

Estimating Mortality from Mean Length Data in Nonequilibrium Situations, with Application to the Assessment of Goosefish

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Abstract.—The Beverton–Holt length-based mortality estimator has received widespread use primarily due to its applicability in data-limited situations. The mean length of animals that are fully vulnerable to the sampling gear can be used to estimate total mortality from basic growth parameters and a known length at first capture. This method requires equilibrium conditions because the mean length of a population will change only gradually after a change in mortality. In this study, we derive the transitional behavior of the mean length statistic for use in nonequilibrium conditions. We investigate conditions affecting the reliability of the Beverton–Holt results and then develop a new procedure that allows a series of mortality rates to be estimated from mean length data representing nonequilibrium conditions in multiple years. We then examine an assessment of goosefish *Lophius americanus* that was criticized for its use of the Beverton–Holt estimator under nonequilibrium conditions. Using data from the 1963–2002 National Marine Fisheries Service annual fall groundfish surveys off the northeastern United States and assuming a single change in total mortality, we used the maximum likelihood method to estimate that the total mortality of goosefish in the southern assessment region increased from 0.31 to 0.60 per year in 1977. Estimates of the new mortality rate made three or more years after the change were relatively stable and only ranged from 0.55 to 0.71 per year, while estimates from the standard Beverton–Holt approach ranged from 0.37 to 1.1 per year. The results for goosefish in the northern assessment region showed that total mortality changed from 0.14 to 0.29 per year in 1978 and then to 0.55 per year in 1987. The new nonequilibrium estimator allows a change in mortality to be characterized reliably several years faster than would occur with the use of the Beverton–Holt estimator.

Baranov (1918, cited in Ricker 1975) was apparently the first to deduce that the equilibrium mean length in a fish population is inversely related to the mortality rate experienced by the population. Beverton and Holt (1956, 1957) observed the same thing for a more realistic situation in which length is an asymptotic, rather than linear, function of time. They also derived an expression for estimating the total instantaneous mortality rate (Z) from the mean length (\bar{L}).

The Beverton–Holt mortality estimator has received widespread use, especially in data-limited situations, because the only required information is the von Bertalanffy growth parameters (K and L_∞), the so-called length of first capture (L_c , i.e., the smallest size at which animals are fully vulnerable to the fishery and to the sampling gear), and the mean length of animals larger than L_c .

The Beverton–Holt mortality estimator is based on the assumption of equilibrium conditions. Hilborn and Walters (1992:426) presented a graph that showed the transitional behavior of a similar estimator when the population experiences a change in total mortality to a higher level. Essentially, if the mortality estimator is

applied continually to mean length data over time, the resulting estimates will show a gradual increase over time and will approach the true (new) value as the new equilibrium condition is approached. Hilborn and Walters (1992) used this example merely to illustrate the pitfalls of applying analytical techniques based on assumptions of equilibrium to situations in which the assumption is not met. They did not present any expression to describe the transitional behavior of the estimator, and they obtained their results by simulation.

In this study, we derive the transitional behavior of the mean length statistic for use in nonequilibrium conditions. We investigate conditions affecting the reliability of the Beverton–Holt results and then develop a new procedure that allows a series of mortality rates to be estimated from mean length data representing nonequilibrium conditions from multiple years. We then examine an assessment of northeast U.S. goosefish *Lophius americanus*, which was criticized for its use of the Beverton–Holt estimator under nonequilibrium conditions. Data from the 1963–2002 National Marine Fisheries Service (NMFS) annual fall groundfish surveys off the northeastern United States were analyzed by use of the maximum likelihood method to estimate the years in which changes in mortality occurred and to reconstruct the mortality history.

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The Beverton–Holt Estimator

Assume deterministic asymptotic growth, as described by the von Bertalanffy equation

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}, \quad (1)$$

where L_t is the length at age t and L_∞ , K , and t_0 are the parameters. Also assume that the instantaneous total mortality rate is constant over time and over age for all ages greater than t_c , where t_c is the age at which animals are fully vulnerable to the fishery and to the sampling gear. Denote this mortality rate as Z per year. Further, assume that recruitment is continuous over time at a constant rate (R). The mean length of those animals above the length L_c corresponding to the age t_c is

$$\bar{L} = \frac{\int_{t_c}^{\infty} N_t L_t dt}{\int_{t_c}^{\infty} N_t dt}, \quad (2)$$

where L_t is given by equation (1) and $N_t = R \exp[-Z(t - t_c)]$. When the integrations in equation (2) are performed and the results are simplified,

$$L = L_\infty \left\{ 1 - \frac{Z}{Z + K} \exp[-K(t_c - t_0)] \right\}. \quad (3)$$

Equation (3) is easily solved for the mortality rate. Thus,

$$Z = \frac{K(L_\infty - \bar{L})}{\bar{L} - L_c}. \quad (4)$$

Note that the parameter t_0 has been eliminated from the solution through algebraic manipulation using equation (1).

This method is based on six assumptions:

1. asymptotic growth with known parameters K and L_∞ , which are constant over time;
2. no individual variability in growth;
3. constant and continuous recruitment over time;
4. the mortality rate is constant with age for all ages greater than t_c ;
5. the mortality rate is constant over time; and
6. the population is in equilibrium (i.e., enough time has passed after any change in mortality that mean length now reflects the new mortality level).

Some of these assumptions will be considered further in the Discussion.

Transitional Behavior

We now deal with the situation in which assumption 6 is violated. Suppose the mean length in a population is determined d years after a permanent change in total mortality from Z_1 to Z_2 per year. Let age $g = t_c + d$. The

mean length in the population d years after the change in mortality is

$$\begin{aligned} \bar{L} = & \left\{ \int_{t_c}^g R \cdot \exp[-Z_2(t - t_c)] L_t dt \right. \\ & + \int_g^\infty R \cdot \exp(-Z_2d) \cdot \exp[-Z_1(t - g)] L_t dt \left. \right\} \\ & \div \left\{ \int_{t_c}^g R \cdot \exp[-Z_2(t - t_c)] dt \right. \\ & + \int_g^\infty R \cdot \exp(-Z_2d) \cdot \exp[-Z_1(t - g)] dt \left. \right\}. \end{aligned} \quad (5)$$

In the numerator and the denominator, the first integral represents fish recruited after the change in mortality; these animals have experienced just the mortality rate Z_2 . The second integral represents fish that were recruited before the change in mortality; these fish have experienced both the old and the new mortality rates.

