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STABILITY ANALYSIS OF A DIFFERENCE EQUATION POPULATION MODEL WITH DELAYED RECRUITMENT

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Ricker's and Goh's four-parameter population models with delayed recruitment, have been generalized to five and six parameter models and stability analysis has been carried out for these models. The special form of the characteristic equations for these models enables us to make a statement about the effect of increasing delay. This statement had earlier been conjectured on the basis of particular cases. Stability analysis has also been carried out for Chapman's recruitment function model. In the case of no delay, the condition for instability is found to be the same as the condition for the existence of two-period fixed points.

1. DIFFERENT MODELS

Let $N(t)$ denote the density of a breeding population at time t, then Clark's (1976) difference equation model for the population growth is given by

$$N(t+1) = SN(t) + F[N(t-\theta)] \qquad \ldots(1)$$

where S is the survival coefficient and $F[N(t-\theta)]$ is the recruitment to the breeding population at time t produced by the breeding population at time $t-\theta$.

Four commonly used forms for $F(x)$ are:

(i) logistic model : $F(x) = rx(1 - xK^{-1})$ ...(2)

(ii) Ricker's model : $F(x) = Axe^{-Bx}$ ...(3)

(iii) Goh's model : $F(x) = Axe^{-Bx^2}$ ...(4)

(iv) Chapman's model : $F(x) = A(1 - e^{-Bx})$. ...(5)

The logistic model is considered inappropriate for population levels above K since the model implies negative recruitment in this case. We can however consider an alternative model

$$F(x) = \frac{Ax}{(1 + Bk^{-1}x^r)^k} \qquad \ldots(6)$$

which does not suffer from this defect. As $k \to \infty$, this gives

$$F(x) = Axe^{-Bx^r} \qquad \ldots(7)$$

which includes both Ricker's and Goh's models as particular cases.

We thus get the following models with delayed recruitment:

$$\text{I}: \quad N(t+1) = SN(t) + AN(t-\theta)\exp[-BN(t-\theta)] \qquad \ldots(8)$$

$$\text{II}: \quad N(t+1) = SN(t) + AN(t-\theta)\exp[-BN^2(t-\theta)] \qquad \ldots(9)$$

$$\text{III}: \quad N(t+1) = SN(t) + AN(t-\theta)\exp[-BN^r(t-\theta)] \qquad \ldots(10)$$

$$\text{IV}: \quad N(t+1) = SN(t) + AN(t-\theta)[1 + Bk^{-1}N^r(t-\theta)]^{-k} \qquad \ldots(11)$$

$$\text{V}: \quad N(t+1) = SN(t) + A[1 - \exp(-BN(t-\theta)]. \qquad \ldots(12)$$

Models I, II and V involve four parameters viz. S, A, B, θ. Model III involves five parameters viz. S, A, B, θ and r, while Model IV involves six parameters viz. S, A, B, θ, r and k.

As $k \to \infty$, Model IV reduces to Model III. When $r = 1, 2$, Model III reduces to Models I and II respectively. Here r and k are assumed to be positive, but need not be integers.

Goh and Agnew (1978) have considered the stability of Model II and compared some of their results with those for Model I. By considering Model III, we can discuss the effect of variation parameter r on the equilibrium position and its stability. Similarly by considering Model IV, we can discuss the effects of variations of both r and k. Goh and Agnew (1978) have also considered the effect of delay parameter θ by examining the special cases $\theta = 0, 1, 2$ only and then making a conjecture for other values of θ. We find it possible to give a proof of this conjecture.

An alternative method to discuss the stability for the case of no delay is in terms of the existence of two-period fixed points. We show that the two considerations give the same criteria for stability in the case of the first four models.

