those for older ages. This outcome was a result of the smaller, young fish that dominated the random part of the combined sample. The result changed the shape of the sampled growth curve in a way that depressed K and elevated L_{∞} (Figures 3–5; Tables 1–3, A.1, and A.2). Consequently, the mixed scheme was sometimes worse than the fully size-stratified design.

Species Differences

Size-stratified sampling would have little impact on estimates of growth for species with very low variation in sizes at age (Figure 1D). However, size frequency distributions of most species exhibit an overlap of sizes at age that make the issue important. Inspection of Table 3 and Tables A.1 and A.2 reveals that the analyses for Striped Marlin were somewhat more prone to error than those for Vermilion Snapper. Otherwise, the results of the analyses using the two species were similar. For each, the results became more strongly biased when greater proportions of the total sample were affected by length stratification (Figures 1, 3–5; Tables 3, A.1, and A.2). However, for Striped Marlin, the VB parameters fitted using means at age were more strongly biased than when the VB model was fitted to all observations (Figure 1; Tables 1–3). The results were reversed for Vermilion Snapper (Figures 4 and 5; Tables A.1 and A.2). Additionally, the larger number of ages in the Vermilion Snapper example permitted inclusion of means determined by fewer observations. As a consequence, the VB fits to means at age became

somewhat erratic because of means that were poorly estimated, particularly for the 26-age assumption (Figure 5). The results for models fitted to the individual observations were much less affected.

Other Size-Selective Processes that Affect Samples

Data collected for a growth study may misrepresent sizes at age because of gear or habitat features as well as an overt experimental design. The range of possibilities from mixing such effects with variable year-class strengths, mortality schedules, etc., with size-stratified sampling could be expected to result in a high variability in the estimates of growth from different studies for the same species. The Vermilion Snapper is a prime example, where results of L_{∞} varied from 298 to 707 mm TL (sexes combined) within and between studies (Potts et al. 1998; Hood and Johnson 1999; Lombardi et al. 2015; Moncrief 2017). When added to real-world size-selectivity of gears, the additional effect of size-stratified sampling would make the estimation of biologically meaningful growth coefficients a matter of conjecture. These features need not compromise within-study objectives to compare growth rates in time or space that can be addressed with appropriate statistical control or experimental design (e.g., Nate and Bremigan 2005; Tyszkowski and Pritt 2017). However, they may result in misleading analyses in subsequent studies that adopt the VB estimates for other purposes. Investigators who have studied the impact of size selectivity on model parameter estimation have long been aware of problems (Ricker 1969; Gwinn et al. 2010), but even a casual reading of the literature reveals a great heterogeneity of awareness both about the effects on parameter estimation and how these effects propagate into derivative analyses.

Corrective Measures

Age-length keys.—If the sampling methods that collect specimens for a study randomly sample the population, a size-stratified sampling scheme can be corrected with a proactively designed ALK (Ketchen 1950; Kimura 1977; Miranda and Colvin 2017). The properties of the ALK for this purpose are well studied (e.g., Bettoli and Miranda 2001; Chih 2009a, 2009b; Coggins et al. 2013). The method removes the bias in the size-stratified data by expanding the size-age composition of the bins to estimate the age composition of the total sample. The growth model is fitted to the adjusted data rather than to the specimens that were actually aged. An ALK requires that meticulous details be maintained about the size distributions of the samples from which the aged subset was obtained. For whatever reason, growth studies continue to fit the VB equation to the stratified size-age data without correction (e.g., Potts et al. 1998; Hwang and Kim 2008;

García-Contreras et al. 2009; Marshall et al. 2009; Sidons et al. 2016; O'Malley et al. 2017). Notably, even when an ALK is applied, the original data samples must have accurately represented the mean sizes at age. Otherwise, the expanded data will retain any size bias that existed in the original sampling, and growth estimates will be misleading.

Integrated assessment methods.—Stock assessments are a primary client for information about growth. The overall confidence in results would be enhanced by fixing growth to known true values, so methods to quantify and remove bias from growth estimates are increasingly the subject of research (e.g., Maunder et al. 2016; Xu et al. 2016; Piner et al. 2018). Methods that have been investigated to correct for size-selective mortality (e.g., Vaughan and Burton 1994; Schirripa and Trexler 2000) and gear selectivity (Taylor et al. 2005; Gwinn et al. 2010) are situation dependent and add their own uncertainties. Gwinn et al. (2010) showed that corrections for gear selectivity required precise, accurate knowledge of the selectivity curves; otherwise, the methods can increase the biases they were intended to diminish. The results of the strategies evaluated in the examples here highlight the difficulty because the selectivity curves can be unpredictable functions of growth, mortality, study design, and sampling effort—and by analogy, gear, space, and year-class strengths. Ad hoc supplementation of large individuals that might have been intended to improve knowledge about L_{∞} could be especially problematic. The development of integrated statistical assessment methods, such as stock synthesis (Methot and Wetzel 2013), allow simultaneous estimation of growth and mortality that can account for many sources of bias with appropriate data (Maunder and Punt 2013; Maunder et al. 2016). However, the added complexity involves rigorous assumptions about the adequacy of the data and the embedded models. Even getting the assessment model to converge can sometimes be an issue (Ono et al. 2015; Monnahan et al. 2016; Zhu et al. 2016). Consequently, the growth estimates emerging from the analyses are conditioned on the accuracy of the other variables estimated at the same time (Maunder and Punt 2013; Aires-da-Silva et al. 2015). Integrated stock assessment methods have been developed to assimilate information for estimating stock status but not growth. Nonetheless, assessment-related studies are at the forefront of research about methods to quantify growth, nearly always with the assistance of simulated data (e.g., Maunder and Piner 2017; Piner et al. 2018). Unfortunately, modest studies that are intended to include estimates of growth cannot generally hope to match the scope of data required to implement modern integrated assessment methods. Such studies should adopt methods that are best able to estimate true mean sizes at age and, where possible, should

explore the circumstance of their particular study design using simulation or other means.