After integration and simplification (see Appendix 1), we obtain

$$\begin{aligned} \bar{L} = & L_\infty - Z_1 Z_2 (L_\infty - L_c) \\ & \times \left\{ Z_1 + K + (Z_2 - Z_1) \exp[-(Z_2 + K)d] \right\} \div \\ & \left\{ (Z_1 + K)(Z_2 + K) [Z_1 + (Z_2 - Z_1) \exp(-Z_2d)] \right\}. \end{aligned} \quad (6)$$

Note that when d equals 0, equation (6) provides the equilibrium mean length for the case where Z is equal to Z_1 , as expected. As d approaches infinity, equation (6) provides results approaching the equilibrium mean length when Z is equal to Z_2 , as expected. When Z_1 equals Z_2 , equation (6) gives the same result as equation (3). In Appendix 2, we generalize equations (5) and (6) to allow for multiple changes in mortality rate over time.

For any amount of elapsed time after a known change in mortality, we can determine the mean length in the population; by inserting this value into equation (4), we can determine how the Beverton–Holt estimator responds. We examined the effect of the von Bertalanffy parameter K on the estimates for the case where Z increased suddenly from 0.4 to 1.0 per year (Figure 1). The estimates approached the new equilibrium value faster when K was higher. Thus, after 3 years, the estimate reflected 76% of the increase in Z when K was equal to 0.1 per year, 83% of the increase when K was equal to 0.5 per year, and 87% when K was equal to 1.0 per year. Changing the value of L_∞ while holding K and L_c constant had no effect on the rate at which the estimator approached equilibrium.

The time required to reach equilibrium is also

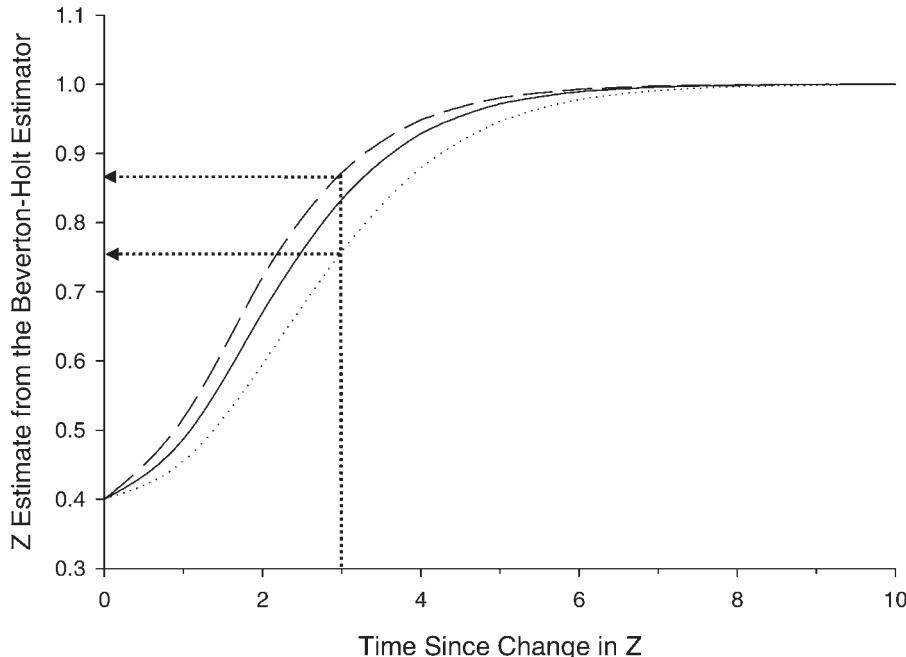


FIGURE 1.—Response of the Beverton–Holt mortality estimator to a change in the total mortality rate (Z) from 0.4 to 1.0 per year when the von Bertalanffy growth coefficient (K) is 0.1 (dotted line), 0.5 (solid line), and 1.0 per year (dashed line) and when L_∞ is 129.2 cm and L_c (the smallest size at which animals are fully vulnerable to the fishery and to the sampling gear) is 30 cm. These conditions approximate the situation for goosefish. After 3 years, the estimates approach the new value of Z if K is large. With a low K , an additional year is necessary.

TABLE 1.—Lag time (years) for the mean length of individuals that are fully vulnerable to the fishery and sampling gear to approach equilibrium and provide an estimate of mortality (Z) within 10% of the new level after a change in mortality from Z_1 to Z_2 . In this example, growth parameters for goosefish in the southern management region (Middle Atlantic Bight) of the northeastern United States were used in the calculations ($K = 0.1198$ per year, $L_\infty = 129.2$ cm, and $L_c = 30$ cm, where K = growth parameter, L_∞ = maximum attainable length, and L_c = minimum length at which fish are fully vulnerable to the gear). Note that the natural mortality of goosefish is believed to be around 0.2 per year, so the first row and first column do not appear to be possible. The value in bold italicics ($Z_1 = 0.4$, $Z_2 = 1.0$) is the example used in Figure 1.

Z_1	Z_2									
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0.1		16	14	12	11	10	9	8	7	7
0.2	23		9	9	8	8	7	7	6	6
0.3	26	11		6	6	6	6	6	6	5
0.4	27	13	7		4	5	5	5	5	5
0.5	28	14	8	4		3	4	4	4	4
0.6	28	15	9	6	3		2	3	4	4
0.7	29	15	10	7	5	2		2	3	3
0.8	29	15	10	7	5	4	2		2	2
0.9	29	16	10	8	6	4	3	2		2
1.0	29	16	10	8	6	5	4	3	2	

dependent on the magnitude and direction of the change in mortality (Table 1). The time required to reach equilibrium is greatest when fishing pressure has been significantly reduced to near-virgin levels. In this scenario, only growth over time can restore the original population structure and affect the mean length. On the other hand, the response to increases in fishing pressure occurs more rapidly, as the removal of the larger, older animals has an immediate effect on the mean length of the population.

