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Effects of Growth Variability on Estimation of the Biological Reference Point $F_{0.1}$, with Examples from Chesapeake Bay, USA

by

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SPECIAL SESSION ON MANAGEMENT UNDER UNCERTAINTIES
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Abstract

The biological reference point $F_{0.1}$ is used with yield-per-recruit models as a conservative alternative to fishing at F_{max}, i.e., to maximizing yield per recruit at a given age of entry. As with other management benchmarks based on dynamic pool models, estimation of $F_{0.1}$ requires estimates of growth parameters obtained from size-at-age data. Those parameter estimates have variability arising from sampling error and the intrinsic variability in growth itself. Using Monte Carlo methodology and size-at-age data from several Chesapeake Bay fisheries, we examined the effects of that variability on resulting estimates of $F_{0.1}$. The bias in estimating $F_{0.1}$ was small in most cases, but the variance of the estimate was sometimes large. We also noted that many of the age data collected for Chesapeake Bay species do not seem to fit the von Bertalanffy growth model very well, and that growth during the ages sampled could equally well be described by a straight line.

Introduction

Estimating the ages of samples from a fish population, or *aging*, is a fundamental step in quantifying growth. The aging of fish, like any laboratory procedure, is subject to both error (lack of accuracy) and variability (lack of precision). The result is that growth parameter estimates derived from aging will themselves contain error and variability. Even length-based models that do not involve aging (e.g., Pauly 1987; Fournier et al. 1990) produce growth parameter estimates with nonzero variance and possible bias. Moreover, parameter estimates from length-based models are generally less certain than those from aging-based models, since under any but the most restrictive assumptions, the former must contain subjective elements (Fournier et al. 1990). Because estimates of growth parameters are imprecise, estimates of management benchmarks that rely upon the parameter estimates are also imprecise, and may be biased, even when the original parameter estimates are unbiased.

We conducted a Monte Carlo study to examine the propagation of aging uncertainty (variability) on the Beverton and Holt (1957) yield-per-recruit (YPR) model when used with the

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management measure $F_{0.1}$ (Gulland and Boerema 1973). Size-at-age data from several anadromous fish species found in Chesapeake Bay (eastern USA) provided examples. While these particular species are not managed by $F_{0.1}$, and indeed may not be particularly well suited to management by $F_{0.1}$, the simulations based on their growth data serve to illustrate the issues involved.

The management benchmark $F_{0.1}$ was proposed to obtain relatively high yields while avoiding overfishing (Gulland 1983). The unique estimation of $F_{0.1}$ for any age at entry t_c is possible because a curve of YPR against instantaneous fishing mortality F exhibits a monotonically decreasing slope; i.e., for all F, $\frac{\partial^2 \mathrm{YPR}}{\partial F^2} < 0$. $F_{0.1}$ is defined as the value of F at which the slope of such a curve is 0.1 times its slope at the origin. (Deriso 1987 gives the equivalent mathematical definition.) Because $F_{0.1}$ is defined in terms of the Beverton–Holt yield-per-recruit model, it requires estimates of the three von Bertalanffy (1938) growth parameters W_∞, t_0, and K, making it vulnerable to variability in the underlying size-at-age data. The purpose of this study was to characterize the sensitivity of $F_{0.1}$ to variability in aging, using representative example data sets.

We are aware of two previous studies that examined the effects of error and variability in size-at-age data on dynamic pool models. Lai and Gunderson (1987) compared age estimates made from otoliths, dorsal and pectoral fin rays, and scales of walleye pollock (*Theragra chalcogramma*). Although Lai and Gunderson described theirs as a study of the effects of aging error, and in some ways it was, they made no attempt to verify the absolute accuracy of any age determinations, but arrived at their estimates of error by comparing age determinations made by different readers and methods. Thus they used lack of precision, rather than lack of accuracy, as their basis for estimating the general magnitude and distribution of aging errors and their effects.

In their simulation study, Lai and Gunderson (1987) showed that the effects of aging error on estimated growth and survival parameters of walleye pollock can range from insignificant to substantial. In the presence of aging error, the average mean length at age was typically overestimated for ages 1 through 4 and underestimated for older ages. The bias increased with increasing aging error and appeared to arise from misallocation of younger fish to older age-classes and vice versa. From a management point of view, the most serious biases occurred from underaging. When ages are underestimated, the optimal fishing mortality F_{max} for a given t_c is overestimated, and the optimal value of t_c for a given F is underestimated. Either error results in a less conservative management regime that could encourage growth overfishing or even reduce the expected recruitment of the stock.

In a Monte Carlo study, Restrepo and Fox (1988) examined the effects of parameter uncertainty on a three-parameter relative yield-per-recruit model (Holt 1962, Beverton 1963). The study randomly drew sets of parameters from predetermined probability distributions chosen to reflect the relative importance of uncertainties in the parameters. The equilibrium relative yield per recruit Y'_i was given by

$$Y_i' = E_i(1-C_i)^{(M/K)_i} \sum_{n=0}^{3} \frac{U_n(1-C_i)^n}{1+n(M/K)_i^{-1}(1-E_i)}, \qquad (1)$$

where E is the exploitation rate (the ratio of fishing to total mortality, F/Z); C is the ratio of the mean length at first capture, l_c, to the asymptotic length, L_∞; M/K is the ratio of the rates of natural mortality and von Bertalanffy growth; and i indexes the current set of three parameters (E, C, and M/K).