Limitations

The current investigation examined the importance of bias in the size component of observational information that makes it difficult to accurately estimate growth. The scope of relevant issues not addressed here is practically limitless. The analyses assumed stationary age distributions, whereas real populations are in constant flux resulting from variations in year-class strength and mortality. Such effects would not eliminate the size-selective bias on average but could diminish or exacerbate the effect depending on the vagaries of the particular study. Furthermore, a study of mixing size- and age-selected samples in the same growth analysis would be instructive. The population models also assumed that sizes were normally distributed about age with constant CV and that growth was independent of population density. The selection of bin intervals, alternatives for selecting study maximum sizes, and alternatives for populating the size-bins that may affect cumulative age-at-length probabilities were not evaluated.

Size selection that favors small fish was not examined. From the results here, the effect would likely depress L_{∞} and would increase K and Pauly's \dot{M} . Understanding of these features could be enhanced with additional research. The relatively large sample-size target of 10,000 observations was intended to elucidate the behavior of expected values for the treatments. Smaller design targets would produce more variable results but might be more useful for work intended to interpret historical growth studies. I did not investigate issues related to what information, if any, might be derived from the estimated precision of VB model parameters. Initial trials confirmed the general perception that bias is not reflected by residual errors because highly significant statistics were commonly obtained for strongly biased model fits. Finally, this study does not address how sampling may affect estimation of the shape and magnitude of distributions of sizes about the means at ages. For many applications, this information is equally important for understanding and modeling the size structure and dynamics of populations (e.g., Parma and Deriso 1990; Goodyear 2004, 2015).

Combining Data from Multiple Sampling Gears

Wilson et al. (2015) showed that it is possible to improve accuracy of growth models by combining samples from multiple gears when they sample selectively, particularly when individual gears exclude representation of different sizes or ages. However, Wilson et al. (2015) cautioned that their approach did not lead to a rule applicable across species and selectivity scenarios that will always lead to improved parameter estimates. Age-selected and size-selected data can be superficially indistinguishable

based on aggregated size frequencies. The results here show that age-selected data accurately estimate mean size at age for the ages sampled. Model fitting will benefit from pooling age-selected data, even if the samples from different gears have much different mean sizes (because of differences in ages collected). In contrast, when sampling gears are size selective, the sizes at age in samples will typically not accurately estimate true mean sizes at age. In such cases, accurate growth models require the fitted model to balance offsetting size biases. Even changing the total numbers of observations from each of the contributing gears can systematically vary the fitted model from one trial to the next. Combining data from different gears does not guarantee that the resulting pooled data will yield accurate growth parameters. However, samples that include the full size-range present in the population should be less prone to produce L_{∞} values that are larger than values possible for the species. Even here, investigators must exercise caution: due to the effects of mortality, L_{∞} can actually exceed the largest individuals that could exist. Conclusions about the reliability of such results should be formed on a case-by-case basis after careful analyses of the accuracy required by the intended model applications.

Alternative Growth Models

I used the VB model here because it is the most widely employed growth equation in fisheries. In addition, the implications of estimation errors caused by potential biases could be illustrated via the Pauly (1980) equation, which is often used to estimate M . However, the VB function is only one of several growth models that are applicable to fishes. Other examples, including the Gompertz, logistic, Richards, and Schnute models, are summarized by Ogle et al. (2017) and elsewhere. Each model attempts to describe mean length at age in the population. Model selection is not an alternative that can be relied upon to offset bias in the growth data. The sampling biases that distorted the sampled mean lengths at ages in Figure 1 would equally undermine the accuracy of any fitted growth model that might successfully predict the observed mean sizes at age in the data. Even our perception about which model is applicable for a particular species is framed by the overall scatter of data that include biases embedded in the distribution of the observations. Likewise, these issues will extend to more complicated growth patterns that partition growth into stanzas, such as the biphasic models (e.g., Wilson et al. 2018), if some of the applicable growth data were collected with size-selective sampling.

Natural Mortality and Other Derivative Uses

Natural mortality is one of the most important life history variables needed for research and management

(Clark 1999). Direct estimation of M is data intensive or impossible, so investigators often use indirect methods that rely on VB parameter estimates (e.g., Pauly 1980), longevity (e.g., Hoenig 1983), or both (Alverson and Carney 1975). Then et al. (2015) reported that the Pauly (1980) method using VB parameter values was the most common empirical method and had been cited 2,129 times as of August 2014. With 936 citations, the next most common empirical method used a longevity metric, T_{max} , which is the oldest observed age in a population (Hoenig 1983). Then et al. (2015) reported that longevity-based approaches outperformed Pauly-based methods, which is not surprising since longevity is directly affected by mortality, while the VB parameters must rely on correlations that result only from evolutionary selection (Pauly 1980). Data collected during growth studies can affect these mortality estimates in two basic ways: (1) through VB parameters that are then substituted into Pauly's predictive equations; and (2) by facilitating the estimate of T_{max} with the sample data. The current study evaluated the first.

