

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 (α) and small noise levels, the dynamics are nearly linear. Increasing variability in α elevates nonlinearity and increases variability (Fig. 1). This effect is more pronounced as age-selective fishing increases α (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.

George Sugihara^{a,1}, John Beddington^b, Chih-hao Hsieh^c, Ethan Deyle^a, Michael Fogarty^d, Sarah M. Glaser^e, Roger Hewitt^f, Anne Hollowed^g, Robert M. May^h, Stephan B. Munchⁱ, Charles Perretti^a, Andrew A. Rosenbergⁱ, Stuart Sandin^a, and Hao Ye^a

^aScripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093; ^bDivision of Biology, Faculty of Natural Sciences, Imperial College London, London SW7 2AZ, United Kingdom; ^cInstitute of Oceanography and Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei 10617, Taiwan; ^dNational Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA 02543; ^eDepartment of Biology, College of William and Mary, Williamsburg, VA 23185; ^fNational Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA 92037; ^gNational Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, WA 98115; ^hDepartment of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom; ⁱFisheries Ecology Division, Southwest Fisheries Science Center, Santa Cruz, CA 95060; and ¹Department of Science and Knowledge, Conservation International, Arlington, VA 22202

- Shelton AO, Mangel M (2011) Fluctuations of fish populations and the magnifying effects of fishing. *Proc Natl Acad Sci USA* 108:7075–7080.
- Anderson CNK, et al. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* 452:835–839.
- Sugihara G (1994) Nonlinear forecasting for the classification of natural time series. *Phil Trans R Soc Lond Ser A* 348:477–495.
- Hassell MP, Lawson JH, May RM (1976) Patterns of dynamical behavior in single-species populations. *J Anim Ecol* 45:471–487.
- Hsieh CH, Glaser SM, Lucas AJ, Sugihara G (2005) Distinguishing random environmental fluctuations from ecological catastrophes for the north Pacific ocean. *Nature* 435:336–340.

Author contributions: G.S., J.B., R.M.M., A.A.R., and S.S. designed research; G.S., C.-h.H., E.D., M.F., S.M.G., R.H., A.H., S.B.M., C.P., and H.Y. performed research; G.S., C.-h.H., S.M.G., S.B.M., and H.Y. analyzed data; and G.S., J.B., C.-h.H., M.F., S.B.M., and S.S. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. E-mail: gsugihara@ucsd.edu.