Restrepo and Fox (1988) repeatedly made random changes to E, C, or both and computed corresponding values of relative YPR. The percent change in yield-per-recruit for the ith set of values was then computed as

$$\mathrm{PCY}_i = 100\,(Y_i'' - Y_i')\,/\,Y_i' \tag{2}$$

where Y_i'' is the equilibrium relative yield per recruit after the parameters are changed. A non-negative change in YPR always occurred when C was increased by 0.0 to 0.1 and E remained constant. Other results demonstrated that improving knowledge of E could reduce the coefficient of variation of PCY significantly, while improved knowledge of M/K and C, did not result in a substantial reduction. The degree to which the results could be generalized beyond the examples used by Restrepo and Fox was not stated.

In the present study, we examined the effects of intrinsic variability in the size-at-age data when estimating $F_{0.1}$ for several actual sets of growth data. We used the full Beverton-Holt (1957) seven-parameter yield-per-recruit model and examined estimates both of $F_{0.1}$ and of yield at $F_{0.1}$, which we designate $Y_{0.1}$.

Methods

Length-at-age data were supplied by colleagues at the Maryland Department of Natural Resources and the Virginia Institute of Marine Science (VIMS) as part of a survey to determine the availability of such data for Chesapeake Bay species (Prager et al. 1990). The only species with substantial bodies of aging data were American shad *(Alosa sapidissima)*, alewife *(Alosa pseudoharengus)*, blueback herring *(Alosa aestivalis)*, and striped bass *(Morone saxatilis)*. Population and management parameters (other than growth parameters) for these species are summarized in Table 1. Because of substantial sex-related differences in growth, analyses of alosid stocks were performed using both pooled data and data separated by sex. The data for shad were collected geographically; results were computed separately for data from each geographical area. The stock structure of these alosid species is at present not well known.

The simulation procedure for each data set began with estimation of a reference set of von Bertalanffy growth parameters (L_∞, K, and t_0; Table 2) and their covariance matrix. Estimation was by nonlinear least-squares (Marquardt 1963) as implemented in the FISHPARM computer program (Prager et al. 1989). Parameter estimates for several data sets did not converge within the 150 iterations allowed (Table 2), but since the parameter estimates at that stage seemed to characterize mean growth well, the analysis was continued. To compute asymptotic weight (W_∞) from asymptotic length (L_∞), we assumed that weight was proportional to length and divided by 200 as a scaling factor. Because W_∞ appears in the yield-per-recruit equation as a constant only, its absolute magnitude was not important in this study, where the main concern is change in yield, rather than its central value.

The second step of the analysis was to estimate a reference value of $F_{0.1}$ based on management and growth parameters (Table 1; Table 2). We estimated $F_{0.1}$ with an iterative bisection method, chosen for robustness and simplicity. Because growth in some of the example data sets appeared quite linear, it was important that final estimates of $F_{0.1}$ did not imply substantial harvest beyond the oldest age present in the data. We verified that, under the postulated values of mortality, no more than 1% of an initial population would survive to the oldest observed age. This confirmed that estimates of $F_{0.1}$ were not based on artificially large size estimates for unrealistically old fish.

The next step in the analysis was simulation of the natural variability in aging and parameter estimation. For each data set, 1000 random triplets (3-vectors) of the growth parameters (L_∞, K, and t_0) were generated from a trivariate normal distribution whose mean vector was the reference set of growth parameter estimates and whose covariance matrix was their estimated covariance matrix. Trivariate normal random numbers were generated by the algorithm of Fishman (1978). A scatterplot of 1000 pairs of simulated values of K and L_∞ for American shad demonstrates the elliptical shape typical of bivariate normality (Figure 1a). In some data sets, the growth parameter estimates were very highly correlated (Figure 1b). When the estimates of K and L_∞ were correlated in the extreme ($r > 0.999$), the random number generator failed, and random triplets could not be generated. The simulation procedure was abandoned for these stocks, identified in Table 2. In the few instances where a negative growth rate (K) was generated, the vector of three growth parameters was discarded. In addition, we truncated the normal distribution at ±3.5 standard deviations to ensure numerical stability. Because of this, some simulations included slightly fewer than 1000 realizations.

The final step in the simulation was estimation of $F_{0.1}$ for each of the approximately 1000 vectors of growth parameters. This was done using the same bisection algorithm used for the reference value; the resulting $F_{0.1}$ and $Y_{0.1}$ were recorded for each vector. Analyses of the variability and bias of $F_{0.1}$ and $Y_{0.1}$ were then made for each data set. The bias was defined as the difference between the mean simulated $F_{0.1}$ and the reference value. To judge whether 1000 random vectors of growth parameters would adequately describe the results, several additional simulations were conducted using 5000 random vectors.

Results and Discussion

The growth data collected for these Chesapeake Bay species are very variable. In many cases, the range of sizes within an age is as large as the range of mean sizes for all ages. Despite this variability, many of the data sets can still define a model of mean size at age fairly well. However, not all of the data sets support unique estimation of a three-parameter model like the von Bertalanffy. This is indicated by the large coefficients of variation on the parameter estimates (Table 2) and the very high estimated correlations between parameters. This phenomenon was associated with a pattern of nearly linear growth in the observed data and fitted growth models.

The problems we encountered with apparent linear growth violate an important assumption in yield-per-recruit modeling, and such data should be analyzed cautiously. Of the 29 data sets that we originally analyzed, 12 exhibited this pattern, and 8 could not be examined by Monte Carlo simulation as a result. While this was not a study on the quality of age data collected in Chesapeake Bay, the topic deserves further investigation.

The relationship of simulated growth parameters to the resulting estimates of $F_{0.1}$ varied considerably. (Since the three growth parameters were highly correlated, this discussion is in terms of K only.) In the striped bass data, the estimated $F_{0.1}$ was positively correlated to K, but in the alosid data the opposite pattern was observed (Figure 2). The major difference between these groups is that the alosids have a ratio of M to K of somewhere between 10 and 100, while in striped bass, this ratio is believed to be around 3.