2. The Third Model

The equilibrium value for the model (10) is given by

$$\bar{N} = S\bar{N} + A\bar{N}\exp(-B\bar{N}^r) \qquad \ldots(13)$$

or

$$B\bar{N}^r = \ln\frac{A}{1-S}. \qquad \ldots(14)$$

Obviously for this position to exist, it is necessary that

$$A > 1 - S \qquad \ldots(15)$$

and this condition is independent of B, θ and r. Substituting

$$N(t) = \bar{N} + u(t) \qquad \ldots(16)$$

in (10) and linearizing, we get

$$u(t+1) = Su(t) + (1-S)(1 - rB\bar{N}^r)\, u(t-\theta). \quad \text{...(17)}$$

Trying the solution

$$u(t) = Ke^{\lambda t} \quad \text{...(18)}$$

we get the characteristic equation

$$\lambda = S + \frac{1-S}{\lambda^\theta}\left[1 - \ln\left(\frac{A}{1-S}\right)^r\right]. \quad \text{...(19)}$$

For $r = 2$, we get

$$\lambda = S + \frac{1-S}{\lambda^\theta}\left[1 - \ln\left(\frac{A}{1-S}\right)^2\right]. \quad \text{...(20)}$$

Comparison of (19) and (20) shows that all the results of Goh and Agnew (1978) obtained for $r = 2$ can be generalized for a general value of r by replacing $[A/(1-S)]^2$ by $[A/(1-S)]^r$. Thus the condition for stability is

$$A < A^* \quad \text{...(21)}$$

where for

$$\theta = 0,\ A^* = (1-S)\left(\exp\frac{2}{1-S}\right)^{1/r} \quad \text{...(22)}$$

for

$$\theta = 1,\ A^* = (1-S)\left(\exp\frac{2-S}{1-S}\right)^{1/r} \quad \text{...(23)}$$

for

$$\theta = 2,\ A^* = (1-S)\left[\exp\left(\frac{1-1.5S}{1-S} + \frac{(1+(\frac{1}{2}S)^2)^{1/2})}{1-S}\right)\right]. \quad \text{...(24)}$$

For $\theta = n - 1$, (19) gives

$$P(\lambda) \equiv \lambda^n - \lambda^{n-1}S - (1-S)\left(1 - \ln\left(\frac{A}{1-S}\right)^r\right) = 0. \quad \text{...(25)}$$

For applying Jurys' version (Jury and Blanchard 1948) of the classical Schur-Cohen conditions, we have

$$a_n = 1,\ \ a_{n-1} = -S,\ \ a_0 = -(1-S)\left(1 - \ln\left(\frac{A}{1-S}\right)^r\right) = M \text{ (say)} \quad \text{...(26)}$$

$$b_{n-1} = -MS,\ \ b_1 = S,\ \ b_0 = M^2 - 1 \quad \text{...(27)}$$

$$c_{n-2} = S^2M,\ c_1 = S(M^2 - 1),\ c_0 = (M^2 - 1)^2 - (MS)^2 \qquad \ldots(28)$$

$$\ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots$$

and all other elements are zero. The non-zero elements are

$$a_n,\ a_{n-1},\ a_0;\ b_{n-1},\ b_1,\ b_0;\ c_{n-2},\ c_1,\ c_0;\ \ldots\ . \qquad \ldots(29)$$

What is important is that all the elements in (29) are independent of n. Jury's criteria for stability are:

$$P(1) > 0;\ P(-1) > 0 \quad \text{for } n \text{ even};\ \ P(-1) < 0 \text{ for } n \text{ odd} \qquad \ldots(30)$$

$$|a_0| < a_n,\ \ |b_0| > |b_{n-1}|,\ \ |c_0| > |c_{n-2}|,\ \ |d_0| > |d_{n-3}|,$$
$$\ldots \quad ,\ |s_0| > |s_2|\ . \qquad \ldots(31)$$

In view of (15), the condition $P(1) > 0$ is satisfied for all n.

For n even, $P(-1) > 0$ is easily seen to be satisfied

For n odd $P(-1) < 0$ gives

$$-2 + (1 - S)\ln\left(\frac{A}{1-S}\right)^r < 0 \qquad \ldots(32)$$

which is the same as (22)

$$|a_0| < a_n \Rightarrow \left|1 - \ln\left(\frac{A}{1-S}\right)^r\right| < \frac{1}{1-S}$$

$$\Rightarrow -\frac{1}{1-S} < 1 - \ln\left(\frac{A}{1-S}\right)^r < \frac{1}{1-S}$$

$$\Rightarrow \frac{2-S}{1-S} > \ln\left(\frac{A}{1-S}\right)^r \qquad \ldots(33)$$

which is the same as (23).

