Effect of Seasonal Recruitment on Bias of the Beverton–Holt Length-Based Mortality Estimator

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Abstract.—The Beverton and Holt mortality estimator is a length-based formulation often applied to tropical fish stocks. Although constant uniform recruitment of fish to the exploitable phase is an important condition of its derivation, the robustness of the estimator when this assumption is violated has never been studied. This is important because evidence from the literature shows that in the tropics (i.e., Hawaii) both recruitment and spawning are distinctly seasonal events. Thus, to study properties of the estimator when recruitment is variable, a simple model with seasonal reproduction was developed and analyzed. I show that if age is measured discretely in units equal to the period of the recruitment function, typically 1 year, the age distribution is stationary. The model is extended to length distributions and used as a basis for Monte Carlo simulation of the estimator. Results show that, seasonally, the time of sampling has a major effect on the relative bias of mortality estimates. Bias is negative during periods of increasing recruitment and vice versa, whereas no bias exists at times of maximal and minimal recruitment. Likewise, as the underlying mortality rate increases, bias becomes more severe. When multiple length-frequency samples are drawn and the data and estimates are aggregated, relatively little bias is evident. These results suggest that, when the estimator is used in situations in which recruitment is periodic, it may be better to obtain many small samples than a single large sample, unless some prior information exists concerning the form of the recruitment function.

There has been a resurgence of interest in length-based methods for fishery stock assessment (Jones 1981; Pauly and Morgan 1987). In many situations, these techniques represent an attractive alternative to more conventional stock assessments (Pauly 1982), especially for tropical fishes whose ages are difficult to determine.

In one of the earliest length-based formulations, Beverton and Holt (1956) derived an equation for estimating the total instantaneous mortality (Z) of a fish stock under exploitation. The specific conditions under which their equation is derived are (1) individual fish grow according to a deterministic von Bertalanffy growth curve (i.e., there is no variation among fish within the population in length at age); (2) all fish greater than a minimum length, l_c, are equally vulnerable to the fishing gear and experience a constant total mortality rate (i.e., there are no age- or size-specific differences in mortality); and (3) recruitment to the exploitable stock occurs at a constant uniform rate. When these three conditions are satisfied, mortality can be estimated as

$$Z = K \frac{(L_\infty - \hat{l})}{(\hat{l} - l_c)};$$ (1)

K and L_∞ are the growth coefficient and asymptotic length, respectively, of the equation, and $\hat{l}$ is the mean length of fish in the catch greater than l_c. Others have investigated and extended this finding (Ssentongo and Larkin 1973; Powell 1979; Wetherall et al. 1987). The estimator has often been used to estimate mortality of fishes in tropical environments (e.g., Munro 1983; Brouard and Grandperrin 1984; Polovina and Ralston 1986), where spawning is more seasonally protracted than in temperate and boreal climates.

In this paper, I investigate the bias of the Beverton–Holt mortality estimator (equation 1) when it is applied under conditions that depart from those for which it was intended. In particular, I relax the assumption of constant uniform recruitment because, contrary to conventional wisdom, most tropical species do not spawn and recruit uniformly throughout the year (Thresher 1984).

Seasonality of Spawning and Recruitment in Hawaii

In a recent summary of spawning and recruitment patterns of Hawaiian fishes, Walsh (1987)

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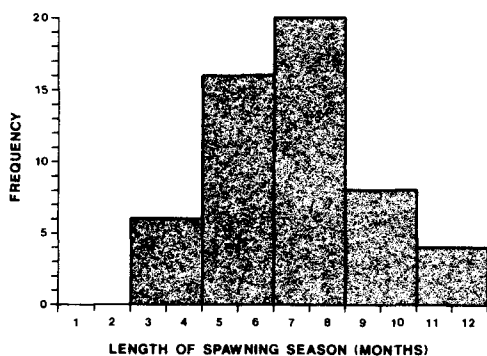
190

FIGURE 1.—Frequency distribution of the duration of seasonal spawning by fishes in Hawaii (data from Walsh 1987).

tabulated the results of 54 studies involving 48 taxa. In the subtropical Hawaiian environment, spawning lasts for 3–12 months but the average reproductive season is 7 months (Figure 1). Generally, this life history pattern is incompatible with recruitment at a constant uniform rate because larval periods for these fishes typically range from 0.5 to 2.5 months (Brothers et al. 1983; Brothers and Thresher 1985).

