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Analysis of Two Length-Based Mortality Models Applied to Bounded Catch Length Frequencies

by

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Abstract - We performed an assessment of the length-based total mortality model of Beverton and Holt, assuming that catch length frequency distributions in tropical artisanal fisheries are constrained by 1) the selective properties of multiple gears used, and 2) the temporal-spatial availabilities of certain size classes to operationally restricted fleets. Positive bias always resulted with the Beverton and Holt Z-estimator, which assumes an infinite exploitable life span. Z-estimates were unreasonably biased when exploitable life spans were less than or equal to 50% of the biological life span of the species considered in the analyses. Biases were larger at lower levels of fishing mortality rates. We developed a new method from a truncated equation for average length. It considers length at first capture and the maximum retainable length actually observed in the fishery catch. The method has no explicit solution for total mortality rate Z, so we used numerical methods to provide its solution. The new estimator has zero bias at equilibrium. We determined variance of the new Z estimator by bootstrap techniques.

Management of tropical fisheries is difficult due to the remoteness and the varied characters of the fishing activities, and by the complex population dynamics exhibited by tropical fish species (Pauly and Murphy 1982). Efforts to assess the effects of fisheries exploitation on these resources are usually marred by the considerable uncertainties associated with age (growth) and mortality estimates derived from usually sparse fishery statistics, and inadequate biological and oceanographic information. To resolve this dilemma, a number of simple methods aimed at estimating mortality rates based on frequently available length frequency data have been either developed for or adapted to tropical fisheries. This is because less expensive length frequency data series are more often collected in tropical fisheries than the possibly more important, but labor- and cost-intensive catch-and-effort statistics or age composition data.

Development of length-based assessment methodologies have been the focus of several papers (see Pauly and Morgan 1987 for references); however, due to its simple computational formula, the equation of Beverton and Holt (1956) has been widely used for calculating total instantaneous mortality rates (Z). The model estimates Z as a function of average length in the landings and the length at first capture. Statistical evaluations of the Beverton and Holt Z-estimator by Wetherall et al. (1987) indicate that the estimator is the only one applicable among several other methods when the available information is limited to the mean length in a sample of fish above the length at first capture; L_c,

and to an independent estimate of the asymptotic length, L_∞.

The Beverton and Holt model assumes steady state conditions, and that species exhibit infinite exploitable life spans. This latter assumption, however, may be less realistic in tropical fisheries where most species are subjected to high rates of growth and natural mortality, and are therefore relatively short-lived. Furthermore, tropical fisheries are characterized by numerous and heterogeneous artisanal fleets that have restricted operational ranges and highly selective gears. The aforementioned conditions result in catch length frequency distributions which are usually truncated at lower L_c and upper L_λ boundaries because of 1) temporal-spatial differences in availability of cohorts, and 2) differential gear selection of certain age or size classes in the fisheries.

Although Ralston (1989) recommended caution in the use of Beverton and Holt's estimator, he suggested that over a broad range of simulated conditions, bias in the formulation is negligible and the estimator is robust with respect to seasonal recruitments. In contrast, we will show that the efficacy of the Beverton and Holt Z-estimator tends to be highly biased when the maximum age in the catch t_λ (i.e., fishery life span) is somewhat less than the theoretical infinite life span t_∞.

The objectives of our paper have therefore been 1) to examine the bias of the Beverton and Holt estimator when length distributions are constrained by gear selectivity within the range defined by L_c and L_λ, and 2) to develop an alternative

model which may be more appropriate to availability or selectivity patterns observed in tropical fisheries.

Methods

The mortality model developed by Beverton and Holt (1956) is based on a deterministic expression for the mean length of fish in the catch above a length at first capture, L_c. Assuming a population in equilibrium, average length is written

$$\bar{L} = \frac{\int_{t_c}^{\infty} N_t L_t dt}{\int_{t_c}^{\infty} N_t dt}. \tag{1}$$

If growth can be adequately expressed by a simple von Bertalanffy growth equation (Beverton and Holt 1957), such that

$$L_t = L_\infty\left(1-e^{-K(t-t_0)}\right), \tag{2}$$

where L_t ≡ length at age t, L_∞ ≡ asymptotic length, K ≡ the growth coefficient, and, t_0 ≡ fitted parameter corresponding to L_t=0, and population size can be expressed by an exponential mortality model, such that

$$N_t = R' e^{-(F+M)(t-t_c)}, \tag{3}$$

where N_t ≡ abundance in numbers of individuals at age t, R' ≡ recruitment in numbers to exploitable ages, F ≡ instantaneous fishing mortality rate, M ≡ instantaneous natural mortality rate, then substituting L_t by equation 2 and N_t by equation 3 into equation 1, and integrating from t_c *to* ∞ results in an explicit expression for average length

$$\bar{L} = L_\infty \left(1 - \left[\frac{(F+M)}{(F+M+K)}\right] e^{-K(t_c - t_0)}\right). \tag{4}$$