Pauly's (1980) method is known to explain much of the variance in M in the taxa to which the model was fitted, partly because of the large contrast in scale (Griffiths and Harrod 2007; Then et al. 2015). However, the equations were also poor predictors (Griffiths and Harrod 2007), with 95% confidence intervals about 2.5 times the estimated value (Gulland and Rosenberg 1992). Consequently, point estimates of \hat{M} are very uncertain even before considering error in the VB parameters used. The Pauly results can be seriously further eroded whenever the growth data are biased by size-selective processes, such as the size-stratified sampling examined here. For example, the calculated levels of acceptable catch could vary over a range of twofold to more than tenfold using the rule of thumb that F_{MSY} is a constant multiple of M with the Striped Marlin results in Table 1. In addition, the collective variation of VB parameters and \hat{M} would have important consequences for analyses of yield per recruit and spawning potential ratios or other analyses that depend on growth. The impact of selective sampling on T_{max} was not evaluated here. However, selection of large fish, either by size-selective gear or size-stratified sampling, would tend to also increase the probability of collecting older fish and hence would tend to increase T_{max} . The result would appear as a decreased estimate of M . However, the bias is likely important only for an unfished population because the value of T_{max} is strongly confounded (decreased) by fishing that would increase \hat{M} (Kenchington 2013). Overall, the results here support Kenchington's (2013) conclusion that "fisheries scientists measure M by more advanced methods whenever possible" and that uncertainty and error arising from empirical estimators should be acknowledged and propagated into derivative studies.

A Plea for Reporting

The Striped Marlin was selected here because the data necessary to conduct the evaluation were available from a single source in which the authors used a published VB model for another purpose and had also estimated M using Pauly's (1980) method (Pine et al. 2008). Although a value for M was required for their analysis, their finding that catch and release can be a useful management tool for marlins is not dependent on a particular value. Pine et al. (2008) noted that there was uncertainty in M , but their decision to only use the Pauly estimate may be interpreted by some readers as a (possibly unintended) tacit endorsement of the accuracy of the method and a judgement of the accuracy of its estimate for the species. That interpretation could influence parameter selections by other investigators for future studies, either directly or by inclusion in meta-analyses of M values appearing in peer-reviewed publications. The more often we do it, the more legitimate it seems to be.

Melo-Barrera et al. (2003) authored the source paper that estimated VB parameters for Striped Marlins, and these parameters were later adopted by Pine et al. (2008) and used here. Melo-Barrera et al. (2003) reported that their size-age data were from a subsample of 399 of the total 1,044 Striped Marlins sampled from recreational catches during the study. However, their documentation failed to discuss how the subsampling was performed, so it is impossible for readers to (1) tell whether the distributions of length at age used to fit the VB equation were affected by size stratification or (2) know whether the gear was size selective. Such information is important for those hoping to extract parameter estimates that are important inputs for subsequent research projects. However, as in the Melo-Barrera et al. (2003) example, discussion of sampling issues is often insufficient (e.g., Chen et al. 2012; Gervelis and Natanson 2013; Dunton et al. 2016). Studies would be improved if authors routinely documented potential size biases of their samples with the same care given to the methods used to age specimens.

Final Thoughts

There will always be a need for growth and mortality information as cornerstones of analyses and touchstones for evaluating modeling results. The results here support the attention being devoted to research to improve growth estimation within stock assessments. They also illustrate underappreciated consequences of size-selected data on growth and derivative estimates of \hat{M} from traditional, small-scale studies. Growth parameters are highly susceptible to sampling bias, and these errors propagate to values of \hat{M} calculated therefrom. Both the VB parameters and \hat{M} are used in all manner of ecological and fish population models, usually without knowledge or acknowledgment of the uncertainty. The results here suggest that estimates of \hat{M} from Pauly's (1980) method should be avoided wherever the underlying

uncertainty may compromise results. The potential that size-selective bias has affected growth estimation and the impact of such uncertainty should be explicitly evaluated when modeling growth. Furthermore, as evident in Figure 1, the basic bias from size selection is in the data; that is, the bias cannot be removed by selecting a different growth equation, even if the change in scatter may favor one model over another. Those of us who use published data for subsequent studies should caution about uncertainties that accrue from the original study as well as those added by new research. That will remain difficult until researchers provide the same level of detail about possible biases that affect mean sizes at age as they do for age determinations. Finally, VB and other growth models can be fitted using methods other than the analysis of size–age data. Examples include mark–recapture experiments and progressions of modes in population length frequencies. Ultimately, a well-fitted model just describes the data and does not necessarily equate to biological realism. The source and extent of potential biases should be included with the primary publication and in subsequent reports of research where the parameter values are used for other purposes.

ACKNOWLEDGMENTS

This study was supported by The Billfish Foundation. I thank W. Pine and several anonymous reviewers for comments and suggestions on an early draft of the manuscript. There is no conflict of interest declared in this article.

