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Mean Size at Age: An Evaluation of Sampling Strategies with Simulated Red Grouper Data

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Abstract.—The influence of sampling protocol on estimation of mean lengths at age was evaluated by computer simulation of a population of red grouper *Epinephelus morio.* Variation in length at age was simulated with platoons of different lengths within each year-class. Mean length of each platoon was assigned with the normal distribution and mean size at age from a previous growth study. Natural mortality was assumed to be 0.2. Simulated samples were obtained at random or with length stratification from either the population or its fishery. Fishing mortality was assumed to be a function of either fish age or fish length. Estimates of mean length at age contrasted with known true mean lengths indicated that reliable estimates of mean size at age requires random sampling of lengths within ages. Stratification of samples by length biases the estimates of mean length at age. Similarly, samples drawn from size-selective gears or fisheries yield biased estimates of mean length at age. Growth models fitted to such data will not generally reflect the mean growth of individuals in the population, and even slight changes in sampling protocol can result in misleading temporal shifts of estimates of size at age.

Determination of mean lengths at age is an important task in many fishery investigations. Such data are often used to characterize growth and can lead to models of growth with age or studies of density-independent and density-dependent effects of environmental conditions on population structure and dynamics. The application of age-structured methods for assessing population status requires estimating age composition of the catch. Such estimates may be derived from random samples of the catch for age composition, or from samples of the catch for lengths with subsamples stratified by length so that age–length keys can be obtained and expanded to the entire catch. Both procedures require long-term dedication of substantial resources. Consequently, growth models are sometimes used to estimate age composition from length samples of the catch. This practice requires the assumption that the samples used to construct the model of size at age are representative of size at age for each gear encountered in the fishery. Factors such as gear selectivity, bias in sampling protocol, or variability in actual growth may seriously constrain the utility of growth models for estimating age composition of the catch.

Recent evaluations of the growth of red grouper *Epinephelus morio* showed an important increase in size at age through time for specimens sampled from the U.S. Gulf of Mexico (Eklund 1992; Goodyear and Schirripa 1993; Johnson and Collins 1994). This trend led to the development and application of a time-corrected growth model based on the von Bertalanffy growth equation to estimate the age composition of the catch (Goodyear and Schirripa 1993). The results of applying virtual population analysis methods (Gavaris 1988; Powers and Restrepo 1992) to the resulting catch-at-age data led to widely disparate views of the status of the stock (Goodyear and Schirripa 1993). Inadequate estimates of age composition of the catch may have contributed to this unsatisfactory result.

Vaughan and Burton (1994) simulated red grouper growth in the presence of size-selective mortality to explore methods to reduce the influence of Lee's phenomenon on estimates of the parameters of the Von Bertalanffy growth equation. In the present paper, I use a similar approach to explore the influence of gear selectivity and sampling protocol on the accuracy of estimates of mean size at age with computer simulation.

Methods

The potential magnitude of bias in the red grouper growth estimates was evaluated from measurements of lengths of fish at capture and measurements of radii from focus to annulus on otoliths. These data represent a subset of those presented by Johnson and Collins (1994) that were available at the time of the Goodyear and Schirripa study (1993). These data were partitioned by time and gear of capture into four sets: members of set A were captured by recreational hook and line in 1979–1981, fish in set B were from commercial hook and line in 1980–1981, fish in set C were

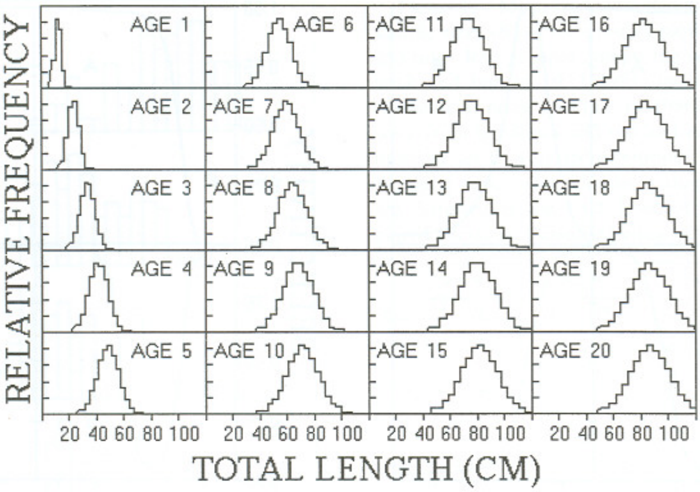

FIGURE 1.—Length compositions of a simulated red grouper population used to compare estimated mean lengths with underlying true values for several sampling situations.

from handlines and rod and reel in 1991–1992, and fish in set D were from bottom longline in 1991–1992. I back-calculated lengths at prior annulus formation for each set and compared across sets with Student's *t*, assuming equal variance. For the remainder of the present study, I used simulation techniques to evaluate conditions that might contribute to the disparity in mean size at age observed among these data sets.