The length of a fish at age of first capture, L_c, may be expressed as a function of t_c according to equation 2 from which

$$e^{-K(t_c - t_0)} = \frac{L_\infty - L_c}{L_\infty}. \tag{5}$$

Substituting (5) into expression (4) and rearranging terms results in Beverton and Holt's (1956) formula

$$Z = \frac{K(L_\infty - \bar{L})}{(\bar{L} - L_c)}, \tag{6}$$

which estimates total instantaneous mortality rate, Z, from the mean length, $\bar{L}$, in a random sample of fully recruited fish in the catch.

In the particular case where the hypothetical infinite life span assumed by Beverton and Holt (1956) is restricted such that life span is defined by a size L_λ corresponding to age t_λ, chosen to correspond either with the greatest size for which adequate data is represented in the catch, or with maximum selection size, then equation 1 may be expressed as

$$\bar{L} = L_\infty [1 - \frac{e^{Kt_0} \int_{t_c}^{t_\lambda} e^{-(Z+K)t} dt}{\int_{t_c}^{t_\lambda} e^{-Zt} dt}]. \tag{7}$$

Integrating from t_c to t_λ in equation 7 results in an expression for average length in the catch as

$$\bar{L} = \frac{L_\infty \left[\frac{e^{-Zt_c} - e^{-Zt_\lambda}}{Z} - \frac{e^{Kt_0}\left(e^{-t_c(Z+K)} - e^{-t_\lambda(Z+K)}\right)}{Z+K} \right]}{\left[\frac{e^{-Zt_c} - e^{-Zt_\lambda}}{Z} \right]}. \tag{8}$$

We used this expression to calculate the average length of length frequency distributions bounded between t_c and t_λ according to several values of t_c and intrinsic total instantaneous mortality rates, Z^0. We then used the resulting average lengths to estimate Z^1 according to the Z-formulation of Beverton and Holt (equation 6). Biases in Z^1 due to bounding of length frequency distributions were estimated as the relative difference between the intrinsic mortality rate (Z^0) used in equation 8 and the estimated mortality (Z^1) resulting from equation 6, as

$$Relative\ bias = \frac{Z^1 - Z^0}{Z^0}. \tag{9}$$

Analysis

For analysis purposes, we selected growth parameters from a range of possible values corresponding to tropical fish species. Growth of these species has been extensively reviewed by several authors, more importantly by Pauly and Ingles (1981), Munro (1982), and Manooch (1987). Estimates for L_∞ and t_λ given in the above references were used to generate Figure 1. Three species, i.e., lane snapper (Lutjanus synagris), yellowfin grouper (Mycteroperca venenosa), and snowy grouper (Epinephelus niveatus), were selected from the figure (triangles) such that a

representative range of life histories could be included in the analyses. Parameter estimates pertinent to the three selected species are given in Table 1.

Relative bias estimated for various combinations of exploitable life spans (number of years individuals from a cohort are effectively recruited to the fishery) and fishing mortality rates indicated that the formulation of Beverton and Holt unreasonably overestimates total mortality rates if exploitable life spans are short (Table 2). However, the amount of bias decreases considerably as exploitable life spans approach the total life span of the species. Note that in the three species considered, an increase in fishing mortality reduced the amount of bias and Z was noticeably more overestimated for lower values of F (Table 2).

We also calculated the magnitude of the bias in Z-estimates with reference to exploitable life spans measured relative to the maximum age of the species. When an arbitrarily selected fishing mortality rate of F = 0.1 was used and when the relative exploitable life span was 33% of the maximum, bias in Z-estimates varied from 21% for the species with a maximum age of 27 years (snowy grouper) to 46% for the species with a maximum age of 6 years (lane snapper) (Figure 2a). Bias was reduced when relative exploitable life span was increased to 50%; bias varied from 7% for the longer-lived species (snowy grouper) to 18% for the shorter-lived species (lane snapper). Finally, bias in Z-estimates reached levels below 10% when exploitable life span

represented at least 66% of the maximum age. At F = 0.3, Z-estimates were significantly biased when the relative exploitable life span was 33% of t_λ (Figure 2b). Bias was nil when exploitable life spans are 66% of maximum age of yellowfin grouper, and 50% and 66% of maximum age of snowy grouper. However, at the latter percentages biases were still significant (31.17% and 3.73%, respectively) in the shorter-lived species (lane snapper).

