STABILITY ANALYSIS OF CONTINUOUS AND DISCRETE POPULATION MODELS

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(*Received* 14 *March* 1978)

The stabilities of corresponding continuous and discrete population models for interacting species with same points of equilibrium have been examined for a general case. The special cases of the host-parasite models of Leslie and Gower and Watts have been considered in detail. While in most cases the continuous and discrete models may be both stable or both unstable, it is also possible that one may be stable and the other may be unstable. For the operator used in this paper, we have given a case where the difference equation model is less stable, but for other operators, this model may be even more stable than the other. The conclusions of stability analysis of two types of models need not therefore be the same.

1. INTRODUCTION

The choice between continuous and discrete population models from the point of view of stability has been discussed by a number of authors including Driessche (1974), Innes (1974), May (1973a, 1973b), and Usher (1969). From his discussions, May (1973b) concluded that :

"It is widely understood that difference equations tend to be less stable than their differential equations twins, because the finite time lapse between generations of growth will have the destabilizing effects associated with any time lag in an interacting system. Our discussion makes it explicit; clearly stability of the difference equation implies stability of the differential equation one, but the converse is not necessarily true."

However, Driessche (1974) gave an operator for which the difference equation system is as stable as the differential equation one. Later we (Kapur and Khan 1978) gave another operator for which the difference equation system can be even more stable than the differential equation one.

Recently Biswas (1975) has recommended the use of difference equation systems for their simplicity in numerical computation. For the difference equation analogue

$$N_i(t+h) = \lambda_i^h N_i(t)/[1 + (\lambda_i^h - 1) f_i(N_1, N_2, \ldots, N_m)] \quad (i = 1, 2, \ldots, m) \quad \ldots(1)$$

of the differential equation model.

$$\frac{dN_i}{dt} = N_i \ln \lambda_1 [1 - f_i(N_1, N_2, ..., N_m)], \qquad (i = 1, 2, ..., m) \qquad ...(2)$$

he showed that for $h = 1$, there will be stable oscillations about the equilibrium position $(\bar{N}_1, \bar{N}_2, ..., \bar{N}_m)$ if the absolute values of the roots of the equation

$$\det | A - zI | = 0 \qquad ...(3)$$

are less than unity where

$$A_{ij} = \delta_{ij} - \bar{N}_i \frac{\lambda_i - 1}{\lambda_i}\left(\overline{\frac{\partial f_i}{\partial N_j}}\right). \qquad ...(4)$$

In particular he considered the well-known host-parasite interaction model of Leslie and Gower (1960) viz.

$$\frac{dH}{dt} = (a_1 - c_1 P) H, \; \frac{dP}{dt} = \left(a_2 - c_2 \frac{P}{H}\right) P. \qquad ...(5)$$

For $a_1 = 1$, $c_1 = 0.1$, $a_2 = 1$, $c_2 = 2.5$, Pielou (1969) had shown that the differential equation model gives stable oscillations about $\bar{H} = 25$, $\bar{P} = 10$. Biswas (1975) showed that his difference equation model also gives stable oscillations in this case. Neither of them discussed the stability for general values of a_1, c_1, a_2, c_2.

In the present paper, we show that even though a differential equation system and a difference equation system may have the same points of equilibrium, it is possible that one may be stable and the other may be unstable. As such, for discussion of stability, we cannot always replace the differential equation system by a difference equation system in spite of the fact that in some cases both the systems may be simultaneously stable or simultaneously unstable.

2. Stability Analysis of the Two Systems

By carrying out the usual stability analysis, it can be shown that the equilibrium position $\bar{N}_1, \bar{N}_2, ..., \bar{N}_m$ given by

$$f_i(N_1, N_2, ..., N_m) = 1, \qquad i = 1, 2, ..., m \qquad ...(6)$$

of the system (2) will be stable if all the m roots of the determinantal equation

$$\left|\lambda \delta_{ij} + \bar{N}_i \ln \lambda_i \left(\overline{\frac{\partial f_i}{\partial N_j}}\right)\right| = 0 \qquad ...(7)$$

have their real parts negative. Similarly the same equilibrium position for the system (1) will be stable if all the m roots of the equation