Estimation in Nonequilibrium Situations

Estimation of mortality rates in nonequilibrium situations can be accomplished by selecting the year of change and the values of Z_1 and Z_2 that cause predicted mean lengths from equation (6) to best match a time series of estimated mean lengths. We used the method of maximum likelihood estimation. The probability density function of a normally distributed sample mean (\bar{x}) for a sample size of m is

$$f(x; \mu, \sigma^2) = \frac{\sqrt{m}}{\sqrt{2\pi\sigma^2}} \cdot e^{-\frac{m}{2\sigma^2}(\bar{x}-\mu)^2}. \quad (7)$$

The product likelihood function (Λ) for n years of observed mean lengths results in, by substitution with

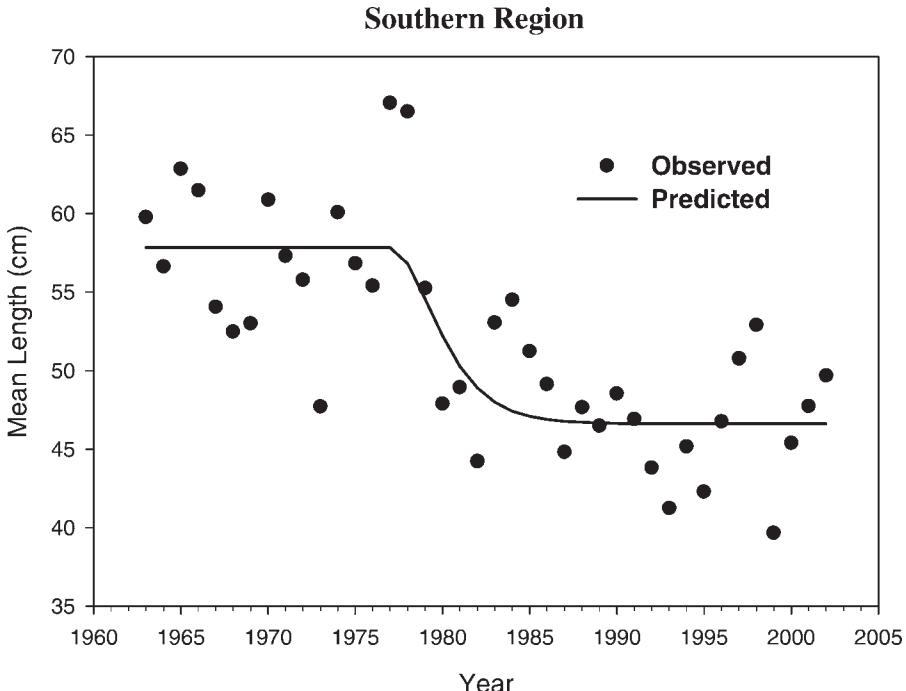


FIGURE 2.—Observed mean lengths of goosefish from the 1963–2002 National Marine Fisheries Service annual groundfish surveys in the southern management region (Middle Atlantic Bight) and predicted values from the transitional length statistic derived in this paper.

equation (6): $\mu = E(\bar{L})$ and $\sigma^2 = \text{Var}(L)$, which is the variance of lengths that are greater than L_c . Thus,

$$\Lambda = \prod_{y=1}^n \frac{m_y}{\sqrt{2\pi\sigma^2}} \cdot e^{-\frac{m_y}{2\sigma^2}(\bar{L}_y - L_{\text{pred},y})^2}, \quad (8)$$

where m_y is the number of fish greater than size L_c measured in year y , \bar{L}_y is the observed mean length in year y , and $L_{\text{pred},y}$ is the mean length computed with equation (6) or, more generally, from equation (A.2.1). The log likelihood is proportional to

$$\log_e(\Lambda) \propto -n \cdot (\log_e \sigma) - \frac{1}{2\sigma^2} \cdot \sum_{y=1}^n m_y \cdot (\bar{L}_y - L_{\text{pred},y})^2. \quad (9)$$

Equation (9) was maximized and confidence intervals were generated for each variable using the PROC NLP procedure in version 8 of the Statistical Analysis System (SAS Institute 1999). The year in which the mortality change occurred was specified, and Z_1 , Z_2 , and the variance (σ^2) were estimated. If the year in which a change in mortality occurs is unknown, the model can be fitted separately for each year in which the change is possible. The year of change that maximizes the likelihood provides the maximum

likelihood estimates. Alternatively, the year of change can be estimated along with the other parameters.

Application to the Assessment of Goosefish

Length frequency data from the NMFS annual fall groundfish trawl surveys were obtained for two defined management zones. Although this survey was not designed specifically for the purpose of sampling goosefish, and sample sizes are relatively low, changes in the mean length of goosefish have been observed over the 40-year time series. The survey is described in detail by the Northeast Fisheries Science Center (NEFSC 2002). In the NMFS assessment of goosefish in the northeastern United States, estimates of mortality from the Beverton–Holt length-based method applied to the NMFS survey data have been used to describe the historical pattern in fishing mortality rates (NEFSC 2002). As in the NMFS assessment, we analyzed data from the Middle Atlantic Bight (southern management region) and from the Gulf of Maine, southern New England, and Georges Bank (northern management region) separately.

Analysis of Southern Management Region Data

Consider the mean length data recorded in the NMFS annual fall groundfish survey in the southern