Under the conditions simulated, the Beverton and Holt (1956) estimator showed large positive bias at low levels of total instantaneous mortality rate. High mortality rates artificially truncated length frequency distributions and thus apparently forced less biased estimates. The difference between $\bar{L}$ and L_c, on which the estimate of total mortality is critically dependent, would be small and sensitive to factors such as flawed sampling design and fluctuations in cohort strength or growth rates.

Holt (1965) considered the problem of an aged catch distribution truncated at some age less than t_∞ for cases where data for the ages of the oldest fish in the samples are to be used. Holt solved the problem for the mean age of fish above age t_c and less than some upper limit t_λ as a generalized censored exponential distribution. For length-based data the Holt (1965) method has at least two problems 1) the ages of fish in the samples are presumed unknown, and 2) the generalized solution considers only the limiting values of the exponential distribution to compute the mean of the exponential series,

rather than explicitly solving the integral. Holt's (1965) Z-estimate is also biased.

An Alternate Model

Biases associated with the Z-estimators of Beverton and Holt (1956) and Holt (1965) suggested the need to improve the Z-estimator to represent conditions that are more closely associated with tropical artisanal fisheries and typical catch compositions in general. For this purpose, we developed a (t_λ-t_c)-bounded expression for Z from equation 8.

Rearranging terms in (8) we obtain

$$\frac{e^{Kt_0}\left(e^{-(Z+K)t_c}-e^{-(Z+K)t_\lambda}\right)}{e^{-Zt_c}-e^{-Zt_\lambda}} = \left[\frac{L_\infty-\bar{L}_c}{L_\infty}\right]\left[\frac{Z+K}{Z}\right]. \tag{10}$$

Similar to equation 5, but with a von Bertalanffy growth function for L_λ as a function of t_λ, we make

$$e^{-K(t_\lambda-t_0)} = \frac{L_\infty-L_\lambda}{L_\infty}. \tag{11}$$

Replacing (5) and (11) in (10), and arranging some of the terms, we have

$$e^{-Zt_c}-e^{-Zt_\lambda}\left[\frac{L_\infty-L_\lambda}{L_\infty-L_c}\right] = \frac{(L_\infty-\bar{L})\,(Z+K)}{(L_\lambda-L_c)\,Z}. \tag{12}$$

From equation 12 an expression for survival during the exploitable life span (t_λ-t_c) can be obtained after some simplifications as

$$e^{-Z(t_\lambda - t_c)} = \frac{Z(L_c - \bar{L}) + K(L_\infty - \bar{L})}{Z(L_\lambda - \bar{L}) + K(L_\infty - \bar{L})}. \tag{13}$$

Making

$$e^{-Z(t_\lambda - t_c)} = e^{-Z(t_\lambda - t_0)}\, e^{-Z(t_c - t_0)}, \tag{14}$$

and

$$e^{-Z(t_\lambda - t_c)} = \left[e^{-K(t_\lambda - t_c)}\right]^{\frac{Z}{K}}, \tag{15}$$

then equation 14 can be expressed as

$$\left[e^{-K(t_\lambda - t_c)}\right]^{\frac{Z}{K}} = \left[e^{-K(t_\lambda - t_0)}\, e^{K(t_c - t_0)}\right]^{\frac{Z}{K}}. \tag{16}$$

We note that the term on the right hand side of (16) may be expressed in terms of two von Bertalanffy growth functions for t_λ and t_c, as

$$\left[\frac{L_\infty - L_\lambda}{L_\infty - L_c}\right]^{\frac{Z}{K}}. \tag{17}$$

Therefore, replacing term (17) into (13) results in

$$\left[\frac{L_\infty - L_\lambda}{L_\infty - L_c}\right]^{\frac{Z}{K}} = \frac{Z(L_c - \bar{L}) + K(L_\infty - \bar{L})}{Z(L_\lambda - \bar{L}) + K(L_\infty - \bar{L})}. \tag{18}$$

If estimates of the growth parameters L_∞ and K are available, and if L_c, L_λ and $\bar{L}$ can be estimated from length frequency distributions, then equation 18 contains only one unknown, the instantaneous total mortality rate Z. However, equation 18 does not generate an explicit solution for Z, hence total mortality rate must be obtained by solving equation 18 iteratively. The model requires statistics from censured catch

length frequencies such as the lower limit of the smallest length class that is fully recruited (L_c), the upper limit of the size class representing the largest length class (L_λ), and the weighted average length computed from L_c upward.