The relationship of the simulated values of K to those of $Y_{0.1}$ were very similar in all data sets, exhibiting a maximum at or near the reference value of K (Figure 3). The explanation for this is that the growth equation describes growth during the exploited years similarly, even with simulated growth parameters that are quite far from the reference values. In addition, the reference value of $F_{0.1}$ is close to F_{max}, so that the reference value of $Y_{0.1}$ is close to Y_{max}. Thus a simulated value of K any significant distance from the reference value implies an estimated value of yield lower than the reference value.

The observed frequency distributions of simulated values of $F_{0.1}$ and $Y_{0.1}$ included unimodal, bimodal and some highly skewed distributions. In most cases, the shapes of the distributions of $F_{0.1}$ and $Y_{0.1}$ were dissimilar. The distribution of $F_{0.1}$ for the striped bass data collected in 1983 is approximately symmetrical, while the distribution of $Y_{0.1}$ is skewed to the left (Figure 4). The distribution of $F_{0.1}$ for shad in 1987 is highly skewed to the left, while the distribution of $Y_{0.1}$ is bimodal (Figure 5).

For evaluation of bias and variability, we introduce two quantities, *relative bias* and *relative range*. The relative bias in $F_{0.1}$ is the bias divided by the reference estimate of $F_{0.1}$ and expressed as a percentage. A relative bias of 5%, e.g., means that the bias is 5% of the reference estimate of $F_{0.1}$. The relative range is the interquartile range (the 75th percentile minus the 25th percentile) divided by the reference estimate and expressed as a percentage. A relative range of 10% would indicate that half of the simulated values fell within ±5% of the reference estimate of $F_{0.1}$. Similar quantities were defined for $Y_{0.1}$.

The simulations using 5000 realizations of the growth parameter vector showed patterns of $F_{0.1}$ and $Y_{0.1}$ very similar to the simulations using 1000 sets. The irregularly shaped distributions of $F_{0.1}$ and $Y_{0.1}$ remained irregular with the larger number of realizations. In a few cases, the relative bias in $F_{0.1}$ or $Y_{0.1}$ decreased slightly. For example, the bias for the female shad (1987) data decreased from −7.3% to −6.7%, and the relative range decreased from 13.9% to 13.1%. However, these quantities increased slightly in other cases. Because the differences were inconsequential, the results of the longer simulations are not discussed further. We judged that they demonstrated the adequacy of 1000 realizations for the simulations.

The biases resulting from growth variability were surprisingly small, typically of the order of −0.02/yr in the estimate of $F_{0.1}$. The relative bias for all 21 data sets analyzed was negative, and usually smaller than 1% (Table 3), but had a highly skewed distribution (Figure 7a); the mean was −2.6%, and the median was −1.3%. The examples for which the growth parameters failed to converge were not associated with larger biases, and in fact are concentrated among the examples with little bias (Figure 7), although this distribution is likely to be due to chance.

In only one example was the relative bias in $F_{0.1}$ more extreme than −10%; this was the analysis of female shad from the Nanticoke river in 1989. This analysis, with a bias of −16.9%, exhibited several warning signs. During the simulation, the algorithm failed to converge on $F_{0.1}$ 37 times out of 1000. Although the corresponding trials were discarded (and thus did not affect the results directly), they suggest that the data are pathological. The relative range of simulated values of $F_{0.1}$ for these data was among the highest of all analyses, at 26.0%, and the histogram of these values (Figure 6) reveals an extremely skewed distribution. The simulation indicates the necessity for caution in developing management models that might use such growth data.

The second-largest bias (−7.7%) occurred in the analysis of 1988 data on female shad from the Nanticoke river. The relative range of 29.1%, the highest of all data sets, demonstrates that variability in growth can propagate through dynamic pool models to create a broad distribution of possible outcomes. Here, also, the simulations suggest a cautious approach to using these growth data for management purposes.

Compared to the very small biases, the variability in $F_{0.1}$ was larger but usually moderate (Table 3). The mean relative range was 10.2%; the median, 6.9%. The distribution was highly skewed, with four of the 21 analyses having a relative range over 20% (Figure 7b). For these stocks, half the simulated values of $F_{0.1}$ were more than 10% different from the reference estimate, still not a very large error.

The simulated estimates of $Y_{0.1}$ exhibited more bias and variability than the estimates of $F_{0.1}$ (Table 4). Biases were generally negative, and the examples whose growth parameters did not converge had larger relative biases and larger relative ranges (Figure 8). That bias in yield should be larger than bias in F is not unexpected, because most of the simulated growth vectors for a particular example resulted in estimates of yield lower than the reference value (Figure 3). The relationship of $F_{0.1}$ to the optimum yield was discussed earlier as being instrumental in this phenomenon.

The alosid stocks we examined, which have a very high ratio of M to K and a large spawning mortality, are unlikely candidates for management by $F_{0.1}$. The striped bass data probably provide more representative examples. In those examples, we saw very small relative biases in $F_{0.1}$ (less than 1%) and relatively small relative ranges (less than 20%). However, estimates of yield were biased downwards as much as 40% (the figures for alosids are worse). A reasonable question is how the simulation results are related to specific parameters such as the correlation between L_∞ and K or the ratio M/K. We are initiating additional simulations aimed at answering this question for a range of reasonable parameter values, but those simulations are not complete at this time.

It is likely that our methods certainly underestimate the actual bias and variability that would be expected in using these data for YPR modeling. This is because we considered only the variability in the growth data as collected, without considering such other sources of error and variability as gear selection and other non-random sampling or systematic aging errors. That the Beverton and Holt YPR model assumes weight proportional to length cubed is another source of potential error. Deviations from this assumption would probably increase the variance of the results.

