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Bias in the Wetherall Estimates of Z/K and L_∞ Due to Population Disequilibria

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Abstract

The method of Wetherall (1986, Fishbyte 4(1):12-14) for estimating Z/K and L_∞ from length-frequency data sampled from a population in equilibrium (constant recruitment and mortality) was examined through simulation of population experiencing rapid change in recruitment and fishing mortality. The results show a large bias of Z/K and L_∞ to be generated under non-equilibrium situation; this bias cannot be removed by smoothing. However, departure from equilibrium can be detected, and hence the conditions identified where the method remains applicable.

Introduction

The regression estimator of Z/K and L_∞ developed in Wetherall et al. (1987) has recently received considerable use in cases in which the length frequencies are not multimodal or are from only a single sample (Wetherall 1986; Arellano 1989; Polovina 1989; Rawlinson 1989). This estimator is based on the assumption of an equilibrium population (i.e., a population experiencing fishing effort and recruitment that are constant). Although Wetherall et al. (1987) clearly caution potential users of the bias that may result from applying the method to populations not in equilibrium, no estimates of the likely magnitudes of such bias were provided. This prompted us to investigate the sensitivity of the method to two common types of perturbations: 1) a rapid increase in effort during the fishing-up stage of a fishery and 2) a one-year doubling of recruitment. Here we examine the bias associated with these types of disequilibria.

Assessing the Wetherall Method

Performance of the Wetherall method was assessed by applying it to catch length frequencies generated by a population simulation model. The model - which was configured to simulate a population of opakapaka, *Pristipomoides filamentosus*, a Hawaiian deepwater snapper - accounted for growth, fishing and natural mortality, size selectivity of the fishing gear, and recruitment. Simulations of a rapid increase in fishing effort started with the equilibrium length-frequency distribution that would occur in the absence of fishing. Fishing mortality was set at 0.6 $year^{-1}$, and the model was then run until the new equilibrium length-frequency distribution was obtained. Simulations of a one-year doubling of recruitment started with the equilibrium length-frequency distribution at a fishing mortality of 0.6 $year^{-1}$. Annual recruitment was doubled for one year, and the model was then run to the new equilibrium. In both cases, Z/K and L_∞ were estimated each year subsequent to the perturbation by applying the Wetherall method to the simulated catch length frequencies.

These simulations indicated that the bias in Z/K and L_∞ varies tremendously between the initial perturbation and the subsequent equilibrium. When fishing effort was increased rapidly, the bias in Z/K was initially negative, then became positive before decaying to zero (Fig. 1A). The bias in L_∞ varied similarly with time but was almost always positive and considerably smaller than that of Z/K (Fig. 1A). When recruitment was doubled for one year, the bias of Z/K was initially positive, then became negative (Fig. 1B). The bias of L_∞ varied similarly, but again was considerably smaller than that of Z/K. Although the simulated changes in fishing mortality and recruitment may be more abrupt than those typically experienced by a population, the results clearly demonstrate that disequilibrium can cause large bias in Z/K estimates.

Two possible methods for minimizing the risk of obtaining such biased estimates of Z/K and L_∞ were examined. First, we examined whether

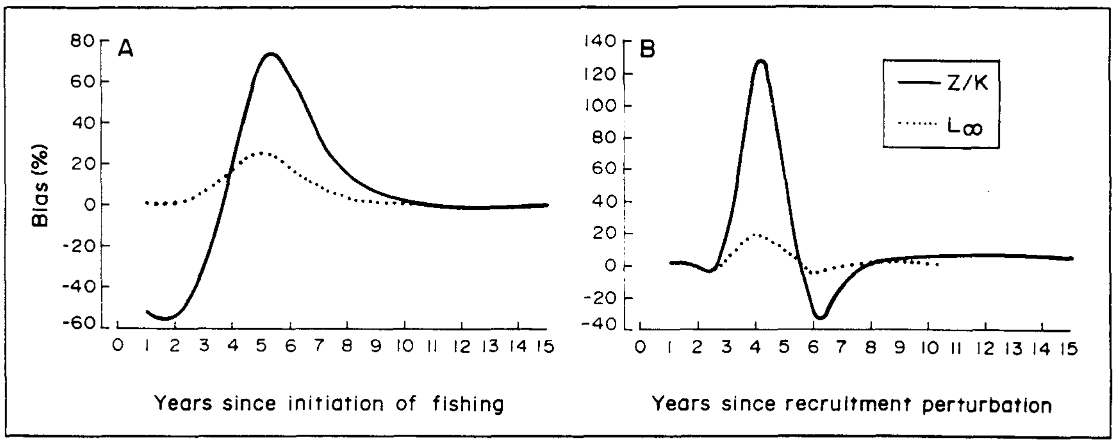

Fig. 1. Time trajectories of Z/K bias and L_∞ bias after (A) a rapid increase of fishing effort and (B) a one-year doubling of recruitment.

smoothing the length-frequency distributions by using a three-year running average before application of the Wetherall method would reduce the effects of the perturbation. The effectiveness of smoothing depended on the type of perturbation. When fishing effort was rapidly increased, smoothing had almost no effect on Z/K bias (Fig. 2A), but when recruitment was doubled, smoothing had a greater effect, especially during periods of maximum bias, when reductions in Z/K bias were up to 30% (Fig. 2B). Overall, however, the three-year smoothing appears to be an ineffective way of reducing disequilibrium bias.