Sensitivity Analyses of the Alternate Model

Testing the accuracy and sensitivity of a method is an essential step before its use can be widely advocated. Because of limitations estimating first and second moments with data derived from tropical fish stocks in which ages are indistinguishable, for the sensitivity analyses we employed the growth and mortality parameters estimates of Ehrhardt (1973) for Chilean hake (Merluccius gayi gayi) (Table 3). Population dynamics parameters for Chilean hake fell within the range of those estimated for tropical fish stocks (c.f. Figure 1). To fully evaluate model (equation 18) sensitivity we used three methods 1) ordinary static analysis, 2) stochastic analysis using Monte Carlo simulation, and 3) the "bootstrap" to approximate model variance for a point estimate of Z.

The objective of our ordinary static sensitivity analysis was the identification of an input parameter that when changed by a fixed percentage produced an effect on the output of equation 18. The method follows Majkowski (1982) who performed a similar analysis on Equation 6. Only one parameter was changed in a single implementation of the model. The relative change in X_i is denoted by U_i. The effects of such changes on the model

performance were determined by the scalar perturbation function D that measures differences between the perturbed (i.e., when an input parameter has been changed) and unperturbed (i.e., associated with best estimates of the input parameters) results from the model. We performed ordinary sensitivity analysis for values of U_i from the U-interval [-B,B] where the value of B should exceed the magnitude of errors in the most uncertain parameters. We calculated sensitivity of the outputs to a percentage change in any given input X_i as

$$S(X,Z,\Delta X) = \frac{Z(X_i + \Delta X_i) - Z(X_i)}{Z(X_i)},$$
$$D_i = S(X,Z,\Delta X) \times 100, \tag{19}$$

where $S(X,Z,\Delta X)$ is the sensitivity of Z to a change in X and Z(X) denotes the unperturbed value of X. The resultant values of D_i are presented in Table 4. The D_i measure is a linear function of U when the K and L_∞ parameters are changed, this is true for any range of perturbations. The D-measure is most sensitive to changes in L_λ and L_c. However, the sensitivity of equation 18 to changes in the L_c and $\bar{L}$ values is on the same order as equation 6 so that the sampling requirements for these parameters are equivalent with use of either model. Nonetheless, it is imperative to ensure that these parameters are estimated reliably, a condition that may be attained by performing appropriate selectivity studies and establishing proper spatio-temporal stratifications in length sampling programs.

We implemented a stochastic sensitivity analysis with the

aid of the Monte Carlo method (Lewis and Orav 1989), running simulations for the full factorial design of model parameters (Table 5). In all relevant combinations of chance parameter variation, equation 18 was more efficient in estimating the true underlying Z than equation 6. This was true for all levels of parameter risk, even in those cases where equation 18 had more parameters varying. Risk refers here to 1) the number of model parameters varying simultaneously, and 2) the degree to which the analysis allows one to choose between options whose outcomes are depicted in probability distributions. While equation 18 had a greater range of coefficient of variation's, principally because the number of varying parameters was greater, it was still far more robust than equation 6. However, equation 18 did show sensitivity to any chance parameter variation involving L_c; this was exacerbated when the parameter L_λ covaried. Deviations in L_∞ seemed to dampen deviations induced by L_c. In general, K and L_∞ affected the solution to equation 18 the least, whereas L_c and L_λ affected it most strongly. Although the parameters L_c and L_λ can be obtained by routine synoptic sampling of the total catch, it is imperative that both parameters be estimated as rigorously and reliably as possible to minimize bias.

We approximated variance for the point estimate of Z associated with equation 18 under varying numbers of chance parameters using the computer intensive bootstrap method (Efron 1979, 1985, 1987). The bootstrap is a small sample method for obtaining variance estimates or confidence intervals for a point

estimate (Lewis and Orav 1989). Parameters and associated standard errors used in the bootstrapping analyses are given in Table 3. The bootstrap method assumes that the data provide an estimate of the parent cumulative distribution function without introducing assumptions regarding its form. We obtained bootstrap sample data vectors from independently identically distributed sampling consisting of 1,250 trial quadruplets of [K, L_∞, L_c, L_λ] of normally distributed deviates selected from uniform distributions with replacement. The model's corresponding parameters L_c and L_λ were estimated by bootstrapping the parameters L_∞, K and t_0 of the von Bertalanffy equation, and then solving the equation exactly at the constrained points.