This conclusion is further confirmed by the seasonal pattern of recruitment of Hawaiian fishes (Walsh 1987). The frequency with which species recruit within each month varies over the year (Figure 2). For example, two species recruit during January, five during February, and so on. In Hawaii, most species recruit during the spring and summer months, March–August. Overall peak recruitment occurs in June and July. Note that no distinction is drawn between recruitment to reefs and recruitment to offshore exploitable populations, despite the often substantial difference in timing between the two. The greater this difference, the more likely recruitment to the exploitable phase can be approximated by a uniform continuous distribution, even if recruitment to the reef is highly seasonal.

These results demonstrate that reproduction and recruitment of fishes in Hawaii are distinctly seasonal events. Recruitment (R) is cyclic and, as a first approximation, can be reasonably modeled by a simple cosine function (solid line and equation in Figure 2) for which time (t) is measured in years.

Because the constant uniform recruitment assumption is violated, application of equation (1) to length-frequency samples of Hawaiian fishes would constitute a misuse of the method. Nonetheless, the method has been used frequently in tropical and subtropical stock assessments (see above). In such cases, an obvious question arises: To what extent
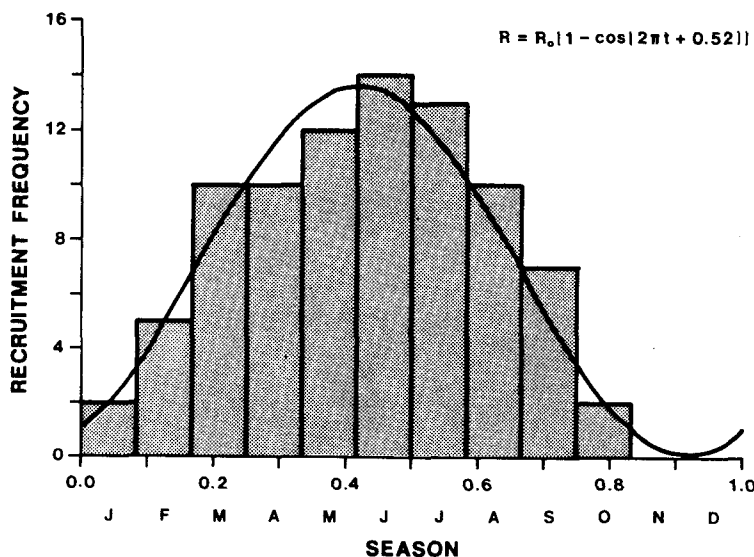

FIGURE 2.—Seasonal frequency of recruitment $(R$, species per month) for fishes in Hawaii (data from Walsh 1987). The solid line represents the fit of the cosine function to the frequency data; R_0 is a recruitment scaling factor; t is time in years.

does the time of sampling affect mortality estimates? It also is unclear how one should proceed to analyze multiple length-frequency samples taken at different times within the recruitment cycle.

