

## Are exploited fish populations stable?

Shelton and Mangel (1) examined patterns of variability in fish populations and concluded that the higher stock variability observed in exploited species results from heightened effects of stochastic forcing in the supposed absence of nonlinear dynamics. In contrast, Anderson et al. (2) found that higher variability in these stocks is attributable to amplified nonlinear behavior in noisy ecological systems under exploitation. Here, we reconcile these apparently conflicting views and demonstrate that stochasticity of demographic parameters directly enhances nonlinearity (2–4), thus challenging assessments of stability based on statistical fits to noise-free models.

Shelton and Mangel (1) concluded that fish populations are stable based on observed values of the maximum growth rate under an assumed Ricker model formulation. This argument requires that the Ricker model is a precise representation of nature—beyond observational error, the model accurately explains all variation in abundances (i.e., no process error) (2, 3). A similar argument for stability of insect populations (4) demonstrates that such analyses are valid only if nature is literally a controlled single-species experiment.

The empirical finding of nonlinearity by Anderson et al. (2) is based on a nonparametric analysis of data that does not depend on specifying a particular underlying structural model (S-map analysis; refs. 2, 3). Further, they explored the properties of the Ricker model with process error to demonstrate that fishing magnifies variability in harvested populations when stochasticity and deterministic nonlinearity interact to amplify overall nonlinear behavior; neither alone suffices to drive this result (2) (figures 4, 5, and S5 in ref. 2).

Unstable dynamics can occur at low values of growth when modest process noise is introduced (i.e., when noisy inputs from, e.g., multispecies factors or environmental factors are acknowledged) (2, 3). Process noise represents dynamics remaining unexplained in a model; it represents the degree to which a single-species model does not fully explain the data. Because stability depends on how process noise (i.e., unknown part) convolves with a noise-free skeleton (i.e., hypothesized deterministic model), one cannot evaluate stability with a model alone if it is an approximation (3, 5). Thus, defining quantitative thresholds for stability in natural populations assuming a purely deterministic model (1) is inappropriate.

In Fig. 1, we repeat the Anderson et al. (2) analysis using simulations from Shelton and Mangel (1) to show how stochastic forcing acting on demographic parameters produces amplified

nonlinear behavior and higher variability. We measure nonlinearity by using the nonparametric S-map procedure (3, 5), wherein  $\Delta\rho$  represents the difference in accuracy between linear and nonlinear forecasts. For small reproductive rate ( $\alpha$ ) and small noise levels, the dynamics are nearly linear. Increasing variability in  $\alpha$  elevates nonlinearity and increases variability (Fig. 1). This effect is more pronounced as age-selective fishing increases  $\alpha$  (2).

The simulations of Shelton and Mangel (1) lend support to earlier results (2) demonstrating how age-selective fishing will increase the relative demographic contribution of recruits and amplify the destabilizing effect of environmental variability. Importantly, magnified fluctuations in exploited fish abundance reflect strengthened nonlinearity emerging as demographic parameters change and are coupled with environmental variability (2). As such, fishing can destabilize exploited stocks.

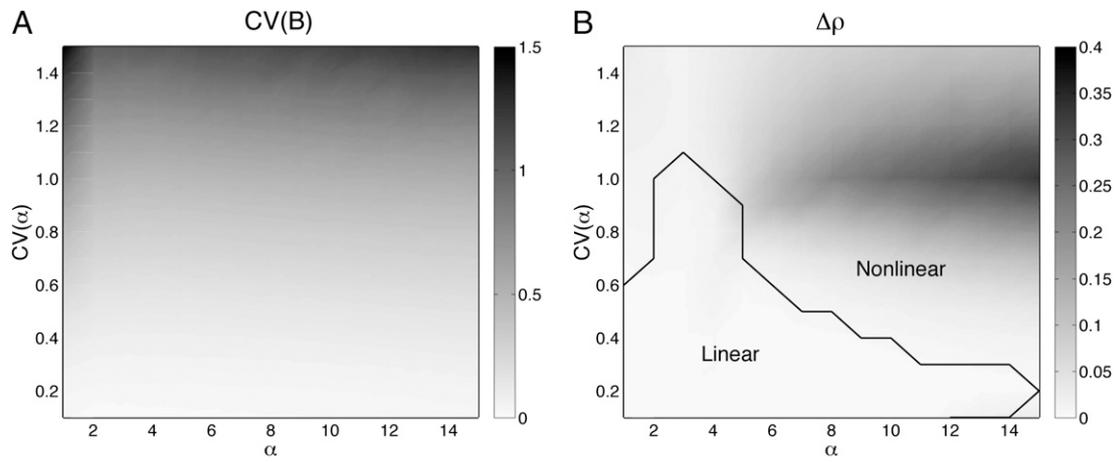
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**Fig. 1.** Coefficient of variation of fish abundance (A) and nonlinearity (B) as a function of  $\alpha$  and coefficient of variation of  $\alpha$  [ $CV(\alpha)$ ]. Simulation follows the procedure described by Shelton and Mangel (2), with a  $\beta$  value of 0.001, total mortality of 0.8,  $\tau$  value of 1,  $\alpha$  values of 1 to 15, and  $CV(\alpha)$ s of 0.1 to 1.5. To account for randomness, 100 simulations were carried out for each parameter combination and the average was presented. Following the S-map procedure,  $\Delta\rho$  is used as a measure of nonlinearity. The 95% confidence limit was computed for each parameter combination, and statistical significance of nonlinearity is determined and illustrated as the solid line in B.