We then formed the mean value of the bootstrap estimates across replications (following Lewis and Orav 1989)

$$\hat{\theta}^*_m(\bullet) = \frac{1}{B}\sum_{b=1}^{B} \hat{\theta}^*_m(b), \tag{20}$$

where $\hat{\theta}^*_m(b)$ are the b replicated bootstrap estimates. The bootstrap estimate of the standard deviation of $\hat{\theta}^*_m(\bullet)$ is

$$S_B = \left[\sum_{b=1}^{B} \frac{[\hat{\theta}^*_m(b) - \hat{\theta}^*_m(\bullet)]^2}{B-1}\right]^{\frac{1}{2}}. \tag{21}$$

The resulting bootstrap estimates of equation 18 are $\hat{\theta}^*_m(\bullet)$=0.477 and S_B=0.258. The correlation matrix for the bootstrap quadruplets of [K, L_∞, L_c, L_λ] was

$$\rho = \begin{bmatrix} 1.000 & 0.0216 & 0.7986 & 0.6646 \\ 0.0216 & 1.0000 & 0.5656 & 0.7541 \\ 0.7986 & 0.5656 & 1.0000 & 0.9620 \\ 0.6646 & 0.7541 & 0.9620 & 1.0000 \end{bmatrix} \tag{22}$$

Discussion

The length-based Z-estimator of Beverton and Holt (1956) is robust if recruitment to the fishery is knife-edge, provided that L_∞ and catch mean length are the only information available (Wetherall et al. 1987). Knife-edge fishing mortality, however, may be questionable in many tropical fisheries where size distributions in the landings represent compounded size ranges defined by the selective characters of the many gears used in these fisheries. This situation may be further complicated by the behavior of some species which makes them more or less available to the usually restricted operational range of most artisanal fleets. Thus, for example, some coastal migratory pelagic species (e.g., scombrids) form dense temporal spatial schools at earlier ages, becoming isolated swimmers at older ages; highly selective gill nets of several mesh sizes used in these fisheries operate seasonally within the restricted size range of schooling migratory fish (Ehrhardt and Die 1988).

For species exhibiting bounded exploitable life spans the Beverton and Holt's (1956) Z-estimator always over-estimated the true value of total mortality, primarily because the model was developed under the simplifying assumption that maximum age was

infinite. Of course, bias in Z will be close to zero when the exploitable life span approaches the biological life span of longer-lived species. However, from a management standpoint, protection of juveniles to avoid growth and possibly recruitment overfishing will always be a desirable strategy to protect the stocks. Reduction in exploitable life span is obviously more significant when minimum fish size management is implemented on shorter lived species. Therefore, estimates of Z derived from Beverton and Holt's (1956) procedure for these species will always be positively biased.

We found that bias of the Z-estimator of Beverton and Holt (1956) decreased as fishing mortality rates, F, increased. This resulted from the upper limits of the population length distribution being numerically obliterated at higher mortality levels. It is expected, therefore, that in fisheries where F is controlled by quotas or limitation of fishing effort the Z-estimator will always be positively biased.

The mortality model expressed by equation 18 by considering catch mean length as a function of L_∞, K, L_c, L_λ, F and M is not affected by bounding exploitable life spans, and hence, under similar conditions equation 18 is more robust than Beverton and Holt's (1956) estimator. However, because of the extra parameter (L_λ) introduced in equation 18, a greater variance must be associated with the new Z-estimator.

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Table 1. Population parameters for three species of tropical fish used in the analysis of relative bias of the Z-estimate of Beverton and Holt (1956).

Species	Parameter estimates				
	K	t_o	M	t_λ	L_∞
Lane snapper	0.35	-0.90	0.82	6	350
Yellowfin grouper	0.17	0.00	0.29	15	860
Snowy grouper	0.09	-1.01	0.18	27	1,320

Table 2. Relative bias (%) of the Z-estimate of Beverton and Holt (1956) for several exploitable life spans and fishing mortality rates for three tropical fish species.

(t_1-t_0) years	Fishing mortality rate F				
	0.1	0.3	0.5	0.7	0.9
			Lane snapper		
0.5	359.43	284.58	232.60	194.48	165.36
1.0	146.18	110.76	86.46	68.91	55.74
1.5	77.95	56.09	41.44	31.16	23.71
2.0	45.97	31.17	21.61	15.18	10.74
2.5	28.43	18.04	11.64	7.57	4.94
3.0	18.02	10.62	6.33	3.79	2.26
3.5	11.56	6.29	3.44	1.88	1.03
4.0	7.46	3.73	1.86	0.93	0.46
4.5	4.81	2.21	1.00	0.45	0.20
5.0	3.11	1.30	0.53	0.22	0.09
			Yellowfin grouper		
1.0	435.21	267.36	185.12	136.62	104.86
2.0	182.50	102.75	64.70	43.09	29.61
3.0	100.81	51.26	28.77	16.86	10.08
4.0	61.87	28.00	13.74	6.93	3.51
5.0	40.00	15.88	6.70	2.86	1.21
6.0	26.61	9.15	3.27	1.16	0.41
7.0	18.00	5.29	1.58	0.47	0.13
8.0	12.28	3.06	0.76	0.18	0.04
9.0	8.42	1.76	0.36	0.07	0.01
10.0	5.79	1.01	0.17	0.03	0.00
11.0	3.98	0.58	0.08	0.01	0.00
12.0	2.74	0.33	0.04	0.00	0.00
13.0	1.87	0.19	0.02	0.00	0.00
14.0	1.29	0.11	0.00	0.00	0.00