Simple Population Model with Seasonal Recruitment

Here, I alter the hypothetical conditions specified by Beverton and Holt (1956) and develop a model that incorporates a form of seasonal recruitment. To simplify the model, population size is normalized to R_0, the recruitment scaling factor (Figure 2). I therefore define $N(x,t)$ as the relative number of individuals age x alive at time t. Both x and t are continuous variables measured in years. I assume that the population experiences a constant total instantaneous mortality Z, so

$$N(x + 1, t + 1) = N(x,t) \exp(-Z).$$

Moreover, I define the age at the time of recruitment to be 0.0 and specify that the rate of recruitment at time t is

$$N(0,t) = 1 - \cos 2\pi t.$$

The rate is highest midway through the annual cycle, whenever the decimal portion of t equals one-half. Conversely, when t is a whole number at the beginning (or end) of the year, recruitment goes to zero. The population undergoes a standardized seasonal range in recruitment of 0.0–2.0. This natality function lacks the phase-shift parameter (0.52) of Figure 2, also for the sake of simplicity.

When the information specified by the mortality and seasonal recruitment function is combined, it follows that

$$N(x,t) = [1 - \cos 2\pi(t - x)] \exp(-Zx); \quad (2)$$

i.e., the scaled number of individuals of age x alive at time t represents the remaining fish that recruited at time $t - x$ and survived x units of time. Equation (2) provides the basis for examining the effect of seasonal recruitment on mortality estimates. In particular, the relative population size at any time t, $N(t)$, is given by

$$N(t) = \int_0^\infty N(x,t) \, dx$$

$$= \frac{1}{Z} - \frac{Z \cos 2\pi t + 2\pi \sin 2\pi t}{Z^2 + 4\pi^2},$$

so that population size depends only on Z and t. It is easily shown that as Z increases, the maximum

in numbers occurs earlier in the annual cycle, and the magnitude of population oscillation increases. Both results are consistent with intuition.

Consider now the age distribution at time t. The population size is $N(t)$, of which $N(x,t)$ are age x. Therefore, the probability density of age x at time t is

$$P_{x,t} = \frac{N(x,t)}{N(t)} = f(x,t,Z).$$

Similarly, the distribution function of age given time is

$$P(X < x_1 | t) = \int_0^{x_1} \frac{N(x,t)}{N(t)} dx$$

$$= 1 - \frac{N(t - x_1)}{N(t)} \exp(-Zx_1). \quad (3)$$

This result leads to a remarkable conclusion if fish age is measured in integer values of years, as is commonly practiced. By convention, the true decimal age of fish classified into the integer age-class i is greater than or equal to i, but less than $i + 1$, i.e., increments of age occur on anniversaries of the birth date. Under these conditions, the age distribution is stationary (Figure 3). Note that the ratio $N(t - x_1)/N(t)$ equals 1.0 for all integer x_1. The effect is simply to lag by x_1 discrete cycles. In this special case, the distribution function reduces to

$$P(X < x_1) = 1 - \exp(-Zx_1).$$

Of course, age stationarity depends strongly on identical annual recruitments, certainly the least realistic aspect of the model developed here. For example, the interannual range in recruitment of Hawaiian fishes can be as great as twentyfold (Walsh 1987).

Because the probability distribution for discrete ages is ergodic, it does not matter when a sample is taken in the cycle; all samples will reflect the same age structure. Therefore, in the absence of aging errors, mortality estimates derived from the analysis of age-frequency data (e.g., Chapman and Robson 1960; Robson and Chapman 1961) are unaffected by the cyclical pattern of recruitment modeled here.