The population simulation model for this analysis (Goodyear 1989) used 20 discrete ages with an instantaneous annual natural mortality of 0.2 for all ages. Each year-class was further stratified into platoons with similar growth attributes. The position of a platoon in the distribution of size at age was fixed so that the larger individuals of a year-class at age 1 remained larger throughout their lifetimes. Mean sizes at age at the beginning of January were assumed to be equal to the values estimated for 1992 from the time-corrected growth model of Goodyear and Schirripa (1993), and the coefficient of variation of length at age was estimated from mean back-calculated length at age 5 (0.16). The mean length of individuals of age a in platoon p, l_{ap}, was determined from mean size at age (L_a) with the normal distribution and the coefficient of variation of length at age (v) for age 5:

$$l_{ap} = L_a + L_a z_p v; \qquad (1)$$

z_p = standard normal deviate for the pth percentile of the distribution, and $v = SD_5/L_5$.

The resulting distributions of size at age in the simulations is given in Figure 1, based on 201 platoons. Although a basic intent of the current exercise is to test the robustness of these estimates, it is less important that they accurately reflect red grouper growth than it is that the simulated population means and variances are known with certainty. Systematic sampling-induced biases in the simulated data would also be expected for actual data collected under conditions similar to those evaluated here.

The simulation model permits specification of temporal fractions of the annual growth, and for this study, growth during the first month was set to zero. This procedure caused the simulated lengths during the first month to remain constant so that mean sizes of the fish in the simulated catch for that period were unaffected by growth or mortality. All sampling from the simulation was restricted to this first month to facilitate comparisons of estimated mean lengths and the true underlying means. Student's *t* was used to test for significant differences between the true and estimated mean lengths at age at the 0.05 level of probability.

Recruitment to the fishery was specified in the model by year-class, and in most simulations examined it was held constant. Several levels of fishing mortality were evaluated, but fishing mortality rates were constant within each simulation. Except when effects of size limit and year-class strength were evaluated, the age distribution of the simulated population was stationary when sampled.

The value of fishing mortality for any platoon in the model is the product of the maximum for

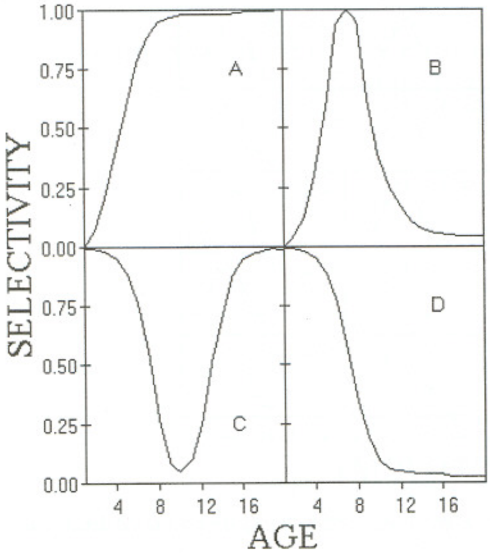

FIGURE 2.—Four schedules (A–D) of age-specific proportions of the maximum exposure to fishing mortality evaluated in the red grouper simulation study.

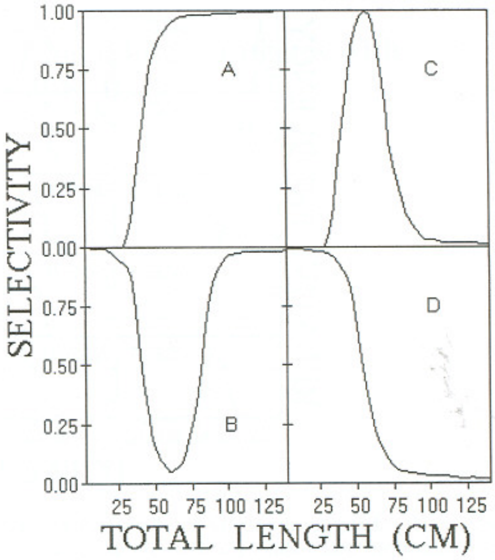

FIGURE 3.—Four schedules (A–D) of length-specific proportions of the maximum exposure to fishing mortality evaluated in the red grouper simulation study.

any platoon and the selectivity for the individual platoon. The consequences of sampling for growth from fisheries in which gear selectivities are age- and length-specific were also examined. For both extremes, the selectivity schedules examined included ones that increased asymptotically and ones that decreased asymptotically with increasing size or age (Figures 2, 3). Each was also evaluated for a U-shaped and dome-shaped selectivity schedule. Other situations evaluated included the impact of size limits when sampling is restricted to the fishery and the effects of abnormally strong and weak year-classes.