$$\left| (z^h - 1)\,\delta_{ij} + \bar{N}_i \frac{\lambda_i^h - 1}{\lambda_i^h} \left(\frac{\overline{\partial f_i}}{\partial N_j}\right) \right| = 0 \qquad \text{...(8)}$$

have their absolute values less than unity. As $h \to 0$, eqn. (8) gives

$$\underset{h \to 0}{\text{Lt}} \left| \frac{z^h - 1}{h}\,\delta_{ij} + \frac{\bar{N}_i}{\lambda_i^h} \frac{\lambda_i^h - 1}{h} \left(\frac{\overline{\partial f_i}}{\partial N_j}\right) \right| = 0 \qquad \text{...(9)}$$

or

$$\left| \ln z\,\delta_{ij} + \bar{N}_i \ln \lambda_i \left(\frac{\overline{\partial f_i}}{\partial N_j}\right) \right| = 0. \qquad \text{...(10)}$$

The two eqns. (7) and (10) are identical if

$$\lambda = \ln z \qquad \text{...(11)}$$

The last equation shows that

$$|\, z \,| < 1 \Leftrightarrow \text{Re}\,\lambda < 0 \qquad \text{...(12)}$$

so that in the limit when $h \to 0$, the two systems are both stable or both unstable. This is otherwise obvious since when $h \to 0$, the difference equation system tends to the differential equation system.

However for non-zero h, (12) may not be satisfied by solutions of (7) and (8). There is no *a priori* reason that whenever Re $\lambda < 0$, for all roots of (7), we should have $|\, z \,| < 1$ for all roots of (8) and vice-versa i.e. there is no *a priori* reason for the two systems to be simultaneously stable or unstable.

3. Some Special Cases

3.1 *The Case of One Specie*

For $m = 1$, the two models are

$$\frac{dN}{dt} = N(a - bN) \qquad \text{...(13)}$$

$$N(t + h) = \frac{e^{ah} N(t)}{1 + \frac{a}{b}\,(e^{ah} - 1)\, N(t)} \qquad \text{...(14)}$$

Equations (7) and (8) give

$$\lambda + a = 0, \quad z = e^{-a} \qquad \text{...(15)}$$

so that Re $\lambda < 0$ and $|z| < 1$. The position $\bar{N} = a/b$ is stable for both models. In fact in this case both (13) and (14) have a common solution viz

$$N(t) = \frac{\frac{a}{b}}{1 + ce^{-at}} \qquad \ldots(16)$$

where c is a constant.

3.2 *The Model of Leslie and Gower*

In this case eqns. (7) and (8) give on simplification

$$\lambda^2 + \lambda a_2 + a_1 a_2 = 0 \qquad \ldots(17)$$

and

$$(z^h - 1)^2 + (z^h - 1)\, k_2 + k_1 k_2 = 0 \qquad \ldots(18)$$

where

$$k_1 = 1 - e^{-a_1 h}, \;\; k_2 = 1 - e^{-a_2 h}. \qquad \ldots(19)$$

It is interesting to observe that in both cases, stability depends only on a_1, a_2 and not on c_1, c_2.

It is easily seen that for both roots of (17), Re $\lambda < 0$ and for both roots of (18), $|z| < 1$. As such both the models will show stable oscillations about the common position of equilibrium for all values of a_1, a_2, c_1, c_2 and h.

3.3 *Watts Host-parasite Model*

Watts (1959) gave the model

$$\frac{dH}{dt} = (a_1 - c_1 P)\, H, \; \frac{dP}{dt} = (a_2 - c_2 P e^{-cH})\, P. \qquad \ldots(20)$$

The equilibrium position is given by

$$\bar{P} = \frac{a_1}{c_1}, \; c\bar{H} = \ln \frac{a_1 c_2}{a_2 c_1} > 0. \qquad \ldots(21)$$

Equation (7) gives on simplification

$$\lambda^2 + \lambda a_2 + a_1 a_2 \ln \frac{a_1 c_2}{a_2 c_1} = 0 \qquad \ldots(22)$$

for both roots of which Re $\lambda < 0$.