Simulated Length Samples

Simulated length data, obtained by transforming ages with an inverted von Bertalanffy growth curve, are now considered. In structuring the simulations, several steps were followed. First, for each length-frequency sample generated, a
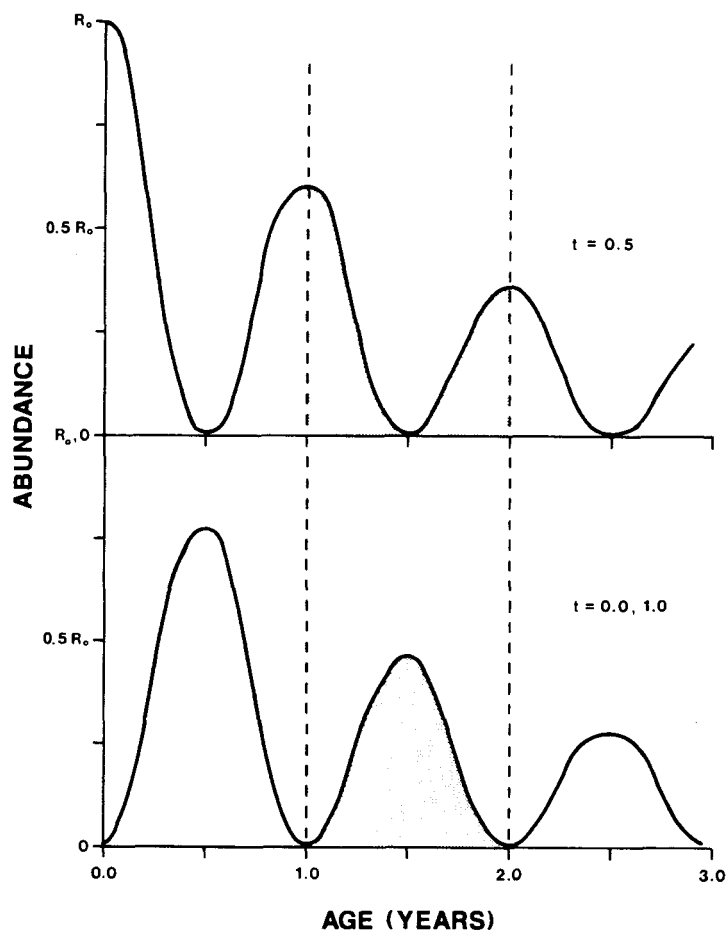
FIGURE 3.—Age-frequency distributions sampled at the beginning (below) and middle (above) of the seasonal recruitment cycle. The numbers of fish of age 1 are represented by the shaded areas under the curves between 1.0 ≤ age < 2.0. In either case, the proportion of fish of age 1 is defined by the ratio of the shaded area to the total area under the curve and does not change with time. R_0 is standardized population size; t is time in years.

value of t was randomly selected from a uniform distribution over the range 0.00–1.00 to represent the specific seasonal time of sampling. Next, the age-distribution function formulated in equation (3) was used to define population age structure. Age thus was expressed as a continuous variable. A random age sample of size N was developed by use of the inverse transformation method (Naylor et al. 1966), wherein N uniform random deviates drawn over the range 0.00–1.00 were used to fix values from the age-distribution function of the model population. Numerical solution to the inverse of equation (3) then provided a random age draw from the popula-