Two sampling strategies were evaluated. In the first, sampling was random without respect to the numbers of samples by length. In the second, samples were stratified by 5-cm length intervals. Simulated observations of length and age were obtained from either the population or its fishery. In either case, a platoon within the population structure or catch was picked at random and evaluated for inclusion as an observation based on the ratio of its abundance (N_{platoon}) to the maximum abundance of any other eligible platoon ($N_{\max}$). To determine this ratio, I drew a uniform random number (R) between 0 and 1.0. If the ratio $N_{\text{platoon}}/N_{\max} \geq R$, the length and age attributes of the platoon were considered eligible to be included as an observation; otherwise, it was discarded. This procedure caused the sampled platoons to be proportional to their abundance in the simulated population. The process was repeated until 50,000 eligible samples had been drawn.

For the random sampling strategy, all eligible samples were retained as observations; for the length-stratified strategy, the first 500 samples in each stratum were retained. This resulted in 50,000 observations for the random-sampling strategy and about 7,500 observations for the length-stratified sampling strategy for each condition evaluated. No error was added to either the age or length attributes to simulate measurement error.

To evaluate performance of each strategy, I plotted error in mean length at age against age, where error = (estimate−true)/true. Estimates of sample means were made only for ages at which sample sizes were 10 or greater.

A minimum size of 50.8 cm total length for red grouper in federal waters of the Gulf of Mexico was established in 1990. One effect of this regulation was to greatly reduce the availability of small fish to biologists sampling fishermen's catches. Consequently, selectivity of fish in the fishery became a function of fish size rather than age. I investigated the possible importance of this phenomenon by sampling simulated catches before and after the size limit was imposed. It was assumed for this test that recruitment was constant, fishing mortality was 0.25, the preregulation selectivity schedules were constant with age, and no

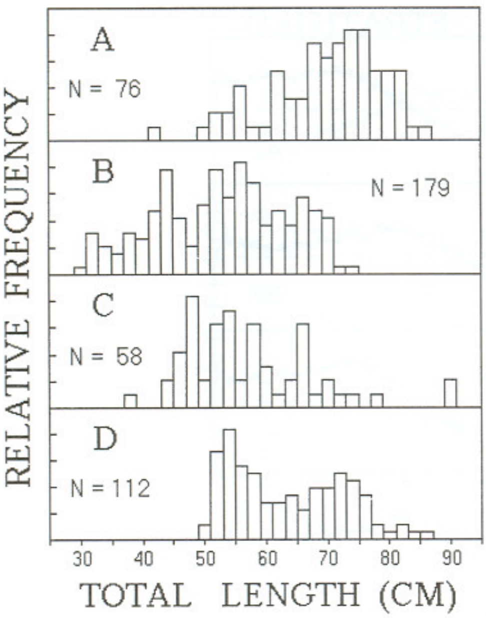

FIGURE 4.—Sample length frequencies for the time–gear stratified age–length data. The hook-and-line data are **(A)** 1979–1981 recreational, **(B)** 1980–1981 commercial, and **(C)** 1991–1992; bottom longline data **(D)** are for 1991–1992.

TABLE 1.—Mean back-calculated total lengths (TL) and sample sizes (N) of red grouper partitioned by capture gear and time. Red grouper composing set A were captured by hook and line in 1979–1981; those in set B were from commercial hook and line in 1980–1981; those in set C were from handlines and rod and reel in 1991–1992; and those in set D were from bottom longline in 1991–1992. Within a row, mean lengths without a letter in common are different at the 0.05 level of probability, based on paired t-tests and assumed equal variances.