REFERENCES

- Aires-da-Silva, A. M., M. Maunder, K. M. Schaefer, and D. W. Fuller. 2015. Improved growth estimates from integrated analysis of direct aging and tag–recapture data: an illustration with Bigeye Tuna (*Thunnus obesus*) of the eastern Pacific Ocean with implications for management. *Fisheries Research* 163:119–126.
- Alverson, D. L., and M. J. Carney. 1975. A graphic review of the growth and decay of population cohorts. *Journal du Conseil International pour l'Exploration de la Mer* 36:133–143.
- Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* 112:735–743.
- Bettoli, P. W., and L. E. Miranda. 2001. Cautionary note about estimating mean length at age with subsampled data. *North American Journal of Fisheries Management* 21:425–428.
- Chen, K. S., T. Shimose, T. Tanabe, C. Y. Chen, and C. C. Hsu. 2012. Age and growth of Albacore *Thunnus alalunga* in the North Pacific Ocean. *Journal of Fish Biology* 80:2328–2344.
- Chih, C. P. 2009a. The effects of otolith sampling methods on the precision of growth curves. *North American Journal of Fisheries Management* 29:1519–1528.
- Chih, C. P. 2009b. Evaluation of the sampling efficiency of three otolith sampling methods for commercial King Mackerel fisheries. *Transactions of the American Fisheries Society* 138:990–999.
- Clark, W. J. 1999. Effects of an erroneous natural mortality rate on a simple age-structured stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1721–1731.
- Coggins, L. G. Jr, D. C. Gwinn, and M. S. Allen. 2013. Evaluation of age–length key sample sizes required to estimate fish total mortality and growth. *Transactions of the American Fisheries Society* 142:832–840.
- Crone, P. R., and J. L. Valero. 2014. Evaluation of length- vs. age-composition data and associated selectivity assumptions used in stock assessments based on robustness of derived management quantities. *Fisheries Research* 158:165–171.
- Dunton, K. J., A. Jordaan, D. H. Secor, C. M. Martinez, T. Kehler, K. A. Hattala, J. P. Van Eenennaam, M. T. Fisher, K. A. McKown, D. Conover, and M. G. Frisk. 2016. Age and growth of Atlantic Sturgeon in the New York Bight. *North American Journal of Fisheries Management* 36:62–73.
- Francis, R. I. C. C. 2015. Growth in age-structured stock assessment models. *Fisheries Research* 180:77–86.
- Francis, R. C., A. M. Aires-da-Silva, M. N. Maunder, K. M. Schaefer, and D. W. Fuller. 2016. Estimating fish growth for stock assessments using both age–length and tagging-increment data. *Fisheries Research* 180:113–118.
- García-Contreras, O. E., C. Quiñónez-Velázquez, R. E. Morán-Angulo, and M. C. Valdez-Pineda. 2009. Age, growth, and age structure of Amarillo Snapper off the coast of Mazatlán, Sinaloa, Mexico. *North American Journal of Fisheries Management* 29:223–230.
- Gervelis, B. J., and L. J. Natanson. 2013. Age and growth of the Common Thresher shark in the western North Atlantic Ocean. *Transactions of the American Fisheries Society* 142:1535–1545.
- Goodyear, C. P. 1989. LSIM—a length-based fish population simulation model. NOAA Technical Memorandum NMFS-SEFC-219.
- Goodyear, C. P. 1995. Mean size at age: an evaluation of sampling strategies with simulated Red Grouper data. *Transactions of the American Fisheries Society* 124:746–755.
- Goodyear, C. P. 2004. FSIM—a simulator for forecasting fish population trends and testing assessment methods. *Collective Volume of Scientific Papers ICCAT* 56:120–131.
- Goodyear, C. P. 2015. Understanding maximum size in the catch: Atlantic Blue Marlin as an example. *Transactions of the American Fisheries Society* 144:274–282.
- Griffiths, D., and C. Harrod. 2007. Natural mortality, growth parameters, and environmental temperature in fishes revisited. *Canadian Journal Fisheries and Aquatic Sciences* 64:249–255.
- Gulland, J. A., and A. A. Rosenberg. 1992. Review of length-based approaches to assessing fish stocks. Food and Agriculture Organization of the United Nations Fisheries Technical Paper 323.
- Gwinn, D. C., M. S. Allen, and M. W. Rogers. 2010. Evaluation of procedures to reduce bias in fish growth parameter estimates resulting from size-selective sampling. *Fisheries Research* 105:75–79.
- Heymans, J. J., M. Coll, J. S. Link, S. Mackinson, J. Steenbeek, C. Walters, and V. Christensen. 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling* 331:173–184.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *U.S. National Marine Fisheries Service Fishery Bulletin* 82:898–903.
- Hood, P. B., and A. K. Johnson. 1999. Age, growth, mortality, and reproduction of Vermilion Snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico. *U.S. National Marine Fisheries Service Fishery Bulletin* 97:828–841.
- Hwang, S. D., and J. Y. Kim. 2008. Age, growth, and maturity of Chub Mackerel off Korea. *North American Journal of Fisheries Management* 28:1414–1425.
- Kenchington, T. J. 2013. Natural mortality estimators for information-limited fisheries. *Fish and Fisheries* 15:533–562.
- Ketchen, K. S. 1950. Stratified subsampling for determining age-distributions. *Transactions of the American Fisheries Society* 79:205–212.