Although the methods described here could readily be used to examine the effects of systematic errors, we looked only at variability. The reason for this was that we could estimate variability from the data at hand. Estimating the magnitude and structure of aging *errors* is best done by a validation study, a major undertaking. Nonetheless, it is logical to expect that aging error is more important than variability. The results of Lai and Gunderson (1987) indicate that substantial bias can be introduced into yield-per-recruit models by the presence of nonsymmetric aging error. Since aging error frequently involves systematic overaging or underaging, it is likely to be nonsymmetric. We expect that such errors would tend to bias estimates of $F_{0.1}$. Although we found that random variability caused only negative biases in $F_{0.1}$, there is no reason to believe that systematic errors cause only negative biases. This is important because negative bias implies a more conservative management scheme; conversely, positive bias in the estimate would suggest less conservative management. Another reason that the detection and correction of systematic errors is particularly important is that the bias and variability caused by systematic errors are not reduced by increased sampling intensity.

The technique presented in this study illustrates a method that could be used to examine similar issues, such as maintaining a particular level of eggs per recruit (Prager et al. 1987) or spawning stock per recruit (Goodyear 1989, Sissenwine and Shepherd 1987). Since the simulation approach is flexible, it could be modified to investigate the effects of systematic errors, random variability, or a combination of the two; the variability can follow any empirical or theoretical distribution. In addition, the method is not limited any particular biological reference point or management benchmark. We chose $F_{0.1}$ for this study as a representative measure in common use. However, it might not be appropriate, e.g., for a species exhibiting large discontinuous mortality, such as spawning mortality. In such a case, a numerical simulation model would be more appropriate, as it could incorporate the discontinuous mortality. For stocks at low population levels, a management benchmark related to reproductive success might be preferable to (or used in conjunction with) one based on yield. However, any model that uses growth parameters can be analyzed by the methods shown here. They can also be used together with aging validation studies to apply any growth-based management scheme with better awareness of the uncertainties involved and the likely outcomes.

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Table 1. Fixed biological and management parameters for the examples used in this study. Parameters are t_c, age at first capture; M, instantaneous rate of natural mortality; t_l, oldest age captured (here set arbitrarily high); t_r, age of recruitment to parent stock (not important to this study).

Species	t_c, yr	M, yr^{-1}	t_l, yr	t_r, yr
Alewife	3	1.1	50	2
American shad	2	1.1	50	1
Blueback herring	3	1.1	50	2
Striped bass	2	0.2	50	1

Table 2. Growth parameter estimates and their coefficients of variation for the examples used in this study.

Species/Sex/Location	Year	N	L_∞	CV	K	CV	t_0	CV	Notes
Alewife (f+m) Nanticoke	1989	435	519.4	0.977	0.041	1.922	−10.92	−0.075	1
Alewife (f) Nanticoke	1989	243	193.4	2.720	0.021	4.071	−13.21	−0.980	1,2
Alewife (m) Nanticoke	1989	192	531.7	3.578	0.028	6.629	−16.78	−2.120	1
Blueback (f+m) Nant.	1989	704	492.1	0.561	0.044	1.146	-10.40	-0.477	1
Blueback (f) Nant.	1989	361	673.4	1.144	0.027	2.330	-11.9	-0.681	1,2
Blueback (m) Nant.	1989	343	552.2	1.161	0.030	2.071	-13.59	-0.679	1,2
Shad (f+m) Upper Bay	1987	642	1587	1.000	0.044	1.411	−2.37	−0.534	1
Shad (f) Upper Bay	1987	216	1074	0.982	0.077	1.709	−2.989	−1.007	
Shad (m) Upper Bay	1987	426	1986	2.991	0.026	3.736	−4.139	−0.754	1
Shad (f+m) Upper Bay	1988	414	704.3	0.061	0.204	0.133	−0.185	−0.886	
Shad (f) Upper Bay	1988	152	3272	7.932	0.016	9.292	−4.689	−1.340	1
Shad (m) Upper Bay	1988	260	771.2	0.323	0.140	0.644	−1.088	−0.808	
Shad (m+f) Nanticoke	1988	159	555.5	0.049	0.422	0.232	0.844	0.495	
Shad (f) Nanticoke	1988	86	577.9	0.084	0.339	0.447	0.024	46.99	
Shad (m) Nanticoke	1988	73	488.3	0.053	0.551	0.304	0.975	0.516	
Shad (f+m) Nanticoke	1989	328	744.2	0.139	0.133	0.319	−1.415	−0.448	
Shad (f) Nanticoke	1989	93	780.1	0.635	0.079	1.608	−5.951	−1.095	
Shad (m) Nanticoke	1989	235	1584	1.733	0.028	2.316	−5.596	−0.526	2
Shad (m+f) Upper Bay	1989	177	4105	6.685	0.134	7.518	−3.380	−0.907	1,2
Shad (f) Upper Bay	1989	57	1452	3.345	0.042	5.005	−4.025	−1.965	2
Shad (m) Upper Bay	1989	120	3039	10.46	0.014	12.16	−5.447	−1.429	1,2
Striped bass Unspec.	1982	945	1937	0.091	0.051	0.133	−1.978	−0.084	
Striped bass Unspec.	1983	841	1423	0.046	0.076	0.084	−1.807	−0.087	
Striped bass Unspec.	1984	565	1529	0.234	0.067	0.341	−1.876	−0.169	
Striped bass Unspec.	1985	1101	2038	0.481	0.038	0.640	−3.481	−0.183	
Striped bass Unspec.	1986	778	701.5	0.054	0.286	0.134	−0.304	−0.455	
Striped bass Unspec.	1987	1994	1124	0.059	0.144	0.098	−0.609	0.115	
Striped bass Unspec.	1988	356	2341	0.513	0.046	0.617	0.484	0.420	
Striped bass Unspec.	1989	457	8043	1.198	0.012	1.281	0.106	1.650	1,2

NOTES:

1. Convergence criterion for growth parameter estimates not met after 150 iterations.
2. These data sets could not be analyzed by Monte Carlo simulation because of extreme correlation of the parameter estimates.