	Set A		Set B		Set C		Set D	
Age	N	TL	N	TL	N	TL	N	TL
1	73	19.1 z	173	19.4 z	58	20.6 y	112	20.8 y
2	73	31.3 z	173	29.9 y	58	31.3 zy	112	32.6 x
3	73	40.9 z	165	37.1 y	54	38.8 y	112	41.1 z
4	73	49.4 z	143	42.8 x	44	45.7 y	112	47.9 z
5	72	55.8 z	121	47.5 x	34	52.0 y	99	53.6 y
6	55	61.2 z	74	50.9 x	24	56.6 y	61	58.9 y
7	47	64.1 z	48	54.7 y	11	63.2 z	37	65.4 z
8	40	66.7 z	31	57.0 y	4	68.9 z	19	68.5 z
9	34	69.1 z	19	59.6 y	4	73.6 z	7	69.3 z
10	32	71.2 z	13	62.0 y	3	77.2 z	4	73.8 z
11	24	71.8 z	12	63.8 y	2	77.4 zy	0	

sublegal fish were available for sampling from the fishery after the minimum size was imposed. Both random and length-stratified sampling strategies were evaluated.

Results

Time–gear Stratification of Field Data

Samples from the recreational fishery in 1979–1981 averaged larger (Figure 4A) and those from the commercial fishery for the same period averaged smaller (Figure 4B) than those from the other strata. The samples from 1991 and 1992 were truncated by the minimum size present at the time, and the effect was most pronounced for the bottom longline stratum (Figure 4D).

Mean back-calculated lengths at age differed among the four strata examined (Table 1). Although estimates of mean length at age differed significantly for at least one age between each combination of strata, the sample from the commercial fishery in 1979–1981 gave estimates of mean size at age that were significantly smaller than those derived from the other samples. The marked difference between estimates from the 1979–1981 recreational and commercial samples suggests that at least one of the two sources of data was not representative of red grouper growth (Figure 5). The cause for the divergent estimates derived from these two samples is unknown but could have arisen from bias introduced through sampling protocol or inherent in the source of animals sampled. In subsequent analyses, I use sim-

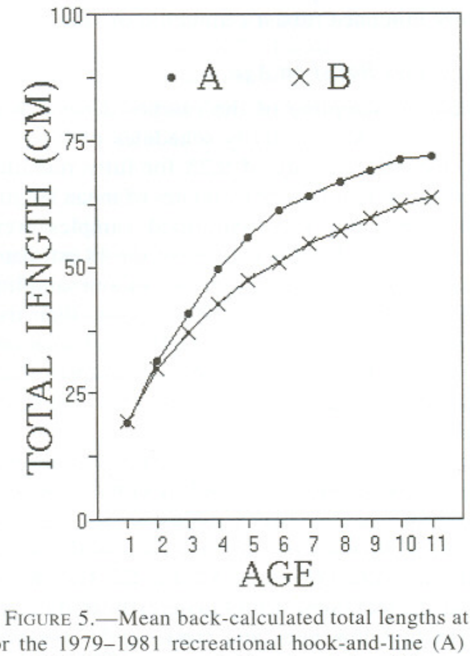

FIGURE 5.—Mean back-calculated total lengths at age for the 1979–1981 recreational hook-and-line (A) and the 1980–1981 commercial hook-and-line (B) samples of Gulf of Mexico red grouper.

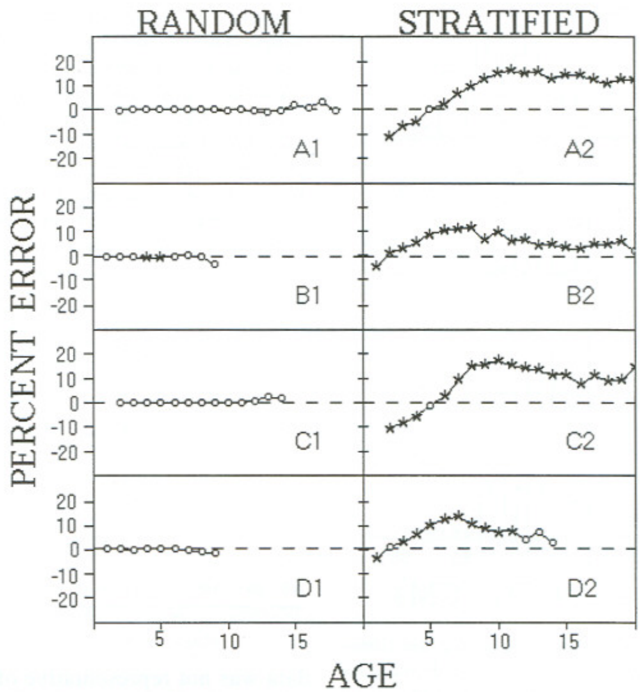

FIGURE 6.—Errors in the estimates of mean length at age for random and length-stratified samples of red grouper catches simulated with the age-specificity selectivity schedules of Figure 2. Letters A–D denote simulations with the respective selectivity schedules of Figure 2. Values denoted by an asterisk (*) are significantly different from the true values ($P < 0.05$).

ulated data to explore the extent to which such factors influence robust estimation of size at age.