Table 2 continued

			Snowy grouper		
2.0	284.64	142.47	85.44	55.52	37.65
3.0	167.93	76.65	41.37	23.89	14.21
4.0	110.80	45.61	21.80	10.96	5.59
5.0	77.50	28.46	11.87	5.10	2.19
6.0	56.12	18.19	6.52	2.36	0.84
7.0	41.54	11.76	3.58	1.08	0.32
8.0	31.20	7.64	1.96	0.49	0.11
9.0	23.66	4.97	1.06	0.22	0.04
10.0	18.06	3.23	0.57	0.10	0.02
11.0	13.82	2.09	0.31	0.04	0.01
12.0	10.63	1.35	0.16	0.02	0.00
13.0	8.18	0.87	0.09	0.00	0.00
14.0	6.30	0.56	0.05	0.00	0.00
15.0	4.85	0.36	0.02	0.00	0.00
16.0	3.74	0.22	0.01	0.00	0.00
17.0	2.88	0.14	0.00	0.00	0.00
18.0	2.21	0.09	0.00	0.00	0.00
19.0	1.69	0.06	0.00	0.00	0.00
20.0	1.30	0.04	0.00	0.00	0.00
21.0	1.00	0.02	0.00	0.00	0.00
22.0	0.77	0.01	0.00	0.00	0.00
23.0	0.59	0.00	0.00	0.00	0.00
24.0	0.44	0.00	0.00	0.00	0.00
25.0	0.34	0.00	0.00	0.00	0.00
26.0	0.26	0.00	0.00	0.00	0.00

Table 3. Parameters of the simulated population of Chilean hake used in the mortality estimation sensitivity analyses. Data from Ehrhardt (1973).

Parameter	$\bar{X}$	$SE_{\bar{X}}$
L_∞	63.90 cm	0.780
K	0.33	0.009
t_o	+0.04	0.021
M	0.38	0.084
t_c	2.50	
t_λ	5.00	
L_c	35.53	
L_λ	51.47	

Table 4. Values of the D measure (equation 19) for various perturbations in the input parameter values for Chilean hake. The perturbed parameter is indicated in the table's first column and the magnitude of the perturbation in the first row. Dashes indicate that the level of parameter change was undefined. The input value of total mortality rate was 0.48.

		Perturbation U_i (percent)									
Parameter	Input value	-40	-20	-10	-5	-1	1	5	10	20	40
K	0.33	-40.01	-20.01	-10.01	-4.86	-0.92	0.90	5.14	9.99	19.99	39.98
L_∞	51.47	–	–	–	–	-15.42	13.42	51.19	75.97	91.23	–
$\bar{L}$	43.01	∞	∞	439.17	161.21	28.80	-27.97	–	–	–	–
L_c	35.53	–	–	-90.25	-53.06	-12.34	13.40	81.51	224.01	3639.4	–
L_m	63.9	–	–	-10.54	-5.22	-1.05	1.02	5.13	10.24	20.39	40.56

Table 5. Results of a Monte Carlo simulation experiment for mortality estimates derived from equations (6) and (18) and based on the data for Chilean hake. [Input Z=0.480, $\bar{L}$ = 43.01, + = stochastic variable, - = deterministic variable, U = undefined response, n/a = not applicable].

Case	Parameters				Equation and Coefficient of Variation (C.V.)			
	K	L_∞	L_c	L_λ	Equation 6	C.V.	Equation 18	C.V.
1	-	-	-	-	0.922	0.0	0.480	0.0
2	+	-	-	-	0.924	2.6	0.482	2.6
3	+	+	-	-	0.928	4.3	0.483	2.9
4	+	-	+	-	0.937	11.9	0.501	26.9
5	+	-	-	+	n/a	n/a	0.484	17.9
6	-	+	-	-	0.920	3.7	0.480	1.2
7	-	+	+	-	0.927	10.4	0.489	19.4
8	-	-	-	+	n/a	n/a	0.482	18.4
9	-	-	+	-	0.924	2.9	0.486	7.8
10	-	-	+	+	n/a	n/a	0.483	9.5
11	-	-	-	+	n/a	n/a	U	U
12	+	+	-	+	n/a	n/a	0.479	27.0
13	+	-	+	+	n/a	n/a	0.510	41.9
14	-	+	+	+	n/a	n/a	0.490	37.7
15	+	+	+	-	0.924	14.4	0.487	29.9
16	+	+	+	+	n/a	n/a	0.499	55.3

Figure 1. Representative ranges of asymptotic lengths and maximum ages of tropical fish species according to references given in the text (circles). The triangles are the species utilized in the sensitivity analyses of this paper. (LS = lane snapper; CH = chilean hake; YG = yellowfin grouper; SG = snowy grouper).