For the difference equation model, Biswas (1975) obtained

$$z^2 - (a + 1)\, z + (a + b) = 0 \qquad \ldots(23)$$

where on simplification

$$a = \frac{1}{\lambda_2},\ b = \frac{\lambda_1 - 1}{\lambda_1}\,\frac{\lambda_2 - 1}{\lambda_2}\ \ln \frac{c_2 a_1}{c_1 a_2}. \qquad \text{...(24)}$$

For both values of $| z |$ to be < 1, we require

$$b > 0,\ \ a + b > 0,\ \ 2 + 2a + b > 0 \qquad \text{...(25)}$$

which are all satisfied.

Therefore in this case both differential equation and difference equation models give stable oscillations.

3.4 *Case of Two Species*

In this case eqns. (7) and (8) reduce to the forms

$$\lambda^2 + \lambda(c_{11} \ln \lambda_1 + c_{22} \ln \lambda_2) + \ln \lambda_1 \ln \lambda_2(c_{11}c_{22} - c_{12}c_{21}) = 0 \qquad \text{...(26)}$$

$$(z^h - 1)^2 + (z^h - 1)\left(c_{11}\,\frac{(\lambda_1^h - 1)}{\lambda_1^h} + c_{22}\,\frac{\lambda_2^h - 1}{\lambda_2^h}\right) + \frac{\lambda_1^h - 1}{\lambda_1^h}\,\frac{\lambda_2^h - 1}{\lambda_2^h}$$

$$\times\ (c_{11}c_{22} - c_{12}c_{21}) = 0. \qquad \text{...(27)}$$

For the food-competition model

$$\frac{dx}{dt} = ax - bxy,\ \frac{dy}{dt} = cy - dxy \qquad \text{..(28)}$$

we get $c_{11} = c_{22} = 0$ and these reduce to

$$\lambda^2 - c_{12}c_{21} \ln \lambda_1 \ln \lambda_2 = 0 \qquad \text{...(29)}$$

$$(z^h - 1)^2 + (c_{12}c_{21})\,\frac{\lambda_1^h - 1}{\lambda_1^h}\,\frac{\lambda_2^h - 1}{\lambda_2^h} = 0 \qquad \text{...(30)}$$

and both give unstable oscillations.

3.5 *Case of m Species*

Consider the special case when $\lambda_1 = \lambda_2 = \ldots = \lambda_m$. Let

$$\ln \lambda_i = k\,\frac{\lambda_i^h - 1}{\lambda_i^h} \quad (i = 1, 2, \ldots, m). \qquad \text{...(31)}$$

In this case eqns. (7) and (8) give

$$\lambda = k(z^h - 1) \quad \text{...(32)}$$

so that

$$|z| < 1 \Rightarrow |\lambda + k| < k \quad \text{...(33)}$$

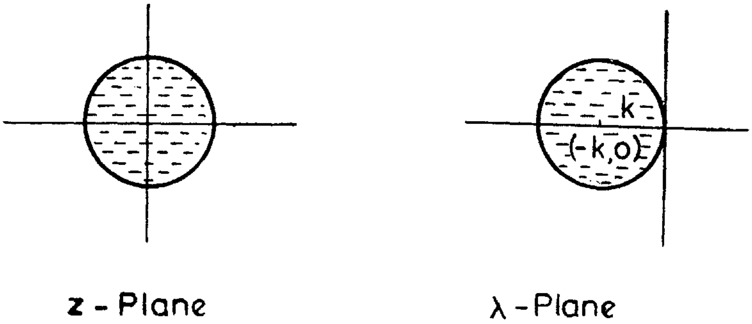

FIG. 1.

If the difference equation system is stable, $|z| < 1$ and $|\lambda + k| < k$ so that the differential equation system is also stable, but if the differential equation system is stable, Re $\lambda < 0$ and $|z|$ can be greater than unity, so that in this case the difference equation system is not stable.

4. Conclusion

In all the cases we have considered, we find that the two systems are both stable or both unstable or the difference equation system is less stable. We have however used that operator for which May (1973b) had drawn his conclusion that the difference equation system tends to be less stable. By using other operators we can construct difference equation models which may be as stable or even more stable than the corresponding differential equation systems. It is obvious however that the stabilities of two systems have to be discussed separately.

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