Selectivities Based on Age

Random sampling of the catches derived with the age-specific selectivity schedules of Figure 2 with fishing mortality of 0.25 for fully recruited fish resulted in unbiased estimates of mean lengths at age, but the length-stratified samples were strongly biased (Figure 6). Two of the 48 estimates of mean lengths derived from the random sampling strategy were statistically different from their true values (Figure 6B1). This result is about what one would expect given the number of sample means compared, so these differences are most likely the result of chance.

In contrast to the results of random sampling, sample stratification by length resulted in significant differences between the estimates and true values for almost every age for each of the selectivities examined (Figure 6A2, B2, C2, D2). Mean size at age was consistently underestimated for the first or first few ages and consistently overestimated for some or all older ages. Errors of plus or minus 10% of the true mean were typical; the maximum error was greater than about 10 cm—about 15% greater than its true value—at about age 8–10, varying somewhat with the selectivity examined.

Length-stratified samples were taken from population simulations at two levels of total mortality (0.25 and 0.75) applied to ages 1–20 for three recruitment conditions. These were constant recruitment (Figure 7A, B), a weak year-class equal to 10% of average (Figure 7C, D), and a strong year-class equal to 10 times normal (Figure 7E, F). Constant recruitment was maintained for all but the perturbed year-class, which was age 4 when samples were taken. Overall, the results showed negative bias for age 1 and positive bias for some or all subsequent ages (Figure 7). Higher total mortality reduced the number of older fish available for sampling for all recruitment conditions (Figure 7) and reduced or eliminated the bias at older ages. The abnormally weak year-class slightly elevated the bias on the corresponding age (= 4) and reduced it slightly for the subsequent age (Figure 7C, D). In contrast, the single stronger-than-normal year-class decreased the magnitude of the bias

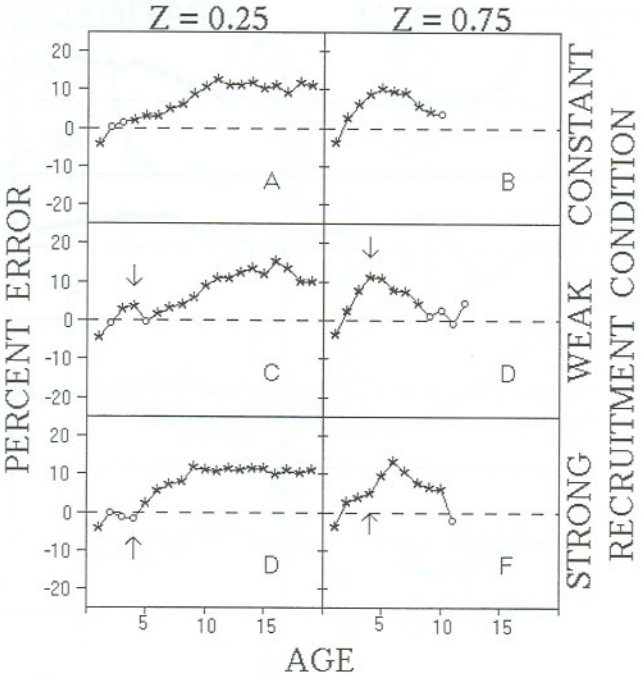

FIGURE 7.—Errors in the estimates of mean length at age for length-stratified samples from the population at two levels of total mortality (Z) and three recruitment conditions. Values denoted by an asterisk (*) are significantly different from the true values ($P < 0.05$). Arrows mark a perturbed age-4 year-class.

evident in the estimates of mean lengths of the corresponding age (Figure 7E, F).

Selectivities Based on Length

Random and length-stratified sampling of the catches derived with the selectivity schedules of Figure 3 with constant recruitment and fishing mortality of 0.25 for fully recruited fish resulted in a strong positive bias in sampled mean size in the youngest ages (Figure 8A1, A2). This pattern disappeared with increasing age for both sampling strategies, but when length-stratified sampling was used, the initial decline in bias with age was followed by an increase in positive bias in the older ages.