Southern Region

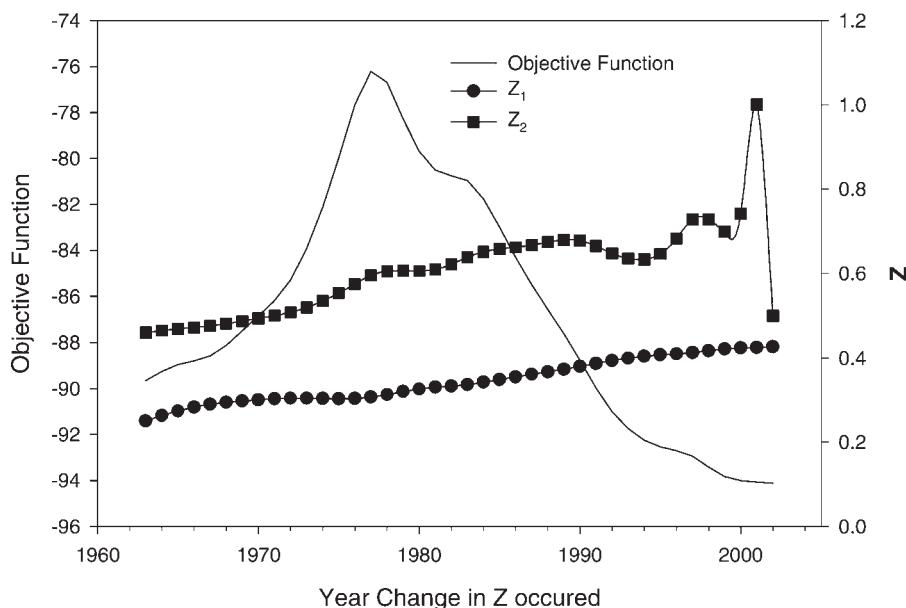


FIGURE 3.—Estimated goosefish mortality rates (Z) in the southern management region (Middle Atlantic Bight) and values of the objective function as functions of the specified year in which mortality changed from Z_1 to Z_2 . The objective function is maximized by specifying the year of change to be 1977.

management region from 1963 to 2002 (Figure 2). Records of goosefish landings began to increase in the southern management region fishery in the late 1970s, and the first step in our analysis was to determine whether the data reflected a change in Z . The model was fitted repeatedly, each time specifying a different year of the time series as the year in which the change in mortality occurred, and the objective function values were evaluated (Figure 3). The objective function was maximized by specifying the year of change to be 1977, which is consistent with the landings data presented in the 34th Stock Assessment Workshop (NEFSC 2002). Mortality was estimated to have changed from 0.31 to 0.60 per year in 1977. We also estimated the year of change directly in the maximization procedure. The parameter estimates were very similar to those obtained by fixing the year of change

(Table 2). The slight discrepancy is explained by the year of change being a continuous variable in the simultaneous estimation scheme and a discrete variable in the grid search (the estimates were 1977.2 years and 1977, respectively, for the year of change). In Table 2, it is seen that Z_1 was estimated quite precisely, while Z_2 was less so. Estimated correlations of the parameter estimates were highest between the two estimated mortality rates and the year of change (0.23 and 0.38 for Z_1 and Z_2 , respectively), and all other correlations were less than 0.04.

The predictive power of the transitional form of the length-based estimator was then evaluated by constructing estimates from data as if an assessment had been done in each year. In other words, estimates of Z_1 and Z_2 were made for each year by the use of data only up to that year, assuming that the year of change was

TABLE 2.—Results for goosefish from the southern management region (Middle Atlantic Bight) when the first level of fishing mortality (Z_1), the second level of fishing mortality, and the year of change are estimated simultaneously; CI = confidence interval.

Variable	Estimate	SE	<i>t</i> -value ^a	95% profile likelihood CI
SD	37.44	4.29	8.72	30.37–47.74
Z_1	0.33	0.02	17.94	0.29–0.37
Z_2	0.58	0.06	9.62	0.48–0.72
Year of change	1977.23	1.00	1973.55	1,975.26–1,979.19

^aAll *t*-values are significant at the 0.0001 level.

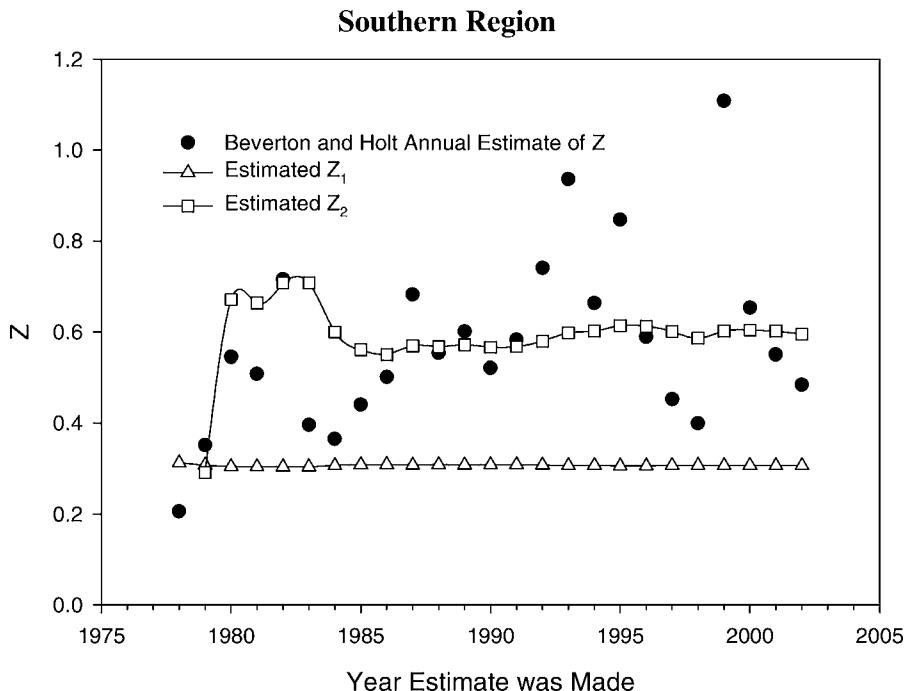


FIGURE 4.—Estimates of goosefish mortality rates (Z) in the southern management region (Middle Atlantic Bight) in various years. Estimates based on a single year's data (Beverton–Holt method) are not very stable. Estimates of Z_1 determined from mean lengths were stable, and estimates of Z_2 were stable if data up to at least 1980 were used. The year of change was specified to be 1977 for all estimates made with this method.

known to be 1977 (Figure 4). The estimates from the transitional form based only on data through 1980 (3 years after the change in mortality) were near 0.7 per year and became very stable at approximately 0.6 per year by 1984. Estimates from the classic annual Beverton–Holt estimator were highly variable and ranged from 0.2 to 1.14 per year (for 1977 and 1999, respectively).