The condition $|b_0| > |b_{n-1}|$ gives (24) and so on. Thus for $n = 1$, we have the condition (22). For $n = 2$, we get the additional condition (23). For $n = 3$, we have the further additional condition (24) and so on. Thus the conditions for stability are of the form:

For $n = 1, \theta = 0 : A < f_1(S)$; for $n = 2, \theta = 1 : A < f_1(S), A < f_2(S)$;
for $n = 3, \theta = 2 : A < f_1(S), A < f_2(S), A < f_3(S), \ldots$

so that the region of stability goes on becoming smaller and smaller as n or θ or delay parameter increases.

From eqn. (22) for $\theta = 0$, we get

$$\frac{1}{A^*}\frac{dA^*}{dS} = \frac{2}{r(1-S)^2}\left[1 - \frac{r}{2}(1-S)\right] \qquad \ldots(34)$$

so that

$$\frac{dA^*}{dS} > 0 \quad \text{if} \quad S > 1 - \frac{2}{r}. \qquad \text{...(35)}$$

This for $r = 1$, A^* is always increasing, for $r = 2$, A^* increases for $S > 0$ for $r = 3$, it decreases up to $S = \frac{1}{3}$ and then increases and for $r = 4$ it decreases up to $S = \frac{1}{2}$ and then increases.

From eqn. (23), for $\theta = 1$, we get

$$\frac{1}{A^*}\frac{dA^*}{dS} = -\frac{1}{1-S} + \frac{1}{r}\frac{1}{(1-S)^2} \qquad \text{...(36)}$$

so that A^* is minimum at $S = 1 - \dfrac{1}{r}$.

Thus for $r = 1$, A^* is increasing for $S > 0$, for $r = 2$ it decreases till $S = \frac{1}{2}$ and then increases, for $r = 3$ it decreases till $S = \frac{2}{3}$ and then increases and so on.

Table I gives the values of A^* for $S = 0.0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9$, for $r = 1, 2, 4$ and for $\theta = 0, 1, 2, \infty$. The value $\theta = \infty$ corresponds to Clark's (1976) condition discussed in section 5. The table shows that

(i) for fixed r and S, the value of A^* for which equilibrium is stable decreases as θ increases;

(ii) for fixed θ and S, the value of A^* for which equilibrium is stable decreases as r increases;

(iii) for fixed r and θ, in general, the value of A^* for static equilibrium first decreases with S and then increases;

(iv) the value of A^* increases sharply as $S \to 1$;

(v) Clarks' values give a great underestimate for A^* except for $S = 0$.

3. The Fourth Model

Here

$$N(t+1) = SN(t) + \frac{AN(t-\theta)}{[1 + Bk^{-1}N^r(t-\theta)]^k}. \qquad \text{...(37)}$$

The equilibrium value is given by

$$\bar{N} = S\bar{N} + \frac{AN}{(1 + Bk^{-1}\bar{N}^r)^r} \quad \text{or} \quad \bar{N} = \left[\frac{k}{B}\left(\left(\frac{A}{1-S}\right)^{1/k} - 1\right)\right]^{1/r}. \qquad \text{...(38)}$$

The condition (15) has still to be satisfied. Making the substitution (16), linearizing and simplifying, we get