Table 3. Summary statistics on simulated values of $F_{0.1}$. The *reference estimate* of $F_{0.1}$ is based on the reference estimates (standard point estimates) of the von Bertalanffy growth parameters. The *relative IQ range* is the interquartile range divided by the reference estimate, multiplied by 100. The *relative bias* is the bias of the simulated values of $F_{0.1}$ divided by the reference estimate, multiplied by 100.

Species	Area(s)	Sex(es)	Year	Reference estimate of $F_{0.1}$	Mean simulated $F_{0.1}$	Relative IQ range (%)	Relative bias (%)
Alewife*	Nanticoke	FM	1989	2.063	2.005	3.7	−2.8
Alewife*	Nanticoke	M	1989	2.148	2.114	2.4	−1.6
American Shad	Upper Bay	F	1987	1.532	1.420	13.9	−7.3
American Shad*	Upper Bay	M	1987	1.570	1.560	3.8	−0.6
American Shad*	Upper Bay	FM	1987	1.359	1.333	5.4	−1.9
American Shad	Nanticoke	F	1988	1.213	1.120	29.1	−7.7
American Shad	Nanticoke	M	1988	0.924	0.891	23.9	−3.5
American Shad	Nanticoke	FM	1988	0.883	0.866	20.3	−1.9
American Shad*	Upper Bay	F	1988	1.601	1.590	5.1	−0.7
American Shad	Upper Bay	M	1988	1.279	1.233	7.3	−3.6
American Shad	Upper Bay	FM	1988	1.091	1.088	4.1	−0.3
American Shad	Nanticoke	F	1989	1.881	1.563	26.0	−16.9
American Shad	Nanticoke	FM	1989	1.354	1.336	7.0	−1.3
Blueback herring*	Nanticoke	FM	1989	2.054	2.006	2.7	−2.3
Striped Bass	Unspecified	FM	1982	0.101	0.101	3.0	−0.4
Striped Bass	Unspecified	FM	1983	0.115	0.115	2.6	−0.4
Striped Bass	Unspecified	FM	1984	0.110	0.109	11.8	−0.6
Striped Bass	Unspecified	FM	1985	0.110	0.109	14.5	−0.6
Striped Bass	Unspecified	FM	1986	0.180	0.179	7.2	−0.3
Striped Bass	Unspecified	FM	1987	0.105	0.105	3.8	−0.2
Striped Bass	Unspecified	FM	1988	0.072	0.072	16.7	−0.0

* An asterisk indicates that the reference growth parameter estimates for that data set did not converge.

Table 4. Summary statistics on simulated values of $Y_{0.1}$. The *reference estimate* of $Y_{0.1}$ is based on the reference estimates (standard point estimates) of the von Bertalanffy growth parameters. The *relative IQ range* is the interquartile range divided by the reference estimate, multiplied by 100. The *relative bias* is the bias of the simulated values of $Y_{0.1}$ divided by the reference estimate, multiplied by 100.

Species	Area(s)	Sex(es)	Year	Reference estimate of $Y_{0.1}$	Mean simulated $Y_{0.1}$	Relative IQ range (%)	Relative bias (%)
Alewife*	Nanticoke	FM	1989	26,870	12,021	73.8	−55.3
Alewife*	Nanticoke	M	1989	26,840	11,342	72.9	−57.7
American Shad	Upper Bay	F	1987	76,330	33,928	72.9	−55.6
American Shad*	Upper Bay	M	1987	59,350	26,992	73.1	−54.5
American Shad*	Upper Bay	FM	1987	52,280	24,940	72.6	−52.3
American Shad	Nanticoke	F	1988	59,260	45,211	44.2	−23.7
American Shad	Nanticoke	M	1988	32,980	29,242	28.7	−11.3
American Shad	Nanticoke	FM	1988	33,890	31,525	22.7	−7.0
American Shad*	Upper Bay	F	1988	85,250	39,708	71.7	−53.4
American Shad	Upper Bay	M	1988	48,600	31,532	50.9	−35.1
American Shad	Upper Bay	FM	1988	42,950	41,867	6.4	−2.5
American Shad	Nanticoke	F	1989	111,000	49,249	73.8	−55.6
American Shad	Nanticoke	FM	1989	48,180	41,836	17.9	−13.2
Blueback herring*	Nanticoke	FM	1989	23,730	12,159	71.0	−48.8
Striped Bass	Unspecified	FM	1982	749,100	728,076	3.8	−2.8
Striped Bass	Unspecified	FM	1983	694,000	687,240	1.9	−1.0
Striped Bass	Unspecified	FM	1984	676,200	567,883	21.3	−16.0
Striped Bass	Unspecified	FM	1985	650,100	395,772	58.6	−39.1
Striped Bass	Unspecified	FM	1986	524,900	516,540	3.5	−1.6
Striped Bass	Unspecified	FM	1987	556,200	549,626	3.8	−1.2
Striped Bass	Unspecified	FM	1988	509,000	311,478	58.0	−38.8

* An asterisk indicates that the reference growth parameter estimates for that data set did not converge.