The results from the transitional model were also consistent with the mean values of the annual Beverton–Holt estimator summarized over different periods of the entire time series ($Z = 0.32$, 0.75 , and 0.65 per year for 1970–1979, 1991–1995, and 1996–2000, respectively). Estimates from the transitional model, however, were stable in each of the years without the need to average over a number of years or wait for future years to smooth the variability in the data. Note that the stability in estimates was achieved even though the annual groundfish survey was not specifically designed for goosefish and despite the fact that sample sizes were very low (the number of fish measured in an annual survey ranged from 14 to 196), leading to a high degree of variability in mean length estimates. Furthermore, sample sizes prior to 1977

were generally larger than those after 1977, which partially explains the smaller standard error for Z_1 than for Z_2 .

Analysis of Northern Management Region Data

Data from the northern management area required a slightly more complex analysis. The model initially assumed a single change in mortality, and the best fit indicated that the change occurred in 1982 (Figure 5, top). However, an examination of the results showed that the residuals were positive from 1986 to 1993 and mostly negative from 1994 to 2002. This pattern in the residuals indicated that our data did not fit the model well and that additional changes in mortality were likely. Thus, the model was modified to incorporate a second change in mortality. All possible combinations of first and second years of change were tried, and a two-dimensional grid search of the change years showed that changes most likely occurred in 1978 and 1987 (Figure 6). The data appeared to fit the model well, and there was no discernable pattern in the residuals (Figure 5, bottom). The model was refitted, and the 2 years of change were estimated simultaneously with the mortality rates and SD (Table 3).

Northern Region

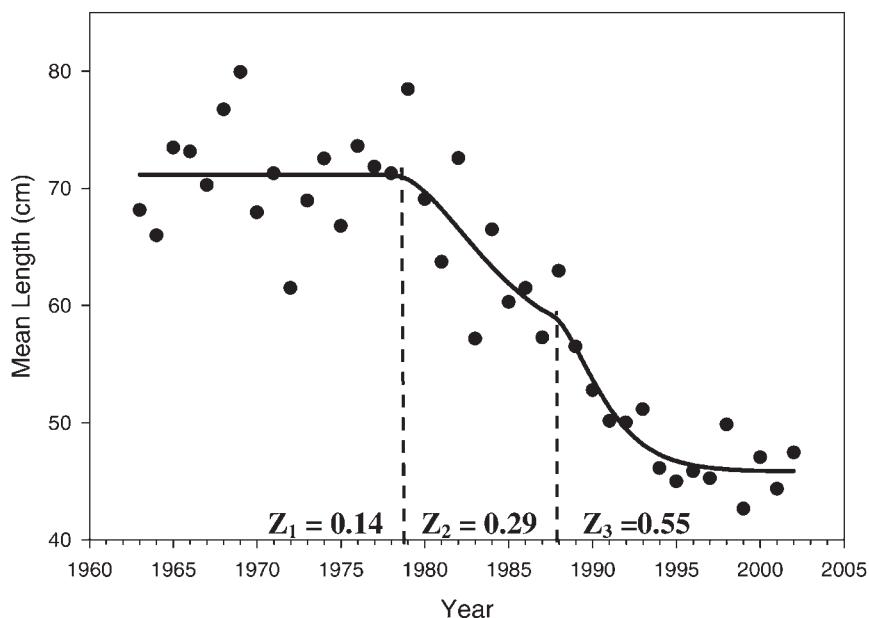
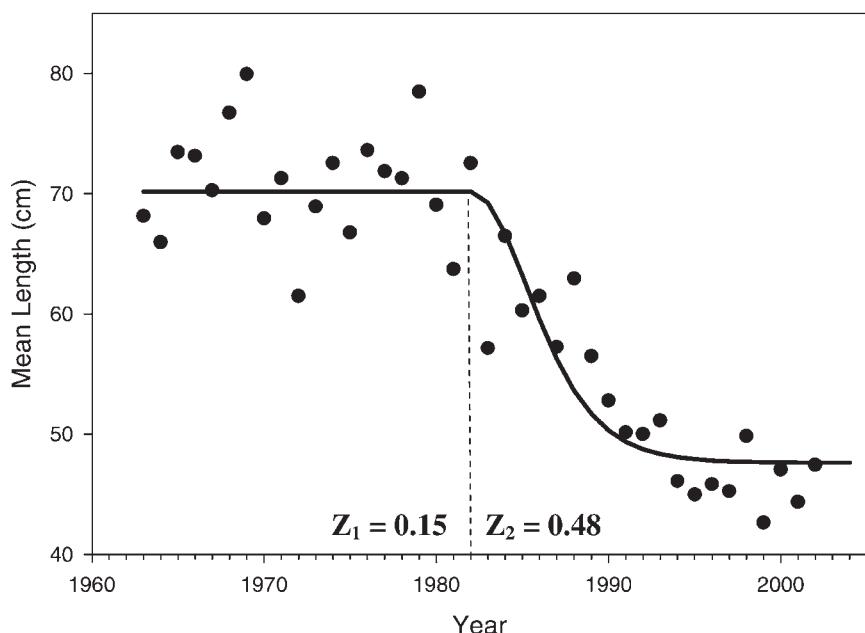


FIGURE 5.—The upper panel shows the results of estimating the mortality rate from goosefish mean length data collected in the northern management region (the Gulf of Maine, southern New England, and Georges Bank) when a change in mortality (from Z_1 to Z_2) in a single year is estimated. Note the pattern in the residuals at the far right, suggesting that mortality may have changed more than once. Dots represent observed mean lengths and the solid line represents the mean lengths predicted by the new nonequilibrium model. The lower panel shows the results when a model with two changes in mortality (from Z_1 to Z_2 and from Z_2 to Z_3) was fitted to the same data.