tion. Finally, the randomly selected ages were transformed to lengths by use of a deterministic inverted von Bertalanffy growth equation in which $K = 0.20$ and $t_0 = -0.1$. Depending on the simulation in question (see below). The L_∞ parameter was set to either 20.5 or 50.5. Length-frequency distributions were developed by rounding all lengths to the nearest integer and aggregating the data into length classes. The result was to draw a length sample from the model population illustrated in Figure 4. Single and multiple length-frequency distributions were then analyzed with equation (1) to estimate the underlying mortality rate.
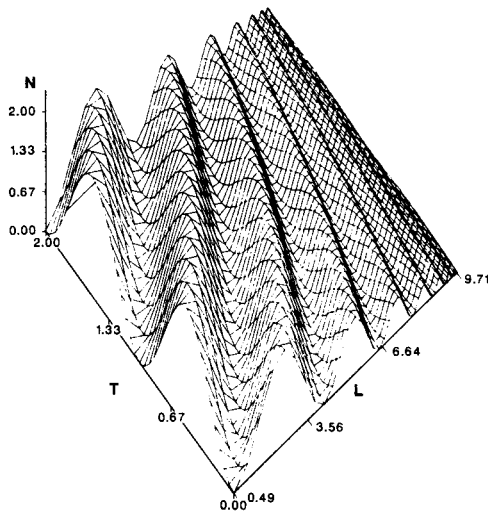
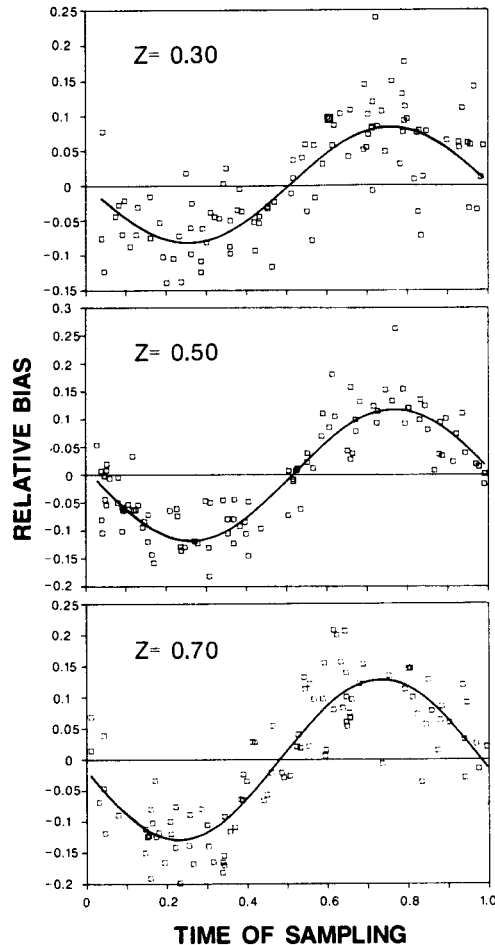FIGURE 4.—Three-dimensional representation of seasonal (T) change in abundance (N) of fish at length (L).

FIGURE 5.—The effect of sampling time and instantaneous mortality (Z) on the relative bias of estimates obtained from the analysis of single length-frequency samples. The unit of sampling time is a year.

To examine the effect of sampling time (t) on mortality estimates, Monte Carlo simulations were performed by using 100 samples of size $N = 500$ at each of three different mortality levels ($Z = 0.30$, 0.50, and 0.70 per year). The relative bias, defined as $(\hat{Z} - Z)/Z$, was calculated for each sample estimation and then plotted against t (Figure 5).

The extent of relative bias arising from application of the Beverton–Holt mortality estimator (equation 1) to populations characterized by seasonal recruitment depends on the seasonal time of sampling. In the situation modeled, a negative bias prevailed in estimations completed during the first half of the year, and a positive bias prevailed during the latter half. Roots, at which time no bias exists, occurred at approximately the beginning and middle of the year.

The data were fitted to a sine wave to examine the effect of mortality on relative bias (RB). The model fitted was RB $= A\sin(2\pi t + \theta)$; A represents amplitude and θ the phase shift. The result (Table 1) is that, as mortality increases, the amplitude of seasonal variation in bias increases. Thus, the greater the underlying mortality, the more serious the consequences of violating the constant uniform recruitment assumption. However, for phase shift, the pattern is not so clear. Over the range $Z = 0.30$–0.70 per year, θ approximated π (3.1416), in which case the roots of the

equation equal 0.00 and 0.50. For samples taken at these times, mortality estimates lack bias. Because these times coincide with periods of minimal and maximal recruitment (see the earlier development of the natality function), it may be possible to design a length-frequency sampling program to overcome the bias if the recruitment function is specified.

Monte Carlo simulations also were performed on multiple length-frequency samples to examine the effects of four factors on the propagation of relative bias in the Beverton–Holt mortality estimator. These factors were (a) the total instanta-

TABLE 1.—The effect of mortality on the seasonal expression of relative bias in mortality. The data presented in Figure 5 were fitted to a sine wave model (solid lines in Figure 5) and the amplitude (A) and phase shift (θ) parameters were estimated (standard errors of the estimates are in parentheses). The error mean square (MSE) and reduction in total sums of squares are also provided.