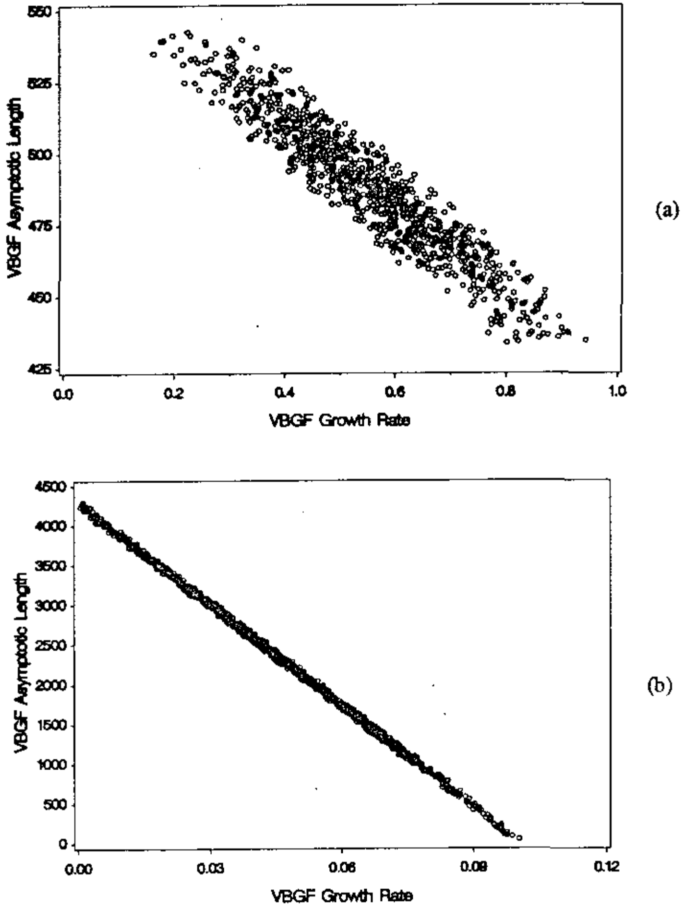

Figure 1. Generated pseudorandom values of von Bertalanffy parameters K (growth rate) and L_∞ (asymptotic length) for two example data sets. (a) Data on male shad data from the Nanticoke River, 1988. The scatterplot exhibits the large negative correlation typical of growth parameter estimates and the ellipsoid shape characteristic of a bivariate normal distribution. (b) Data on striped bass, 1988. The scatterplot shows the extremely large negative correlation that was observed during parameter estimation for this data set.

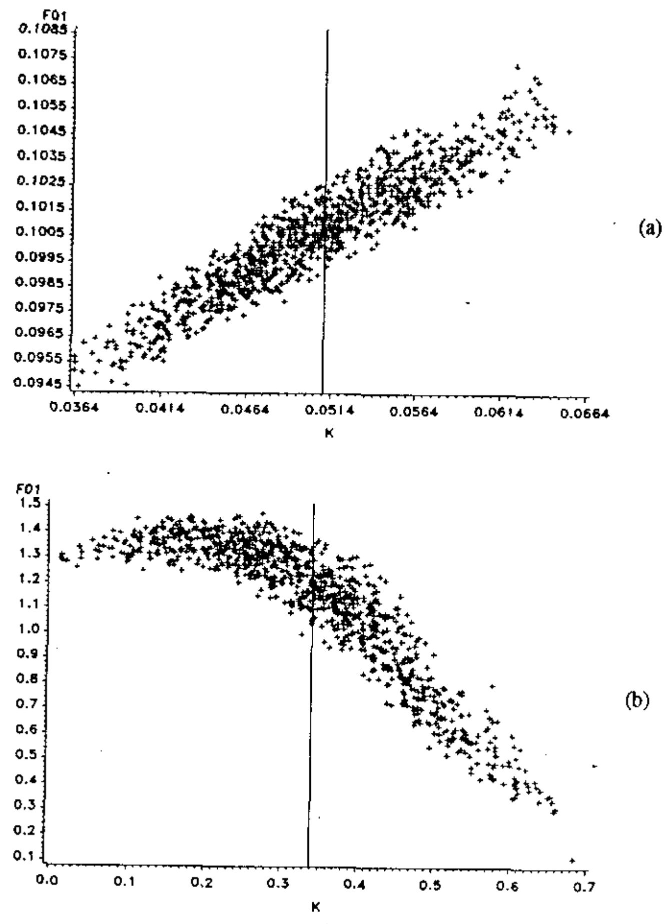

Figure 2. Relationship of estimated $F_{0.1}$ to simulated values of K in two example data sets. (a) Striped bass, 1982. (b) Female American shad from the Nanticoke River, 1988. The vertical lines mark the reference values of K.

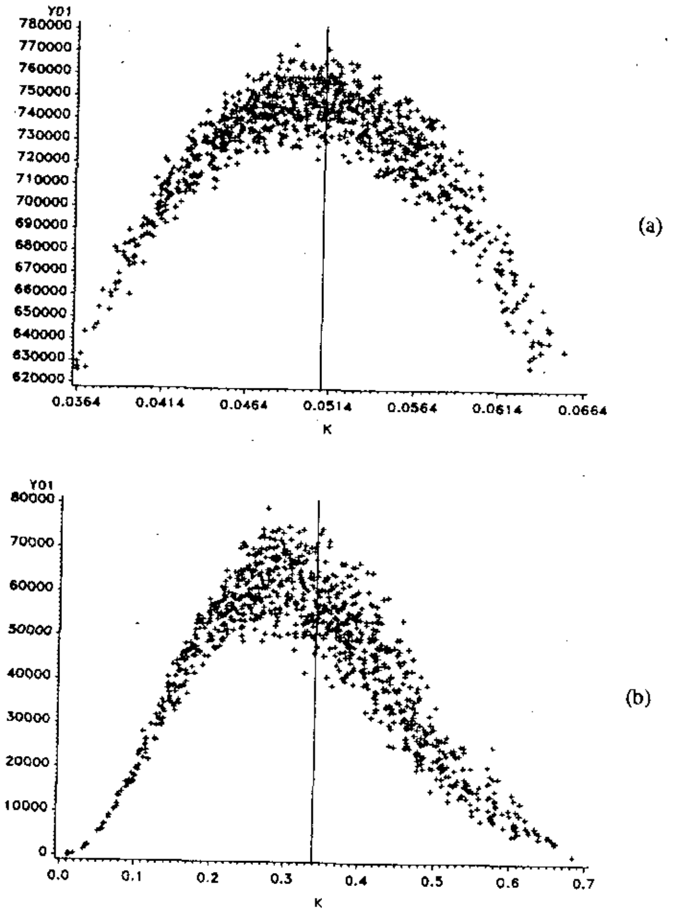

Figure 3. Relationship of estimated $Y_{0.1}$ to simulated values of K in two example data sets. (a) Striped bass, 1985. (b) Female American shad from the Nanticoke River, 1988. The vertical lines mark the reference values of K.