Figure 2. Percent bias of Beverton and Holt's (1956) formula under two levels of fishing mortality (Figure 2A: F=0.1; Figure 2B: F=0.3), three levels of maximum age (6, 15 and 27 years), and three fractions (▪ = 0.33, ▲ = 0.50 and ● = 0.66) of total exploitable life span expressed as t_c/t_λ.

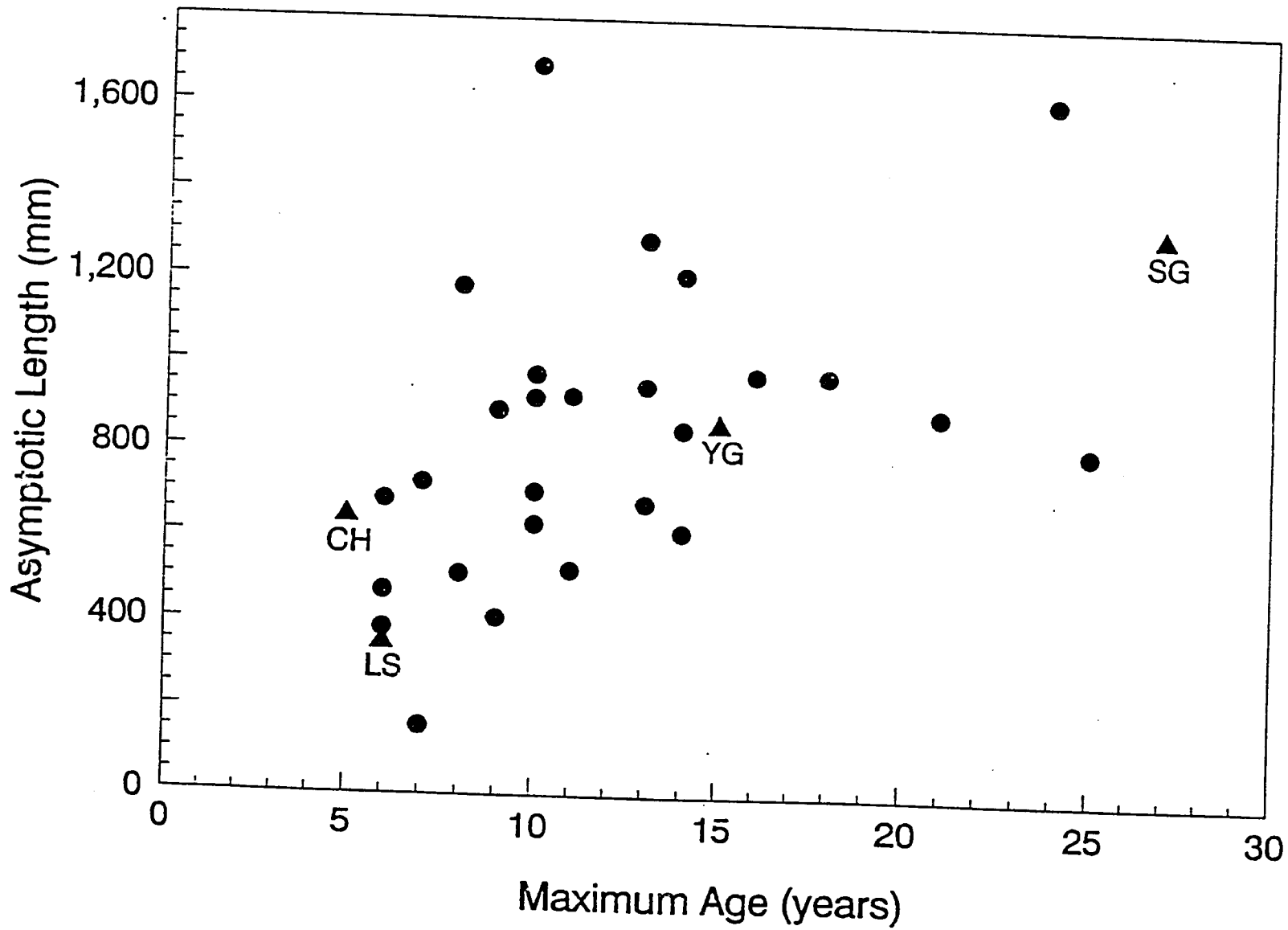
Asymptotic Length (mm)
1,600
1,200
800
400
0
0
5
10
15
20
25
30
Maximum Age (years)
SG
YG
CH
LS

