Sensitivity analysis of density-dependent matrix population models: a generalization of the Takada-Nakajima theorem

Hal Caswell[1] .

In a linear matrix population model

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \tag{1}$$

population performance can be measured by the population growth rate λ, given by the dominant eigenvalue of $\mathbf{A}$. The sensitivity and elasticity of λ to changes in the entries of $\mathbf{A}$ provide a wealth of information about the effects of environmental change, the action of natural selection, and the efficacy of management strategies. It is natural to try to extend this approach to nonlinear models

$$\mathbf{n}(t+1) = \mathbf{A}_{\mathbf{n}(t)}\mathbf{n}(t). \tag{2}$$

When the system converges to a stable equilibrium $\hat{\mathbf{n}}$, some measure of population density is an appealing choice of a measure of population performance. In the special case in which all density effects operate through a single linear combination of stage-specific densities, $N = \mathbf{g}^{\mathbf{n}}$, Takada and Nakajima (1998) showed that the sensitivity of λ calculated from the matrix at equilibrium $\mathbf{A}_{\hat{\mathbf{n}}}$ is proportional to the sensitivity of N.

Here, we generalize this result to the case where $\mathbf{A}_{\mathbf{n}(t)}$ depends on an arbitrary number of measures of density, $N_1 = f_1(\mathbf{n})$, $N_2 = f_2(\mathbf{n})$, $\ldots$, each of which is an arbitrary differentiable function of $\mathbf{n}$. We show that the sensitivity of λ calculated from $\mathbf{A}_{\hat{\mathbf{n}}}$ is always equal to the sensitivity of a *biologically effective density* $\tilde{N} = \sum_i c_i n_i$, which is a weighted sum of

[1] Biology Department MS-34, Woods Hole Oceanographic Institution, Woods Hole MA 02543, USA (e-mail: hcaswell@whoi.edu).

the stage densities n_i; i.e.

$$\frac{\partial\lambda}{a_{ij}} = \frac{\partial\tilde{N}}{a_{ij}} \tag{3}$$

The weight c_i associated with stage i depends on the effect[s] of n_i on the vital rates and the importance of those vital rates to λ at equilibrium. The biologically effective density thus measures population size in a way that incorporates both density-dependence and demography. The close relationship between the sensitivity of λ and the sensitivity of the biologically effective density has implications for studies of evolution, environmental stressors, and conservation biology.

References

[1] Takada, T. and Nakajima, H. (1998) Theorems on the invasion process in stage-structured populations with density-dependent dynamics. Journal of Mathematical Biology, 36:497–514.