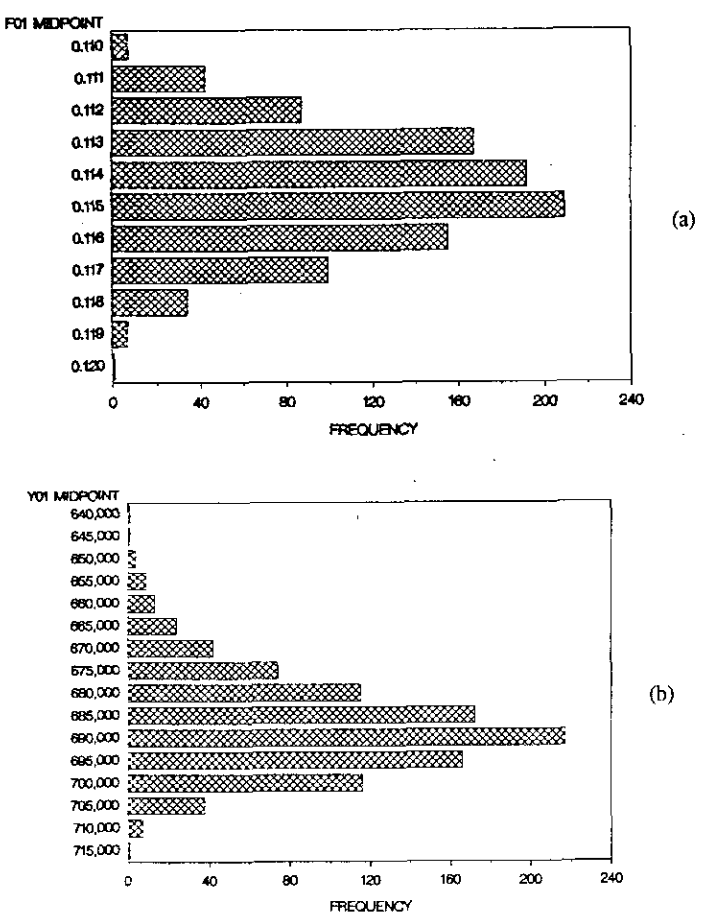

Figure 4. Histograms of simulation results for data on striped bass, 1983. (a) Simulated estimates of $F_{0.1}$ computed from trivariate normal pseudorandom vectors of L_∞, t_0, and K and the management parameters in Table 1. (b) Simulated estimates of $Y_{0.1}$, computed from the corresponding $F_{0.1}$ estimates and the Beverton-Holt (1957) yield-per-recruit model.

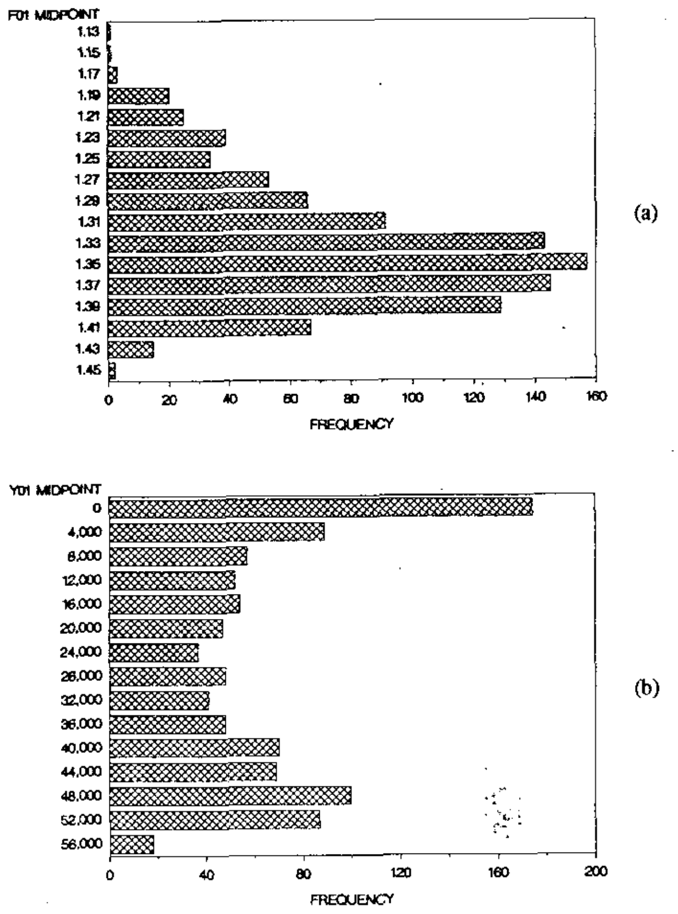

Figure 5. Histogram of simulation results for data on American shad collected in upper Chesapeake Bay,1987. (a) Simulated estimates of $F_{0.1}$ computed from trivariate normal pseudorandom vectors of L_∞, t_0, and K and the management parameters in Table 1. (b) Simulated estimates of $Y_{0.1}$, computed from the corresponding $F_{0.1}$ estimates and the Beverton-Holt (1957) yield-per-recruit model.