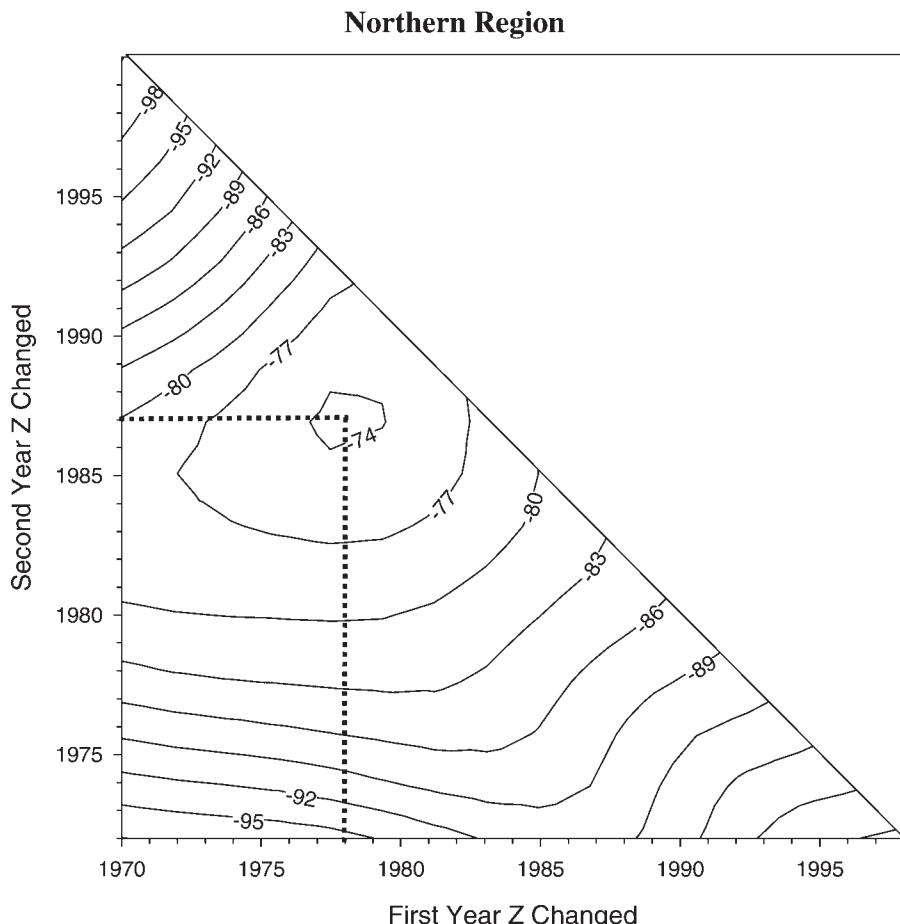


FIGURE 6.—Contour plot of objective function values to determine the 2 years in which the goosefish mortality rate Z changed in the northern management region (the Gulf of Maine, southern New England, and Georges Bank). The objective function was maximized (indicated by a dotted line) by an initial change in 1978 and a second change in 1987.

Parameter estimates were again extremely close to those obtained from the grid search. Estimated correlations of the parameter estimates were less than 0.6 in all cases, and for 11 of the 15 parameter pairs the correlations were less than 0.2.

Model Sensitivity

To test the model's sensitivity to input parameters, we created a simulated data set with a known change in mortality from 0.3 to 0.6 per year in 1977 using growth parameters from goosefish in the southern management

TABLE 3.—Results for goosefish from the northern management region (Gulf of Maine, Southern New England, and Georges Bank) when three different levels of mortality (Z_1 , Z_2 , and Z_3) and the two years of change are estimated simultaneously; CI = confidence interval.

Variable	Estimate	SE	t-value ^a	95% profile likelihood CI
SD	22.93	2.63	8.72	18.61–29.25
Z_1	0.14	<0.01	28.46	0.13–0.15
Z_2	0.30	0.03	8.83	0.24–0.38
Z_3	0.56	0.05	10.78	0.47–0.69
Year of first change	1978.21	0.91	2,167.74	1975.96–1980.26
Years until next change ^b	9.58 (1987.79)	1.33	7.19	6.37–12.85 (1984.58–1991.06)

^aAll t-values are significant at the 0.0001 level.

^bYear indicated in parentheses.

TABLE 4.—Sensitivity of goosefish mortality (Z) estimates to over- or underestimation of actual K (growth parameter) and L_∞ (maximum attainable length). A simulated data set was used with a known change in Z from 0.3 (Z_1) to 0.6 (Z_2) based on growth parameters from the goosefish southern management region (Middle Atlantic Bight) ($K=0.1198$ per year, $L_\infty = 129.2$ cm).

K estimate	L_∞ estimate	Z_1	Z_2
Actual	Actual	0.30	0.60
Actual	10% low	0.25	0.52
Actual	10% high	0.35	0.68
10% high	Actual	0.33	0.65
10% low	Actual	0.27	0.55
10% high	10% low	0.27	0.56
10% low	10% high	0.32	0.62
Actual	20% high	0.41	0.77
Actual	20% low	0.19	0.43
20% high	Actual	0.36	0.71
20% low	Actual	0.24	0.49
20% low	20% high	0.33	0.63
20% high	20% low	0.23	0.51

region ($K = 0.1198$ per year, $L_\infty = 129.2$ cm) and a known L_c of 30 cm. The model was then fitted under the assumption that estimates of K and L_∞ were misspecified by 10–20%. Since estimates of K and L_∞ are generally inversely correlated, we also tested scenarios in which K and L_∞ were mis-specified in opposite directions. Estimates of the change in mortality were most sensitive to the mis-specification of L_∞ and approximately half as sensitive to the mis-specification of K (Table 4). Model results were relatively stable when estimates of K and L_∞ were varied inversely with estimates of Z_1 ranging from 0.23 to 0.33 per year and estimates of Z_2 ranging from 0.51 to 0.63 per year.

Discussion

Fishery managers are continually faced with the challenge of matching methods and data sets such that all the critical assumptions can be met. The method presented in this paper is attractive because it requires minimal data that are commonly available and it does not require the assumption that catch rate is proportional to abundance. It advances a frequently used technique by removing an equilibrium assumption that is typically difficult to meet in real-world situations. This allows for the broader application of a mean length analysis approach and allows the use of an entire time series of data, resulting in increased information. The approach may in some cases represent the best opportunity to reconstruct the mortality history of a stock. In addition, the transitional form of the model allows mortality estimates to be made within a few years of a change rather than having to wait for the mean lengths to stabilize at their new equilibrium level. In other words, as soon as a decline in mean lengths is

detected, our model can be applied and the trajectory of decline can be used to estimate the new Z and determine how mean lengths will change over time. Estimates of multiple mortality rates and the years of change appear to have the desirable property of having only a low to moderate correlation.