Mortality (Z)	A	θ	MSE	r^2
0.30	0.0814 (0.0068)	3.1062 (0.0962)	0.00260	0.594
0.50	0.1175 (0.0060)	3.0523 (0.0497)	0.00175	0.795
0.70	0.1287 (0.0071)	3.2651 (0.0567)	0.00260	0.769

neous mortality, (b) the number of length categories to which the data are assigned, (c) the manner in which a year's sampling is allocated, and (d) the method of condensing the results.

The effect of mortality on relative bias was examined by simulating the same three levels of Z: 0.3, 0.5, and 0.7. The number of length categories (NCAT) was varied by altering L_∞ (see above) and rounding to the nearest integer. All length data, therefore, were classified into either 20 or 50 categories (assignments to the 0 length interval were rejected). The allocation of sampling effort was studied by varying the number of samples (NSAMP) drawn in a year. Either two samples of size 500 were drawn at randomly selected times t, or five samples of size 200 were taken. In either case, the annual sampling effort was $N = 1,000$. Finally, the data were analyzed differently to examine the effect of two methods of condensing the results (COND): averaging or

pooling. For the former, each length-frequency distribution obtained was analyzed with equation (1), and the multiple values of $\hat{Z}$ were averaged to estimate the underlying mortality. In the latter, the data from the multiple samplings were pooled before a single analysis was performed. In all cases, the growth parameters K and L_∞ were specified without error (see Majkowski 1982 for discussion).

All four factors were simulated in a balanced design. Because there were three levels of Z, two levels of NCAT, two levels of NSAMP, and two levels of COND, there were 24 treatment combinations. Each then was replicated 50 times, and the relative bias was calculated. Thus, 1,200 annual samplings of size 1,000 were simulated, and the results were analyzed by a fully interactive factorial analysis of variance (ANOVA). Replication of samples 50 times produced an average coefficient of variation for the standard error of the mean equal to 0.76%. This level of precision is sufficient to detect meaningful levels of bias in mortality estimates.

Tables 2 and 3 summarize the findings of the ANOVA with respect to relative bias, the dependent variable. The fully interactive factorial model was significant, but only reduced the total sums of squares by 9.4%. Of the four main effects examined, only Z and NCAT had a significant effect. The treatment mean relative biases for these two factors became more severe as mortality and the number of length classes increased. In both cases, mortality was underestimated, but only slightly.

TABLE 2.—Factorial analysis of variance to examine the effects of mortality (Z), number of length categories (NCAT), number of annual samples (NSAMP), averaging or pooling results (COND), and all interactive terms on the relative bias of the Beverton and Holt (1956) mortality estimator. Asterisks denote $P < 0.05*$ or $P < 0.01**$.

Source	df	Mean square	F	Probability of a greater F
Model	23	0.01556	5.28**	0.0001
Error	1,176	0.00295		
Z	2	0.02613	8.86**	0.0002
NCAT	1	0.26380	89.44**	0.0001
COND	1	0.00683	2.31	0.1284
NSAMP	1	0.00223	0.76	0.3846
$Z \times$ NCAT	2	0.00817	2.77	0.0632
$Z \times$ COND	2	0.00041	0.14	0.8703
$Z \times$ NSAMP	2	0.00117	0.40	0.6737
NCAT $\times$ COND	1	0.00000	0.00	0.9808
NCAT $\times$ NSAMP	1	0.01171	3.97*	0.0465
COND $\times$ NSAMP	1	0.00087	0.29	0.5874
$Z \times$ NCAT $\times$ COND	2	0.00000	0.00	0.9986
$Z \times$ NCAT $\times$ NSAMP	2	0.00032	0.11	0.8972
$Z \times$ COND $\times$ NSAMP	2	0.00003	0.01	0.9916
NCAT $\times$ COND $\times$ NSAMP	1	0.00000	0.00	0.9723
$Z \times$ NCAT $\times$ COND $\times$ NSAMP	2	0.00000	0.00	0.9996

TABLE 3.—Treatment means of the four main effects in the analysis of variance and the single significant interactive term (NCAT×NSAMP).