Random sampling from the catches produced by the dome-shaped schedule of Figure 3B resulted in a pattern of errors that underestimated mean size at age for ages 3–6 and overestimated it for ages 8 and above (Figure 8B1). Length-stratified samples from the same catches were relatively unbiased for the younger ages and positively biased for the oldest ages (Figure 8B2).

Random sampling from the catches derived with the U-shaped selectivity schedule of Figure 3C led to overestimates of mean lengths for ages 2–5 and underestimates for ages older than 6 (Figure 8C1). The length-stratified samples from the same catches were similarly biased for age 2 but less so for the older ages (Figure 8C2). Further, the bias present in the estimates beyond age 4 was toward overestimating the mean size, and it tended to disappear in the oldest ages.

Random sampling from the catches simulated with the schedule of declining selectivity with size (Figure 3D) caused underestimation of mean lengths at age for all ages above age 3 when the number of observations was at least 10 (Figure 8D1). This trend was also true for the length-stratified samples for ages older than 7, but length at age 1 was underestimated and lengths at ages 3–6 were slightly overestimated (Figure 8D2).

Effects of Minimum Size

Random sampling from the population before size limits were imposed provided unbiased estimates of mean size at age (Figure 9A). However, the mean lengths at age for the youngest ages available after imposition of limits were overestimated with the same sampling strategy (Figure 9B). The length-stratified samples for the preregulation condition (Figure 9C) demonstrated bias

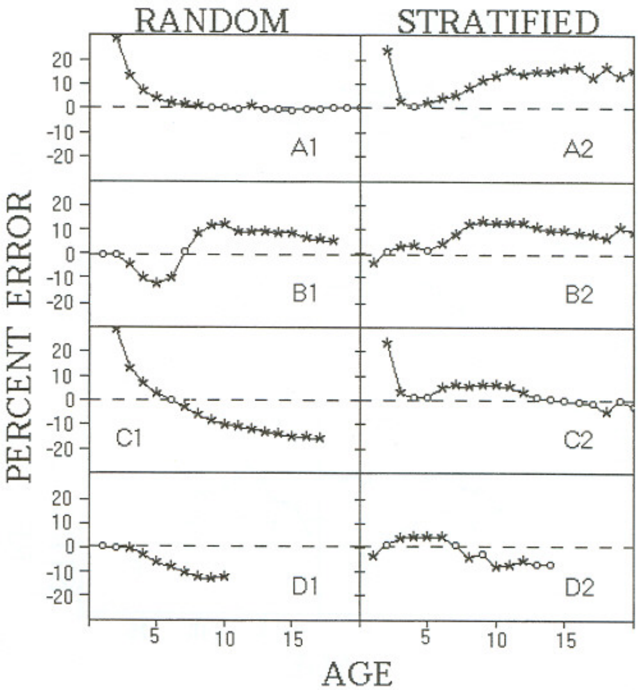

FIGURE 8.—Errors in the estimates of mean length at age for random and length-stratified samples of catches simulated with the length-specific selectivity schedules of Figure 3. Letters A–D denote simulations with the respective selectivity schedules of Figure 3. Values denoted by an asterisk (*) differ significantly from the true values ($P < 0.05$).

similar to that observed for this sampling strategy in previous analyses (Figures 6–8). However, the postregulation samples showed the same strong positive bias for the youngest ages available that was observed for the postregulation random sampling (Figure 9D).

Discussion

Of the sampling strategies I evaluated, only random sampling from gears that were nonselective for fish length produced unbiased estimates of mean size at age, and then only in the absence of size limits. Length-stratified samples and samples drawn from size-selective fisheries all provided biased estimates of mean length at age. Although selectivity patterns that were solely a function of fish age did not result in biased estimates of mean size at age, they often produced samples with strongly biased length distributions. This outcome suggests that it may be difficult to decide from the length composition of samples whether they are from length-selective sources or not.

In the case of red grouper from the U.S. Gulf of Mexico, the mean lengths of fish caught in various components of the overall fishery clearly vary (Goodyear and Schirripa 1993). The selectivity patterns for the three commercial gear types (traps, bottom longlines, and handlines) differ, and recreational anglers generally harvest smaller fish than do their commercial counterparts. However, red grouper harvested recreationally offshore of the Florida panhandle and Alabama average much larger than those in the recreational harvest to the south (Goodyear and Schirripa 1993). Nearly all of the recreational samples available for 1979–1981 came from this area. They were larger than the samples from the commercial fishery for the same period, as were the corresponding mean back-calculated lengths at age.