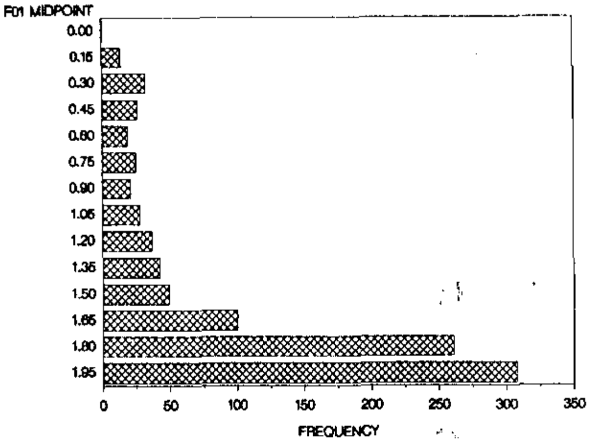

Figure 6. Histogram of $F_{0.1}$ values for female American shad collected in the Nanticoke River, 1989, revealing an extremely skewed distribution.

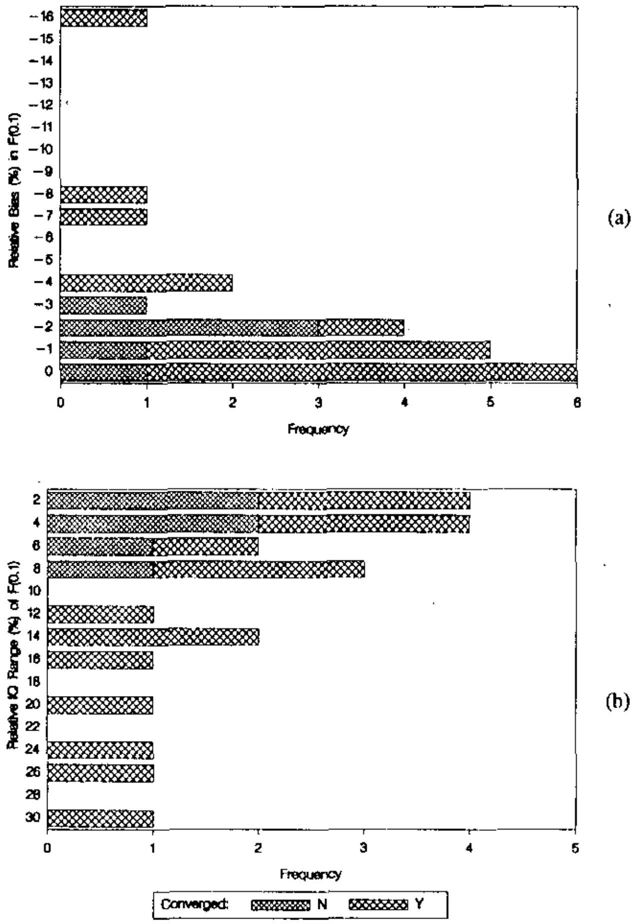

Figure 7. (a) Relative bias and (b) relative range in simulated values of $F_{0.1}$ for the 21 growth data sets analyzed by Monte Carlo simulation. Relative bias is the bias divided by the reference value of $F_{0.1}$; relative range is the interquartile range divided by the reference value. Shading indicates whether the reference von Bertalanffy growth parameter estimates converged or not.

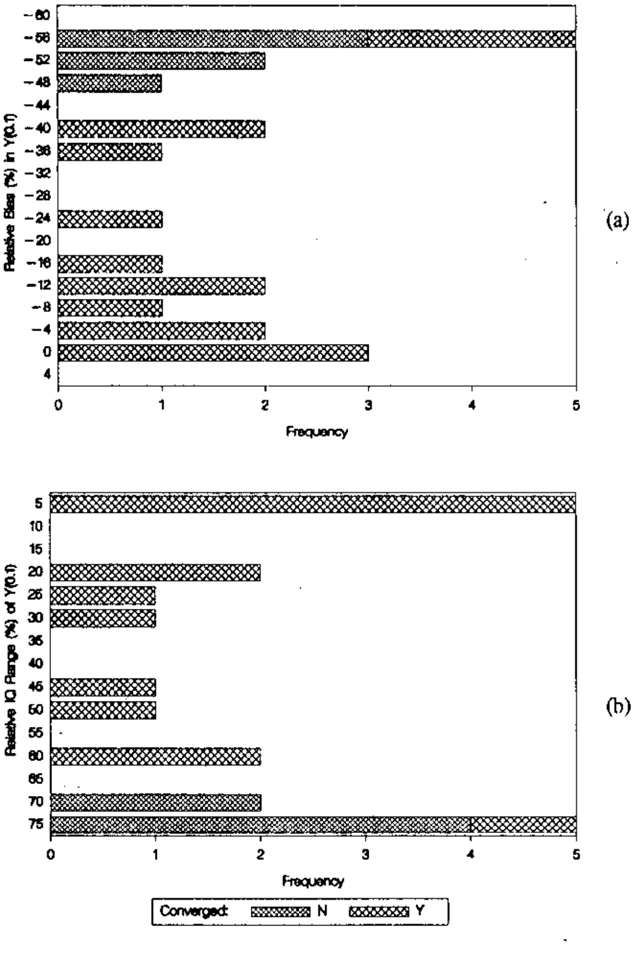

Figure 8. (a) Relative bias and (b) relative range in simulated values of $Y_{0.1}$ for the 21 growth data sets analyzed by Monte Carlo simulation. Relative bias is the bias divided by the reference value of $Y_{0.1}$; relative range is the interquartile range divided by the reference value. Patterns indicate whether the reference von Bertalanffy growth parameter estimates converged or not.