Factor[a]	Level	Mean relative bias (%)
Z	0.3	−0.83
	0.5	−2.04
	0.7	−2.37
NCAT	20	−0.27
	50	−3.23
COND	Averaged	−1.51
	Pooled	−1.99
NSAMP[b]	2 (500)	−1.88
	5 (200)	−1.61
NCAT×NSAMP	20, 2 (500)	−0.09
	50, 2 (500)	−3.68
	20, 5 (200)	−0.44
	50, 5 (200)	−2.78

[a]Z is mortality, NCAT is number of length categories, COND is method of condensing results, and NSAMP is number of annual samples.
[b]Number of samples (sample size).

For none of the 24 treatment combinations did the mean relative bias exceed 5.2%. Due to the large number of F tests in Table 2, the single significance ($P = 0.05$) of an interaction term (NCAT*NSAMP) probably was due to a type-I error. In the absence of real differences the probability of such an error in 15 tests is 0.54; in 13 tests, it is 0.49.

Discussion

The results presented here show that the integer-age probability distribution, developed under a model of seasonal recruitment (Figure 2), is stationary. Although the cosine natality equation represents only one of many potential recruitment functions, the conclusion is more general. As long as (a) recruitment is qualitatively and quantitatively the same from year to year and (b) age is measured discretely in some multiple of the recruitment period, the population age structure will remain stationary in spite of reproductive seasonality (see Figure 3; Keyfitz 1968).

As suggested by Munro (1982), the seasonal time of sampling has a major influence on the relative bias of mortality estimates calculated from samples taken at only one time of the year (Figure 5). This effect is due to seasonal variation in the mean size (l) of individuals in the population (Ebert 1973). The problem may be overcome by sampling at times when recruitment is either maximal or minimal, but to do so requires additional information to specify the recruitment function. Furthermore, the generality of this sampling strategy is open to some question and needs more work.

Still, the average of several mortality estimates obtained by sampling at random times within the year showed little bias. Under these conditions, Monte Carlo simulations demonstrated that the Beverton–Holt (1956) mortality estimator is fairly insensitive to violation of the constant uniform recruitment assumption. Over a broad range of simulated conditions, the maximum relative bias observed was −5.2% of the underlying parameter, and the average relative bias was only −2.1%. Practically speaking, these biases are negligible. The simulations also showed that mortality estimates from several seasonally distinct length-frequency distributions were equivalent, whether individual estimates were averaged or the data were pooled. Similarly, no bias effect was evident when the sampling structure was altered to represent a few large samples or many small ones.

These findings indicate that, if equation (1) is used to estimate the mortality of a population that experiences substantial seasonal variation in recruitment, many small length samples pooled together may be preferable to a single large sample. Pooling of data obtained from throughout the year results in an integrated representation of the average size structure. Moreover, when a field sampling program is planned, advance knowledge of the recruitment function provides the investigator with information useful in determining the optimum times for sampling.

Although the results presented here show that the Beverton–Holt mortality estimator is robust with respect to seasonal recruitment, other difficulties may well arise, due either to sampling error or to violation of one or more of the remaining assumptions. For example, Majkowski (1982) performed a sensitivity analysis to study the effects of misspecifying the four parameters of equation (1). Perturbation of the L_∞ parameter by some percentage δ, for example, alters Z by roughly 2δ. The formula is even more sensitive to changes in l and l_c. Similarly, violations of other assumptions of the model (i.e., constant total mortality rate, constant selectivity, and deterministic von Bertalanffy growth) likely would bias estimates of Z. Because the robustness of the estimator to these types of departures has yet to be examined, caution is recommended with the estimator's use.

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