- Kimura, D. K. 1977. Statistical assessment of the age-length key. *Journal of the Fisheries Research Board of Canada* 31:317–324.
- Lee, R. M.. 1912. An investigation into the methods of growth determination in fishes. *ICES Journal of Marine Science* 1(63):3–34.
- Lee, H. H., L. R. Thomas, K. R. Piner, and M. N. Maunder. 2017. Effects of age-based movement on the estimation of growth assuming random-at-age or random-at-length data. *Journal of Fish Biology* 90:222–235.
- Lombardi, L., R. Allman, L. Thornton, and C. Palmer. 2015. Description of age data and estimated growth for Vermilion Snapper from the northern Gulf of Mexico: 1994–2014. Southeast Data, Assessment, and Review, SEDAR45-WP-01, North Charleston, South Carolina.
- Lorenzen, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: embracing plasticity and its consequences. *Fisheries Research* 180:4–22.
- Manickchand-Heileman, S., and D. A. T. Phillip. 1999. Contribution to the biology of the Vermilion Snapper, *Rhomboplites aurorubens*, in Trinidad and Tobago, West Indies. *Environmental Biology of Fishes* 55:413–421.
- Marshall, M. D., M. J. Maceina, and M. P. Holley. 2009. Age and growth variability between sexes of three catfish species in Lake Wilson, Alabama. *North American Journal of Fisheries Management* 29:1283–1286.
- Maunder, M. N., P. R. Crone, A. E. Punt, J. L. Valero, and B. X. Semmens. 2016. Growth: theory, estimation, and application in fishery stock assessment models. *Fisheries Research* 180:1–3.
- Maunder, M. N., and K. R. Piner. 2017. Dealing with data conflicts in statistical inference of population assessment models that integrate information from multiple diverse data sets. *Fisheries Research* 192:16–27.
- Maunder, M., and A. E. Punt. 2013. A review of integrated analysis in fisheries stock assessment. *Fisheries Research* 142:61–74.
- Melo-Barrera, F. N., R. Felix-Uraga, and C. Quiñónez-Velázquez. 2003. Growth and length-weight relationship of the Striped Marlin, *Tetrapturus audax* (Pisces: Istiophoridae), in Cabo San Lucas, Baja California Sur, Mexico. *Ciencias Marinas* 29:305–313.
- Methot, R. D., and C. R. Wetzel. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research* 142:86–99.
- Miranda, L. E., and M. E. Colvin. 2017. Sampling for age and growth estimation. Pages 107–126 in M. C. Quist and D. A. Isermann, editors. *Age and growth of fishes: principles and techniques*. American Fisheries Society, Bethesda, Maryland.
- Moncrief, T. D. 2017. Age, growth, and reproduction of Vermilion Snapper (*Rhomboplites aurorubens*) in the north-central Gulf of Mexico. Master's thesis. University of Southern Mississippi, Hattiesburg.
- Monnahan, C. C., K. Ono, S. C. Anderson, M. B. Rudd, A. C. Hicks, F. Hurtado-Ferro, K. F. Johnson, P. T. Kuriyama, R. R. Licandeo, C. C. Stawitz, I. G. Taylor, and J. L. Valero. 2016. The effect of length bin width on growth estimation in integrated age-structured stock assessments. *Fisheries Research* 180:103–112.
- Nate, N. A., and M. T. Bremigan. 2005. Comparison of mean length at age and growth parameters of Bluegills, Largemouth Bass, and Yellow Perch from length-stratified subsamples and samples in Michigan lakes. *North American Journal of Fisheries Management* 25:1486–1492.
- Ogle, D. H., T. O. Brenden, and J. K. McCormick. 2017. Growth estimation: growth models and statistical inference. Pages 265–359 in M. C. Quist and D. A. Isermann, editors. *Age and growth of fishes: principles and techniques*. American Fisheries Society, Bethesda, Maryland.
- O'Malley, A. J., C. Enterline, and J. Zydlewski. 2017. Size and age structure of anadromous and landlocked populations of Rainbow Smelt. *North American Journal of Fisheries Management* 37:326–336.
- Ono, K., R. Licandeo, M. L. Muradian, C. J. Cunningham, S. C. Anderson, F. Hurtado-Ferro, K. F. Johnson, C. R. McGilliard, C. C. Monnahan, C. S. Szuwalski, J. L. Valero, K. A. Vert-Pre, A. R. Whitten, and A. E. Punt. 2015. The importance of length and age composition data in statistical age-structured models for marine species. *ICES Journal of Marine Science* 72:31–43.
- Parma, A. M., and R. B. Deriso. 1990. Dynamics of age and size composition in a population subject to size-selective mortality: effects of phenotypic variability in growth. *Canadian Journal of Fisheries and Aquatic Sciences* 47:274–289.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* 39:175–192.
- Pine, W. E., S. J. D. Martell, O. P. Jensen, C. J. Walters, and J. F. Kitchell. 2008. Catch-and release and size limit regulations for Blue, White, and Striped marlin: the role of postrelease survival in effective policy design. *Canadian Journal Fisheries and Aquatic Sciences* 65:975–988.
- Piner, K. R., H.-H. Lee, and M. N. Maunder. 2016. Evaluation of using random-at-length observations and an equilibrium approximation of the population age structure in fitting the von Bertalanffy growth function. *Fisheries Research* 180:128–137.
- Piner, K. R., H.-H. Lee, and L. R. Thomas. 2018. Bias in estimates of growth when selectivity in models includes effects of gear and availability of fish. U.S. National Marine Fisheries Service Fishery Bulletin 116:75–80.
- Potts, J. C., C. S. Manooch, and D. S. Vaughan. 1998. Age and growth of Vermilion Snapper from the southeastern United States. *Transactions of the American Fisheries Society* 127:787–795.
- Quist, M. C., and D. A. Isermann, editors. 2017. *Age and growth of fishes: principles and techniques*. American Fisheries Society, Bethesda, Maryland.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: <http://www.R-project.org>. (April 2016).
- Ricker, W. E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. *Journal of the Fisheries Research Board of Canada* 26:479–541.
- Schirripa, M. J., and J. C. Trexler. 2000. Effects of mortality and gear selectivity on the fish otolith radius-total length relation. *Fisheries Research* 46:83–89.
- Schueller, A. M., E. H. Williams, and R. T. Cheshire. 2014. A proposed, tested, and applied adjustment to account for bias in growth parameter estimates due to selectivity. *Fisheries Research* 158:26–39.
- SEDAR (Southeast Data, Assessment, and Review). 2016. SEDAR 45: Gulf of Mexico Vermilion Snapper stock assessment report. SEDAR, North Charleston, South Carolina.
- Siddons, S. F., M. A. Pegg, N. P. Hogberg, and G. M. Klein. 2016. Age, growth, and mortality of a trophy Channel Catfish population in Manitoba, Canada. *North American Journal of Fisheries Management* 36:1368–1374.
- Taylor, N. G., C. J. Walters, and S. J. D. Martell. 2005. A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. *Canadian Journal of Fisheries and Aquatic Sciences* 62:215–223.
- Then, A. Y., J. M. Hoenig, N. G. Hall, and D. A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science* 72:82–92.
- Tysko, S. M., and J. J. Pritt. 2017. Comparing otoliths and scales as structures used to estimate ages of Largemouth Bass: consequences of biased age estimates. *North American Journal of Fisheries Management* 37:1075–1082.