In our goosefish example, it appears that the population was in equilibrium at the start of our time series. This is not a requirement of the model. A population that is undergoing a change in mean length at the start of a time series can also be successfully analyzed because an initial change in mortality that occurs prior to the start of the time series can be estimated in the model. However, this requires the shape of the trajectory of mean length over time to be well defined. If this is not the case, then it may be possible to set Z_1 equal to the natural mortality rate in situations where observations are initiated shortly after the start of the fishery.

The method presented here is not fully efficient because, in theory, there is information contained in the variability of length measurements within a year (i.e., the sample variance) that is not used in the estimation of mortality rates and change points. That is, under high mortality, there are few large fish and thus the variance in length decreases with increasing mortality rate. An expression for the variance of length measurements as a function of the mortality and growth parameters and the years of change could be derived and incorporated in the likelihood function. This would be appropriate if the sampling design consisted of simple random sampling of lengths. However, such a sampling scheme is uncommon, and sampling almost always involves some form of cluster sampling (e.g., a boat catches clusters of animals from trawl hauls, pot hauls, etc.). Thus, the sample variance of lengths will not be a simple function of the population variance of lengths.

Choice of Cutoff L_c

This method is predicated on the assumption of knife-edge selection in the fishery at a size L_c . Thus, all fish smaller than L_c experience only natural mortality, and all fish larger than L_c experience a total mortality rate of Z . One can thus sample the commercial catch to estimate the mean length of those animals above the size L_c . If the fishery does not have knife-edge selection, then there is a problem. One can define L_c to be the size of full vulnerability to the commercial gear and compute the mean length of fish larger than L_c . However, this means that fish smaller than L_c will experience some fishing mortality, and thus changes in fishing effort may affect the number of fish reaching the size L_c . As a practical matter, this will be important

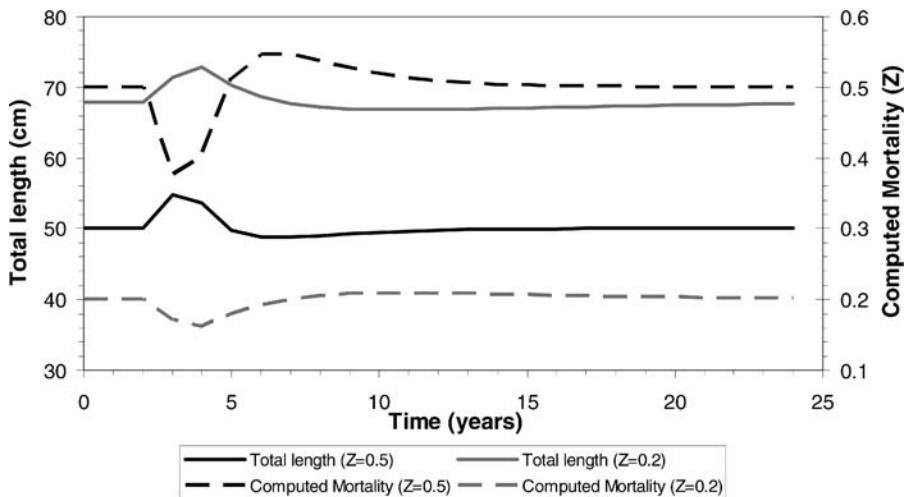


FIGURE 7.—Response of the Beverton–Holt length-based mortality (Z) estimator to a violation of the assumption of constant recruitment in goosefish. A complete reproductive failure under two different levels of fishing mortality is simulated in year 3. Life history parameters for goosefish in the southern management region (Middle Atlantic Bight) were used for this example.

if selectivity increases gradually with length. However, for steep selection curves, this may not be a problem.

Often, length composition data will be available from research surveys. If the size of full vulnerability to the survey gear is less than or equal to the size of full vulnerability L_c in the fishery, one can simply compute the mean of those fish in the survey above the size L_c . In practice, length frequency data are often collected in bins (i.e., as a histogram). The lower limit to one bin is defined to be the cut-off L_c . The mean length in the sample (above the cutoff L_c) is then computed by treating all fish in a bin as being the size at the midpoint of the size range that defines the bin.

We also note that with historical data sets, sometimes only the mean length of the catch is available and one cannot construct size-frequency histograms. The size at first capture L_c may only be known approximately, and there may be some animals below the size L_c that are included in the mean length statistic. If it can be assumed that the selection pattern has remained stable over time, then the method presented in this paper may still be used to study the history of mortality; the results will reflect trends in mortality over time, but estimates of absolute mortality rate will be biased.

Assumption of Constant Recruitment

The method in this paper is based on the assumption of constant recruitment. In reality, recruitment is likely to vary from year to year. This will not cause a bias, but it may lead to autocorrelated errors in a time series of estimates. To study this, we created an extreme case in which there was a complete failure of recruitment in 1

year and we observed the effect over time (Figure 7). The failure of recruitment in an incoming year-class at first raises the population mean length, thus resulting in an underestimate of total mortality. Later, as that missing year-class reaches an age at which there should be large animals, the mean size of the population declines, resulting in an overestimate of mortality rate. In practice, complete year-class failure is rare; to the extent that recruitment variability is random (rather than showing a trend over time), one can expect some cancellation of errors arising from variable recruitment. Thus, recruitment variability should not negate the use of this method, although the reader would be well advised to consider the possibility of a trend in mean length arising from a particularly large or small year-class.

Generalizing the Approach

It may be that observations are available for mean weight but not mean length. This can be accommodated by deriving an expression for mean weight by replacing L_t in the derivations with the age-specific weight W_t , that is,

$$W_t = aL_t^b, \quad (10)$$

where a and b are constants defining the shape of the power function. When the exponent b is exactly 3, an analytical solution can be obtained for the mean weight. Otherwise, the mean weights can be calculated by numerical methods.

In some circumstances, it may be preferable to model reproduction as occurring in an annual pulse rather than continuously over the course of the year.

This can be accomplished by replacing the integrals in the derivations with sums over the discrete age-classes.

A more difficult assumption to deal with is that recruitment is constant over the time series being analyzed. If recruitment varies directly with the stock size, then the model in its current form will underestimate the magnitude of any change in mortality.