Figure 1

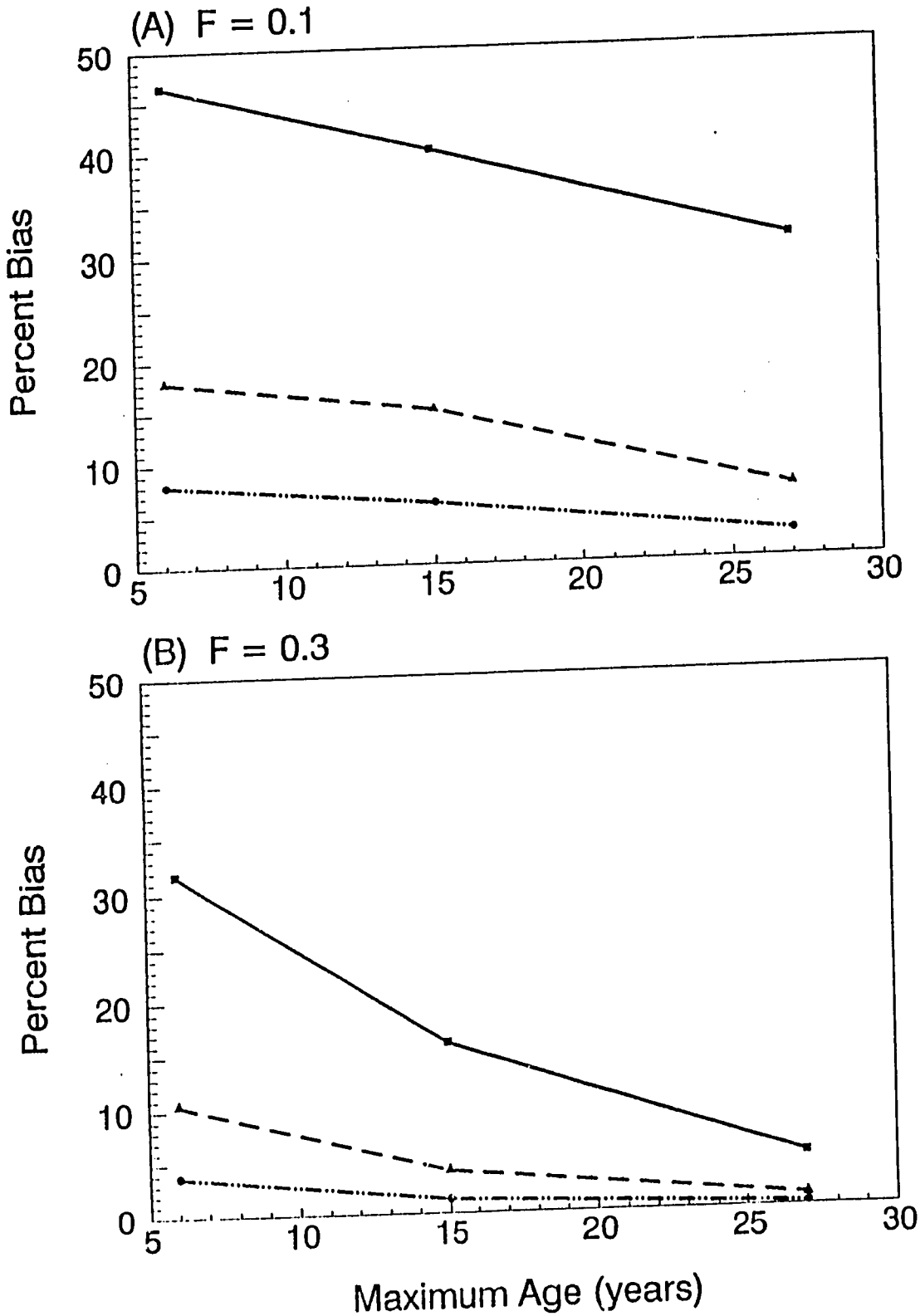
(A) F = 0.1
Percent Bias
50
40
30
20
10
0
5
10
15
20
25
30
(B) F = 0.3
Percent Bias
50
40
30
20
10
0
5
10
15
20
25
30
Maximum Age (years)

Figure 2