- Vaughan, D. S., and M. L. Burton. 1994. Estimation of von Bertalanffy growth parameters in the presence of size-selective mortality: a simulated example with Red Grouper. *Transactions of the American Fisheries Society* 123:1–8.
- Wilson, K. L., A. E. Honsey, B. Moe, and P. Venturelli. 2018. Growing the biphasic framework: techniques and recommendations for fitting emerging growth models. *Methods in Ecology and Evolution* 9:822–833.
- Wilson, K. L., B. G. Matthias, A. B. Barbour, R. N. M. Ahrens, T. Tuten, and M. S. Allen. 2015. Combining samples from multiple gears helps to avoid fishy growth curves. *North American Journal of Fisheries Management* 35:1121–1131.
- Xu, Y., S. L. H. Teo, K. R. Piner, K.-S. Chen, and R. J. D. Well. 2016. Using an approximate length-conditional approach to estimate von Bertalanffy growth parameters of North Pacific Albacore (*Thunnus alahunga*). *Fisheries Research* 180:138–146.
- Zhu, J., M. N. Maunder, A. M. Aires-da-Silva, and Y. Chen. 2016. Estimation of growth within stock synthesis models: management implications when using length-composition data. *Fisheries Research* 180:87–91.

Appendix: Results of Estimating Parameters of the von Bertalanffy Growth Equation and Natural Mortality for Vermilion Snapper

TABLE A.1. Estimates (Est), coefficient of variation (CV), and percent error (err%) for von Bertalanffy parameters (asymptotic length L_{∞} [mm TL] and Brody growth coefficient K) and natural mortality (\hat{M}) estimated from simulated observations from the Vermilion Snapper example with 14 ages by sampling strategy. Tabled values are the means of 10 replicates using simulated data representing stationary vectors of population relative abundances ($N_{a,t}$) with total mortality $Z = 0.57$ and CV of mean size at age = 0.1. For the random strategy, rows are replicates. For the size-stratified, age-stratified, or mixed option 1 strategy, rows are presented in order of increasing sampling effort. For the mixed option 2 strategy, rows are presented in order of increased level of augmentation.

Strategy	N	Means only						All points					
		L_{∞}			K			\hat{M}			L_{∞}		
		Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%
Random	10,000	349.5	2.9	1.6	0.31	12.8	-5.2	0.39	9.2	-4.0	345.5	1.4	0.4
	10,000	346.3	2.9	0.7	0.32	11.9	-2.3	0.40	8.7	-1.8	344.0	1.1	0.0
	10,000	343.1	1.3	-0.3	0.33	6.9	2.2	0.41	4.9	1.5	344.0	0.8	0.0
Age stratified	5,711	341.1	2.2	-0.8	0.34	9.2	5.0	0.42	6.6	3.5	341.7	1.1	-0.7
	7,674	343.6	0.8	-0.1	0.33	4.3	0.3	0.41	3.0	0.2	343.3	0.5	-0.2
	8,934	343.8	1.0	-0.1	0.33	4.8	0.1	0.41	3.4	0.1	344.2	0.8	0.1
	9,806	343.1	0.9	-0.3	0.33	4.6	1.3	0.41	3.2	0.9	343.0	0.7	-0.3
	10,010	342.7	0.5	-0.4	0.33	2.9	1.5	0.41	2.0	1.1	342.8	0.5	-0.3
	10,010	344.3	0.5	0.1	0.32	3.0	-1.0	0.40	2.1	-0.7	344.3	0.5	0.1
	10,010	343.2	0.5	-0.2	0.33	2.3	1.3	0.41	1.6	0.9	343.2	0.5	-0.2
	10,010	343.9	0.6	0.0	0.32	3.3	-1.1	0.40	2.2	-0.7	343.9	0.6	0.0
	10,010	343.2	0.4	-0.2	0.33	2.7	0.0	0.41	1.9	0.1	343.2	0.4	-0.2
	10,010	343.0	0.4	-0.3	0.33	2.2	0.7	0.41	1.5	0.5	343.0	0.4	-0.3
Size stratified	5,844	359.7	1.7	4.6	0.38	8.2	17.6	0.45	5.8	9.8	358.1	1.3	4.1
	7,136	386.8	1.1	12.4	0.38	4.7	16.7	0.43	3.4	7.0	389.3	0.2	13.2
	7,888	405.4	0.9	17.8	0.37	3.9	14.0	0.42	2.8	4.0	412.1	0.3	19.8
	8,494	427.5	0.9	24.3	0.34	2.9	5.9	0.40	2.1	-2.3	435.9	0.5	26.7
	9,055	451.7	1.0	31.3	0.32	3.6	-1.2	0.37	2.6	-8.1	462.7	0.7	34.5
	9,443	467.5	0.6	35.9	0.31	2.5	-4.9	0.36	1.8	-11.1	480.9	0.4	39.8
	9,768	481.6	0.5	40.0	0.30	1.7	-8.8	0.35	1.3	-14.3	496.4	0.4	44.3
	10,017	493.6	0.7	43.5	0.29	2.4	-12.4	0.34	1.8	-17.1	509.5	0.6	48.1
	10,017	493.7	0.5	43.5	0.29	2.2	-12.3	0.34	1.6	-17.1	508.3	0.6	47.8
	10,017	492.9	0.7	43.3	0.29	2.0	-11.6	0.34	1.5	-16.6	508.9	0.6	47.9

TABLE A.1. Continued.