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Appendix 1: Derivation of the Mean Length d Years after a Change in the Mortality Rate

As indicated in the main text, the mean length in the population d years after a change in mortality is

$$\begin{aligned} \bar{L} = & \left\{ \int_{t_c}^g R \cdot \exp[-Z_2(t - t_c)] L_t dt \right. \\ & + \left. \int_g^\infty R \cdot \exp(-Z_2d) \cdot \exp[-Z_1(t - g)] L_t dt \right\} \\ & \div \left\{ \int_{t_c}^g R \cdot \exp[-Z_2(t - t_c)] dt \right. \\ & + \left. \int_g^\infty R \cdot \exp(-Z_2d) \cdot \exp[-Z_1(t - g)] dt \right\}, \end{aligned} \quad (\text{A.1.1})$$

where the notation is as defined in the main text. The denominator (DEN) is

$$\begin{aligned} \text{DEN} &= \frac{1 - \exp(-Z_2d)}{Z_2} + \frac{\exp(-Z_2d)}{Z_1} \\ &= \frac{Z_1 + (Z_2 - Z_1)\exp(-Z_2d)}{Z_1 Z_2}. \end{aligned} \quad (\text{A.1.2})$$

The numerator (NUM) is

NUM

$$\begin{aligned} &= L_\infty \left\{ \frac{1 - \exp(-Z_2d)}{Z_2} \right. \\ &\quad \left. - \frac{\exp[-K(t_c - t_0)] - \exp[-Z_2d - K(g - t_0)]}{Z_2 + K} \right\} \end{aligned}$$

$$+ \frac{\exp(-Z_2d)}{Z_1} - \frac{\exp[-Z_2d - K(g - t_0)]}{Z_1 + K} \Big\}. \quad (\text{A.1.3})$$

We would like to get rid of t_0 in the numerator. Solving the von Bertalanffy growth equation for t_0 , we obtain

$$t_0 = t_c + \frac{\log_e(1 - L_c/L_\infty)}{K}. \quad (\text{A.1.4})$$

Substituting this into NUM and simplifying gives

$$\begin{aligned} \text{NUM} &= \frac{L_\infty[1 - \exp(-Z_2d)]}{Z_2} - \frac{L_\infty - L_c}{Z_2 + K} \\ &\quad + \frac{(L_\infty - L_g)\exp(-Z_2d)}{Z_2 + K} + \frac{L_\infty\exp(-Z_2d)}{Z_1} \\ &\quad - \frac{(L_\infty - L_g)\exp(-Z_2d)}{Z_1 + K}, \end{aligned} \quad (\text{A.1.5})$$

where L_g is defined to be the length at age g ($= t_c + d$). Now the only problem is that we have the parameter L_g , which we would prefer to express as a function of L_c . The difference between L_g and L_c is

$$L_g - L_c = L_\infty b \cdot \exp(-Kt_c) - L_\infty b \cdot \exp(-Kg), \quad (\text{A.1.6})$$

where $b = \exp(Kt_0)$. Solving for L_g and simplifying, we obtain

$$L_g = L_\infty - (L_\infty - L_c) \exp(-Kd). \quad (\text{A.1.7})$$

Substituting this into NUM gives

$$\frac{Z_1 L_\infty + (Z_2 - Z_1) L_\infty \exp(-Z_2 d)}{Z_1 Z_2} - \frac{(L_\infty - L_c) \{1 - \exp[-(Z_2 + K)d]\}}{Z_2 + K}$$

$$-\frac{(L_\infty - L_c) \{1 - \exp[-(Z_2 + K)d]\}}{Z_1 + K}. \quad (\text{A.1.8})$$

Finally, dividing NUM by DEN gives equation (6) in the main text.

Appendix 2. Derivation of the Mean Length after Multiple Changes in the Mortality Rate

Here, we present a general expression for the mean length for situations in which there have been k changes in the mortality rate over time. We define the variable d_i to be the time elapsed between the i th and $(i+1)$ th change in mortality for $i = 1, \dots, k-1$, and we define d_k to be the time from the last change in mortality to the point when the mean length was observed. In other words, d_i measures the duration of the period when Z_{i+1} affected the population. The mean length is

$$\bar{L} = \frac{\sum_{i=1}^{k+1} a_i \int_{\lambda_i}^{\gamma_i} \exp[-Z_{k+2-i}(t - \lambda_i)] L_t dt}{\sum_{i=1}^{k+1} a_i \int_{\lambda_i}^{\gamma_i} \exp[-Z_{k+2-i}(t - \lambda_i)] dt} \quad (\text{A.2.1})$$

where

$$\begin{aligned} \lambda_1 &= t_c \\ \lambda_i &= t_c + \sum_{j=k-i+2}^k d_j \quad \text{for } i = 2, \dots, k+1 \\ \gamma_i &= t_c + \sum_{j=k-i+1}^k d_j \quad \text{for } i \leq k \\ \gamma_{k+1} &= \infty \\ a_1 &= 1 \\ a_i &= \exp\left(-\sum_{j=1}^{i-1} Z_{k+2-j} d_{k+1-j}\right) \quad \text{for } i = 2, \dots, k+1 \\ L_t &= L_\infty [1 - e^{-K(t-t_0)}]. \end{aligned}$$

The denominator (DEN) is

$$\text{DEN} = \sum_{i=1}^{k+1} \frac{a_i (1 - e^{-Z_{k+2-i} d_{k+1-i}})}{Z_{k+2-i}}. \quad (\text{A.2.2})$$

The numerator (NUM) is

$$\text{NUM} = L_\infty \left[\text{DEN} - \sum_{i=1}^{k+1} \frac{\left(1 - \frac{L_c}{L_\infty}\right) r_i s_i}{Z_{k+2-i} + K} \right], \quad (\text{A.2.3})$$

where

$$\begin{aligned} r_1 &= 1 \\ r_i &= \exp \left[\sum_{j=1}^{i-1} -(Z_{k+2-j} + K) d_{k+1-j} \right] \\ &\quad \text{for } i = 2, \dots, k+1 \\ s_i &= 1 - e^{-(Z_{k+2-i} + K) d_{k+1-i}} \\ &\quad \text{for } i = 1, \dots, k \\ s_{k+1} &= 1. \end{aligned}$$