The back-calculated mean lengths at age from the early commercial samples were smaller than those for the other strata and are responsible for the temporal trend of increasing size at age observed by Goodyear and Schirripa (1993) and Johnson and Collins (1994). The simulation results for samples from fisheries with a minimum size limit strongly suggest that the samples from 1991–1992 produced upwardly biased estimates of size at age. It is not clear that any combination of the available samples would constitute a representa-

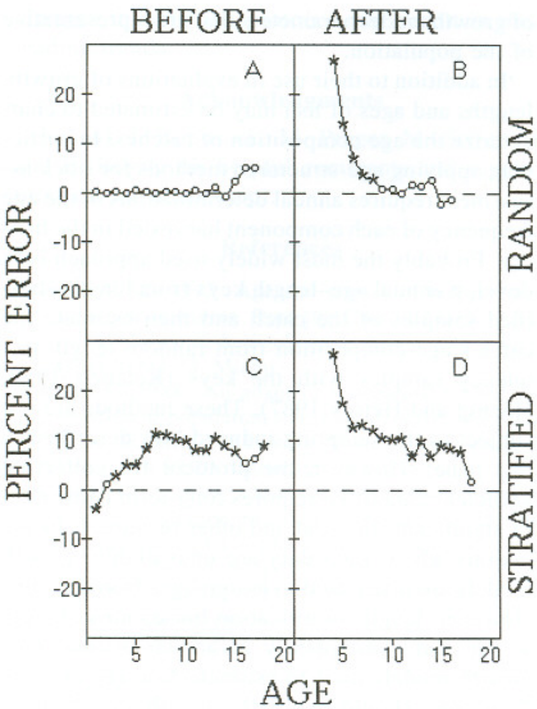

FIGURE 9.—Errors in the estimates of mean length at age from samples before and after imposition of a minimum size in the fishery for random and length-stratified sampling. Values denoted by an asterisk (*) differ significantly from the true values ($P < 0.05$).

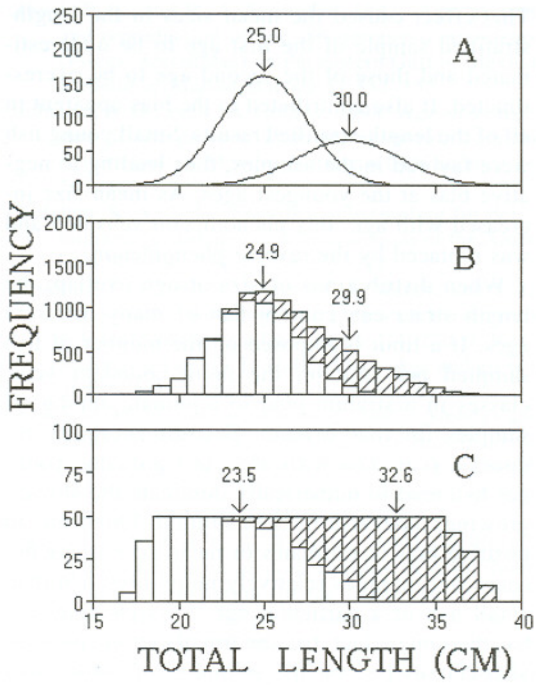

FIGURE 10.—(A) Population distributions of fish length for two age-groups with normally distributed and overlapping length distributions. (B) Sample length frequencies and mean lengths by age generated from 10,000 simple random samples. (C) Sample length frequencies and mean lengths by age for length-stratified samples constructed from the first 50 observations in each 1-cm length stratum of the sample distribution in B. In B and C, hatched frequencies represent the older age-group. Arrows and associated numbers denote mean age-group lengths in the population (A) or in samples (B, C).

tive sample for size at age of red grouper. It also seems likely that the temporal trend of increasing size at age from 1979–1981 to 1991–1992 is an artifact of sampling rather than the result of growth.

The International Biological Programme handbook on methods for assessment of fish production in freshwaters provides the following guidance for the conduct of growth studies: the first step is to "procure a sample of fish representative of all the sizes of the species in the population, as far as possible" (Tesch 1968). This advice favors the adoption of length stratification when simple random sampling would provide overwhelming numbers of individuals of similar sizes and few very large or very small fish. Such sample stratification is relatively common in growth studies (e.g., Miranda et al. 1987; Newman and Weisberg 1987; Gutreuter and Childress 1990; Hammers and Miranda 1991; Hood and Schlieder 1992). Except when all encountered individuals are selected for age determination or some set of procedures are in place to assure random sampling, the occasional very large or small individual would be more likely to be sampled than the average fish of intermediate size.