Second, we examined the possibility of statistically detecting the disequilibrium conditions that lead to bias. This was done by comparing the catch length-frequency distribution in any one year to those from the previous two years by using a chi-square test of independence. The rationale for this type of test is that a population in equilibrium should produce catch length frequencies that, except for sampling variability, are identically distributed over time. Significance of the chi-square test therefore indicates that the population is not in equilibrium. The statistical power of the test was examined in a Monte Carlo experiment where the test was applied to catch length frequencies generated by the population simulation model. For each of the disequilibrium simulations, annual catch length frequencies were subsampled with replacement (N =

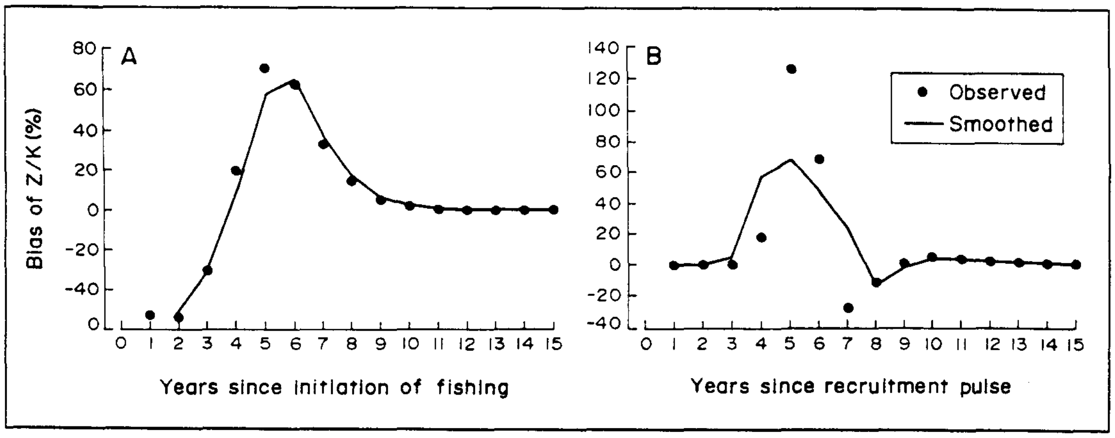

Fig. 2. Time trajectories of Z/K bias after (A) a rapid increase in fishing effort and (B) a one-year doubling of recruitment are shown before and after smoothing catch length frequencies with a three-year running average.

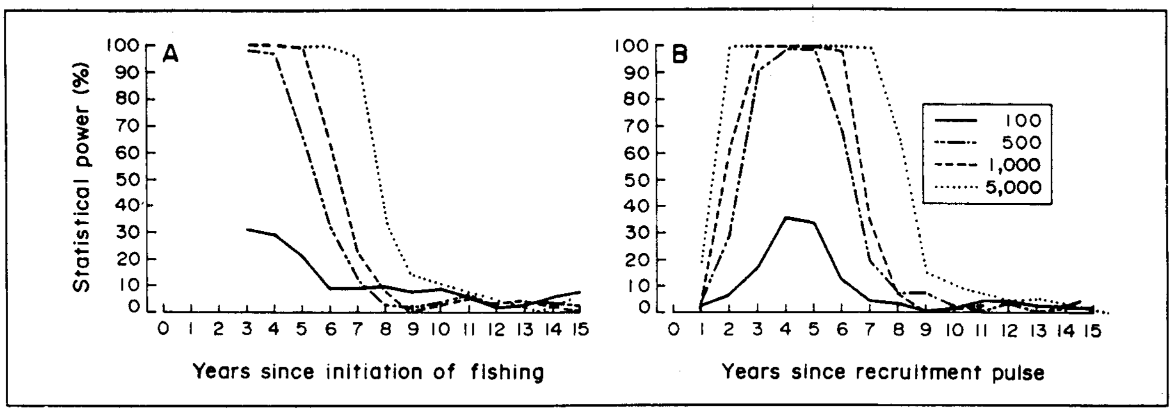

Fig. 3. Time trajectories in the statistical power of a chi-square test to detect population disequilibrium at each of four levels of sampling (N = 100; 500; 1,000; and 5,000 fish) for (A) a rapid increase in fishing effort and (B) a one-year doubling of recruitment (B).

100; 500; 1,000; 5,000 fish). At each level of subsampling, a chi-square test of independence was performed on each three-year sequence of length frequencies. Subsampling and testing were replicated 100 times, and statistical power was estimated as the proportion of the 100 tests that was significant at the 5% level.

The utility of the chi-square test in detecting conditions that likely result in biased estimates can be assessed by comparing the bias curves (Fig. 1) with the power curves (Fig. 3). For example, when fishing effort was rapidly increased and the sample size was 5,000 fish, the power of detecting disequilibria was high (i.e., >0.75) from years 3 to 7 (Fig. 3A). This indicates that, except for the first two years of the series when data were insufficient, the chi-square test had a high probability of detecting perturbations leading to Z/K bias greater than 10%. Compared with the cases of increasing effort, when recruitment was doubled for one year, power was high over a broader time period and tended to stay high with declining sample sizes (Fig. 3B). Thus, provided sample sizes are reasonably large, the chi-square test appears to be an effective way of detecting disequilibrium conditions and thereby avoiding bias.

From the foregoing, it is clear that disequilibrium bias in the Wetherall estimates of Z/K and L_∞ can be large and that averaging length frequencies over time does not remove such bias. Thus, the Wetherall method should be used with extreme caution on new or changing fisheries or species experiencing recruitment fluctuations, and in all cases, its use should be preceded by a statistical verification of population equilibrium.

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