Strategy	N	Means only						All points					
		L_{∞}			K			\hat{M}			L_{∞}		
		Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%
Mixed option 1	9,132	351.6	1.8	2.2	0.31	8.9	-3.5	0.39	6.4	-2.9	351.5	1.2	2.2
	9,624	376.0	2.8	9.3	0.30	10.6	-7.0	0.38	7.7	-7.0	383.8	1.7	11.6
	9,736	391.8	2.3	13.9	0.27	9.3	-16.0	0.35	6.7	-14.0	399.8	1.2	16.2
	9,824	416.3	3.0	21.0	0.24	10.0	-26.8	0.31	7.3	-22.8	421.7	1.8	22.6
	9,905	429.6	3.0	24.9	0.23	9.4	-29.9	0.30	7.0	-25.5	440.4	1.4	28.0
	9,937	431.2	2.4	25.3	0.23	8.7	-29.1	0.30	6.3	-25.0	447.8	1.4	30.2
	9,968	442.9	1.4	28.7	0.22	5.6	-33.1	0.29	4.1	-28.4	459.1	0.9	33.5
	10,001	451.5	2.9	31.3	0.21	9.4	-35.1	0.28	6.9	-30.1	469.0	1.8	36.3
	10,001	452.8	2.9	31.6	0.21	9.0	-36.2	0.28	6.7	-31.0	469.0	1.4	36.3
	10,001	449.3	2.4	30.6	0.21	8.1	-34.5	0.29	6.0	-29.7	467.4	1.4	35.9
Mixed option 2	10,010	360.2	2.3	4.7	0.30	10.1	-8.7	0.38	7.3	-7.1	360.7	0.8	4.8
	10,009	389.7	2.7	13.3	0.23	10.2	-29.1	0.31	7.4	-22.9	378.1	1.0	9.9
	10,008	389.0	2.6	13.1	0.25	10.6	-22.9	0.33	7.5	-18.6	389.6	1.4	13.2
	10,007	410.3	4.7	19.3	0.22	15.6	-31.0	0.30	11.5	-25.4	406.7	1.5	18.2
	10,005	419.1	2.9	21.8	0.22	11.4	-33.2	0.29	8.3	-27.4	419.8	0.6	22.0
	10,005	430.0	2.3	25.0	0.21	7.9	-35.5	0.29	5.8	-29.5	433.8	1.3	26.1
	10,003	438.4	2.8	27.4	0.21	9.1	-36.8	0.28	6.8	-30.8	443.0	1.6	28.8
	10,003	442.5	5.5	28.6	0.21	16.2	-35.1	0.29	12.1	-29.8	452.4	2.1	31.5
	10,001	444.0	3.1	29.1	0.21	9.8	-34.3	0.29	7.3	-29.3	459.4	2.3	33.5
	10,000	454.7	3.2	32.2	0.21	10.3	-36.7	0.28	7.6	-31.4	472.0	1.7	37.2

TABLE A.2. Estimates (Est), coefficient of variation (CV), and percent error (err%) for von Bertalanffy parameters (asymptotic length L_{∞} [mm TL] and Brody growth coefficient K) and natural mortality (M) estimated from simulated observations from the Vermilion Snapper example with 26 ages by sampling strategy. Tabled values are the means of 10 replicates using simulated data representing stationary vectors of population relative abundances ($N_{a,t}$) with total mortality $Z = 0.41$ and CV of mean size at age = 0.1. For the random strategy, rows are replicates. For the size-stratified, age-stratified, or mixed option 1 strategy, rows are presented in order of increasing sampling effort. For the mixed option 2 strategy, rows are presented in order of increased level of augmentation.