The principal bias in estimates of mean size at age from the length-stratified samples was the direct result of sample stratification. Origin of the bias is illustrated by the length frequencies of simulated simple random and length-stratified samples drawn from a population composed of two hypothetical ages with overlapping length distributions (Figure 10). The mean lengths at age for the simple random samples were very close to the parent distributions, whereas the mean lengths at age from the length-stratified samples were biased (Figure 10). Note that length stratification resulted in individuals smaller than the mean size of the first age and larger than the mean size of the older age being included in greater proportion in the sample than they were in the parent population.

This effect caused the mean sizes in the length-stratified sample of the first age to be underestimated and those of the second age to be overestimated. It also contributed to the bias apparent in all of the length-stratified results. Small young fish were favored in the samples, thus leading to negative bias at the youngest ages. As mean size increased with age, this phenomenon subsided and was replaced by the reverse phenomenon.

When distributions of size at age overlap, the length strata can contain fish of many different ages. If a limit is imposed on the number of fish sampled per stratum, the more abundant year-classes in a stratum tend to dominate among all samples for that stratum. Because mortality reduces a year-class with time, fast-growing, younger fish tend to numerically dominate the slower-growing, older fish in each stratum. This leads to positive bias in estimates of mean size at age because one samples relatively more large fish than small fish of a particular age. This phenomenon has the same effect that abnormally strong or weak year-classes had on the estimates of mean sizes seen in Figure 7.

Means of samples drawn from the catches of size-selective fisheries were particularly strongly biased. The pattern depended on the selectivity pattern of the fishery, and to a lesser extent, on whether the estimates were from random or length-stratified samples of the catch. Also, the extent of the bias depended on both the selectivity schedule and sampling strategy. For some selectivity schedules, length stratification reduced the extent of the bias in estimates of mean size at age for some ages compared to the random samples.

Vaughan and Burton (1994) simulated red grouper growth in the presence of size-selective mortality to explore methods to reduce the influence of this phenomenon on estimates of the parameters of the Von Bertalanffy equation. Their results suggested that investigators can obtain the best parameter values for estimating growth by including only lengths back-calculated to the most recent annuli. Although Lee's phenomenon is commonly interpreted as the result of size-selective mortality on mean size at age of the survivors, Ricker (1969, 1975) noted that size-selective gears also produce this phenomenon. It results when size selectivity introduces gradients in the bias into the estimates of mean size at age. The results of the present study imply that if samples are length-stratified or obtained from length-selective fisheries or sampling gears, it may not be possible to obtain estimates of growth model parameters that are representative of the population.

In addition to their use in evaluations of growth, lengths and ages of fish may be estimated to characterize the age composition of catches. In particular, applying age-structured methods for stock assessment requires annual determinations of the age frequency of each component harvested in the fishery. Probably the most widely used approach is to develop annual age–length keys from length-stratified samples of the catch and then estimate the catch's age composition from random length-frequency samples with the keys (Ketchen 1950; Hoenig and Heisey 1987). These methods are not subject to the sampling-induced bias described in this paper. However, the protocol for collecting sufficient data often requires long-term dedication of significant financial and other resources. In situations where such data are unavailable, growth models are often used to assign ages from lengths. However, length stratification biases mean length at age and consequently parameter estimates of growth models used to estimate fish age as well. Thus, one should avoid the length stratification required for applying age–length keys when developing models of fish growth intended for the same purpose.

The major disadvantage of the random sampling strategy is the large numbers of samples required for estimating size at age for the older fish in the catch because of the cumulative effect of mortality. Although I used 50,000 observations in the simulations, only small sample sizes were obtained for the older ages in the catch. It is probably noteworthy that if sample sizes from random samples of the catch suffice to characterize the mean sizes at age, then the sample age-frequency data would probably better characterize the catch than would ages estimated from lengths with a growth model fitted to the size-at-age data.

In summary, it may not be possible to obtain unbiased estimates of size at age if samples come from length-selective sources. Consequently, length-stratified samples should be avoided when data sets are constructed to characterize growth or to develop models of mean length at age. The results of my study also suggest that it will often be difficult to draw robust conclusions about true mean growth or about observed differences in growth unless the selectivity patterns of the collection methods are known to be unbiased with respect to length. The magnitude of sample-induced bias can be important, such that even slight changes in sampling protocol may result in misleading trends.

Acknowledgments

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