Reply to Sugihara et al: The biology of variability in fish populations

Sugihara et al. (1) ask, "Are exploited fish populations stable?" and conclude that they are not. We concur. However, we do not concur that Shelton and Mangel (2) "conclude that fish populations are stable..." or that "higher stock variability observed in exploited species results from heightened effects of stochastic forcing in the supposed absence of nonlinear dynamics" (1).

We (2) started from the observation that many natural populations of fish fluctuate in abundance. By using available data from a diverse range of species, we showed that single deterministic nonlinear dynamics are very unlikely to drive the variability of natural populations. This mismatch between model and data indicates that the variability in natural populations is not well explained by deterministic single-species models. Thus, we agree with Sugihara et al. (1) that nature is not well conceived as a single-species experiment. The question is then "how does one introduce multispecies aspects in a practicable manner?"

We investigated biological mechanisms that could drive fluctuations in populations. We used analytic and simulation approaches to illustrate how the inclusion of variation in measurable biological processes [the maximum reproductive rate (α) or natural mortality] may contribute to temporal variation. We examined published or biologically reasonable ranges of parameter variation and various correlation structures between these parameters to understand how stochasticity from unobserved abiotic or multispecies factors may interact with nonlinear dynamics and fisheries exploitation to generate temporal variation. Although we introduce process stochasticity in a different manner than the S-map (1) and acknowledge that the Ricker model is not the only possible model for this process (i.e., there is model uncertainty; see ref. 2), the implication that we did not consider process stochasticity is incorrect. Furthermore, as we used the nonlinear Ricker model, we concur with Sugihara et al. (1) that the interaction between nonlinear dynamics

and stochasticity must lie at the heart of the variability of populations.

We also showed how fishing pressure increases the variability of populations even if there are no fishing-induced changes to the productivity of a population. The available experimental and observational evidence suggests that the maximum reproductive rate will remain unchanged (e.g., ref. 3) or decrease when large, old fish are removed from the population (e.g., refs. 4, 5). However, our work is silent on the consequences of age-selective harvesting for population dynamics and neither supports nor contradicts the conclusions outlined by Sugihara et al. (1). The role age structure plays in population dynamics and the interaction between age structure and exploitation are both topics that deserve further attention.

In summary, we consider that there are few substantive differences between our conclusions and the critical points made by Sugihara et al. (1). Perhaps our differences arise from distinct motivations. If one is more interested in forecasting, the S-map and associated methodologies that model the data are an excellent route, but if one is interested in understanding the underlying mechanisms, one must model the process, even with its limitations.

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