Strategy	N	Means only						All points											
		L_{∞}			\hat{M}			L_{∞}			K			\hat{M}					
		Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%			
Random	10,000	345.3	4.5	0.4	0.32	22.8	-0.5	0.40	16.4	-0.8	344.0	1.2	0.0	0.32	4.6	-0.3	0.41	3.3	-0.2
	10,000	340.3	5.7	-1.1	0.36	28.9	9.6	0.43	20.7	5.8	344.1	1.1	0.0	0.33	3.4	-0.1	0.41	2.5	-0.1
	10,000	341.6	3.1	-0.7	0.35	15.5	6.4	0.42	11.1	4.1	344.9	1.3	0.3	0.32	3.1	-0.4	0.40	2.3	-0.3
Age stratified	3,163	342.3	3.8	-0.5	0.34	18.1	5.7	0.42	13.0	3.6	343.1	1.2	-0.3	0.34	5.2	3.0	0.41	3.7	2.0
	4,036	350.4	4.3	1.9	0.30	25.9	-8.8	0.38	18.3	-6.8	344.8	0.7	0.2	0.32	4.7	-2.3	0.40	3.2	-1.6
	4,689	344.4	2.6	0.1	0.33	16.2	0.4	0.41	11.5	0.0	343.6	0.6	-0.1	0.33	2.9	1.2	0.41	2.0	0.8
	5,365	340.4	2.5	-1.0	0.34	15.2	4.8	0.42	10.6	3.2	341.8	0.5	-0.6	0.33	2.7	1.5	0.41	1.9	1.2
	6,194	341.8	1.9	-0.6	0.34	12.3	3.2	0.41	8.6	2.1	342.2	0.4	-0.5	0.33	2.8	2.2	0.41	1.9	1.6
	6,856	340.4	1.2	-1.0	0.35	8.6	6.6	0.42	6.0	4.5	342.2	0.3	-0.5	0.34	3.8	3.2	0.42	2.5	2.2
	7,461	343.1	0.9	-0.2	0.33	5.3	0.5	0.41	3.7	0.4	342.7	0.5	-0.4	0.33	3.2	1.3	0.41	2.2	0.9
	8,320	345.5	0.6	0.4	0.32	4.9	-2.7	0.40	3.3	-1.9	343.9	0.4	0.0	0.33	4.0	0.2	0.41	2.7	0.1
	8,888	343.1	0.5	-0.3	0.33	3.8	1.5	0.41	2.6	1.1	343.2	0.4	-0.2	0.33	3.7	1.3	0.41	2.5	0.9
	9,454	343.4	0.4	-0.2	0.33	3.0	0.5	0.41	2.0	0.3	343.4	0.4	-0.2	0.33	2.8	0.3	0.41	1.9	0.2
Size stratified	5,861	366.9	4.4	6.7	0.35	23.2	6.7	0.41	16.2	2.1	357.2	1.4	3.8	0.39	5.2	20.8	0.45	3.8	12.0
	7,149	385.1	2.2	12.0	0.39	10.4	19.1	0.44	7.4	8.5	389.7	0.8	13.3	0.37	2.9	12.9	0.42	2.1	4.6
	7,908	402.6	2.9	17.0	0.38	14.1	17.7	0.43	10.0	6.3	412.7	0.6	20.0	0.34	2.6	5.7	0.40	1.8	-1.5
	8,526	422.7	1.8	22.9	0.36	7.6	12.1	0.41	5.5	1.7	435.2	0.6	26.5	0.32	2.1	-0.9	0.38	1.5	-6.9
	9,100	442.5	3.0	28.6	0.35	12.7	6.8	0.39	9.1	-2.7	458.7	0.6	33.4	0.30	1.7	-7.6	0.36	1.2	-12.4
	9,462	463.3	2.7	34.7	0.32	11.0	-2.9	0.37	8.0	-9.8	475.1	0.4	38.1	0.29	1.6	-12.1	0.34	1.2	-16.0
	9,784	471.6	2.0	37.1	0.32	8.1	-1.8	0.37	5.9	-9.6	491.0	0.6	42.7	0.27	1.7	-16.1	0.33	1.2	-19.3
	10,017	478.8	1.4	39.2	0.32	5.7	-2.7	0.36	4.1	-10.5	500.8	0.5	45.6	0.27	1.7	-17.8	0.32	1.3	-20.8
	10,017	484.1	1.8	40.7	0.30	7.4	-7.4	0.35	5.4	-13.6	502.4	0.4	46.1	0.26	1.5	-19.0	0.32	1.1	-21.6
	10,017	487.9	2.9	41.8	0.29	11.6	-9.6	0.34	8.5	-15.1	503.4	0.4	46.3	0.26	1.5	-19.5	0.32	1.1	-21.9
Mixed option 1	9,141	355.4	6.1	3.3	0.31	28.8	-6.2	0.38	20.8	-5.5	350.3	1.0	1.8	0.32	2.8	-2.8	0.40	2.1	-2.4
	9,632	381.1	4.0	10.8	0.28	19.2	-13.4	0.36	13.7	-11.8	382.5	1.5	11.2	0.28	4.5	-15.1	0.35	3.4	-12.8
	9,744	388.6	4.5	13.0	0.29	20.7	-9.7	0.37	14.7	-9.8	401.8	1.2	16.8	0.25	4.8	-24.0	0.32	3.5	-20.0
	9,822	409.3	6.6	19.0	0.26	25.6	-21.3	0.33	18.9	-18.9	415.1	2.4	20.7	0.23	6.2	-28.4	0.31	4.7	-23.7
	9,907	417.4	6.0	21.4	0.26	28.7	-19.7	0.33	20.0	-18.3	436.2	1.6	26.8	0.21	4.6	-34.8	0.29	3.5	-29.3
	9,938	435.8	9.3	26.7	0.24	29.5	-27.1	0.31	22.2	-24.2	443.4	1.3	28.9	0.21	3.5	-36.7	0.28	2.7	-30.9
	9,966	429.2	5.1	24.8	0.25	22.2	-24.3	0.32	16.2	-21.9	448.5	1.3	30.4	0.20	2.8	-38.0	0.28	2.2	-32.1
	10,001	455.7	5.0	32.5	0.21	20.7	-35.6	0.28	14.8	-30.9	465.5	1.2	35.3	0.19	4.0	-42.5	0.26	2.9	-36.0
	10,001	430.9	5.6	25.2	0.25	18.5	-23.8	0.32	13.9	-21.6	457.8	1.3	33.1	0.19	3.6	-41.1	0.27	2.7	-34.7
	10,001	428.5	3.4	24.6	0.25	15.2	-22.2	0.32	11.0	-20.3	456.6	0.8	32.7	0.19	2.2	40.2	0.27	1.7	-34.0

TABLE A.2 Continued.

Strategy	N	Means only									All points								
		L_{∞}			K			\hat{M}			L_{∞}			K			\hat{M}		
		Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%	Est	CV	err%
Mixed option 2	10,010	363.2	5.0	5.6	0.29	22.9	-12.3	0.37	16.8	-10.0	359.5	1.2	4.5	0.29	3.1	-9.7	0.38	2.3	-7.6
	10,009	379.8	8.5	10.4	0.27	36.4	-15.9	0.35	26.6	-13.9	375.4	1.0	9.1	0.27	2.6	-18.3	0.35	1.9	-14.5
	10,008	407.3	14.5	18.4	0.24	39.3	-27.1	0.31	29.9	-23.0	386.9	1.2	12.5	0.25	3.9	-22.5	0.33	2.9	-18.1
	10,007	416.8	6.9	21.2	0.20	30.5	-38.3	0.28	22.1	-31.3	397.6	1.1	15.6	0.24	3.0	-26.7	0.32	2.2	-21.6
	10,005	409.5	8.1	19.0	0.25	25.3	-24.0	0.32	19.3	-20.7	413.5	1.3	20.2	0.22	3.9	-31.7	0.30	2.9	-26.0
	10,005	402.2	5.5	16.9	0.27	23.9	-15.7	0.35	17.3	-14.7	421.5	0.8	22.5	0.22	2.2	-33.5	0.29	1.6	-27.7
	10,003	450.0	6.6	30.8	0.18	25.2	-43.3	0.26	18.4	-36.2	435.4	2.3	26.6	0.20	6.0	-37.0	0.28	4.6	-30.8
	10,003	427.8	10.3	24.4	0.25	38.9	-23.5	0.32	28.3	-21.7	441.2	1.7	28.3	0.20	4.8	-37.9	0.28	3.6	-31.7
	10,001	424.7	3.1	23.5	0.25	11.9	-23.3	0.32	8.8	-20.8	451.0	0.7	31.1	0.20	1.5	-39.8	0.27	1.1	-33.5
	10,000	451.8	8.5	31.3	0.21	28.1	-34.0	0.29	21.0	-29.6	456.6	1.6	32.7	0.20	5.0	-40.1	0.27	3.7	-33.9