TABLE I

Values of A^* for various values of r, θ and S

$S \backslash \theta$	0	1	2	∞
		$r = 1$		
0.0	7.3891	7.3891	7.3891	7.3891
0.1	8.3050	7.4317	7.0398	6.8502
0.2	9.7460	7.5902	6.7402	5.9113
0.3	12.1882	7.9399	6.5116	5.1693
0.4	16.8190	8.6352	6.3950	4.4335
0.5	27.2990	10.0428	6.4780	3.6945
0.6	59.3653	13.2462	6.9851	2.9556
0.7	235.7316	22.8597	8.6950	2.2167
0.8	445.2931	80.6858	16.0503	1.4778
0.9	485.1652	5987.4142	174.7351	0.7389
		$r = 2$		
0.0	2.7183	2.7183	2.7183	2.3183
0.1	2.7340	2.5862	2.5171	2.4464
0.2	2.7923	2.4642	2.3221	2.1746
0.3	2.9210	2.3575	2.5350	1.9028
0.4	3.1767	2.2762	1.9588	1.6309
0.5	3.6945	2.2408	1.7997	1.3591
0.6	4.8730	2.3008	1.6715	1.0873
0.7	8.4095	2.6087	1.6136	0.8155
0.8	29.6826	4.0871	1.7917	0.5436
0.9	2202.64066	24.4692	4.1801	0.2718
		$r = 4$		
0.0	1.6487	1.6487	1.6487	1.6487
0.1	1.5686	1.5256	1.5051	1.4838
0.2	1.4946	1.4040	1.3630	1.3189
0.3	1.4299	1.2846	1.2225	1.1581
0.4	1.3806	1.1686	1.0841	1.9892
0.5	1.3591	1.0585	0.9486	0.8243
0.6	1.39614	0.9599	0.8177	0.6594
0.7	1.5823	0.8863	0.6958	0.4946
0.8	2.4364	0.89634	0.5986	0.3297
0.9	14.8413	1.5643	0.6465	0.1649

$$u(t+1) = Su(t) + (1-S)\left[1 - kr\left(1 - \left(\frac{1-S}{A}\right)^{1/k}\right)u(t-\theta).\right. \quad \text{...(39)}$$

The characteristic equation is

$$\lambda = S + \frac{1-S}{\lambda^{\theta}}\left[1 - kr\left(1 - \left(\frac{1-S}{A}\right)^{1/k}\right)\right]. \quad \text{...(40)}$$

As $k \to \infty$, this gives

$$\lambda = S + \frac{1-S}{\lambda^{\theta}}\left(1 - r\ln\frac{A}{1-S}\right) \quad \text{...(41)}$$

which is the same as (19). Comparing with (22), (23), (24), we get for our present model:

$$\text{For} \quad \theta = 0 \;:\; \left(\frac{A^*}{1-S}\right)^{-1/k} = 1 - \frac{1}{kr}\frac{2}{1-S}. \quad \text{...(42)}$$

$$\text{For} \quad \theta = 1 \;:\; \left(\frac{A^*}{1-S}\right)^{-1/k} = 1 - \frac{1}{kr}\frac{2-S}{1-S}. \quad \text{...(43)}$$

$$\text{For} \quad \theta = 2 \;:\; \left(\frac{A^*}{1-S}\right)^{-1/k} = 1 - \frac{1}{kr}\frac{1 - 1.5S + (1 + \frac{1}{4}S^2)^{1/2}}{1-S}. \quad \text{...(44)}$$

As $k \to \infty$, these give (22), (23), (24) and when $k \to \infty$ and $r = 2$, these give Goh and Agnew's (1978) results.

The equilibrium would be stable if

$$\text{for} \quad \theta = 0, \; S > 1 - \frac{2}{kr} \quad \text{and for} \quad \theta = 1, \; S > 1 - \frac{1}{kr-1}. \quad \text{...(45)}$$

Let us keep θ fixed at zero and r fixed at 2, then for $k = 2$, the equilibrium is stable for $S \geqslant \frac{1}{2}$ for all A and for $S < \frac{1}{2}$, it is stable if

$$A < (1-S)\left(1 - \frac{1}{2}\frac{1}{1-S}\right)^{-2} \quad \text{...(46)}$$

for $k = 3$, the equilibrium is stable for $S \geqslant \frac{2}{3}$ for all A and for $S < \frac{2}{3}$, it is stable if

$$A < (1-S)\left(1 - \frac{1}{3}\frac{1}{1-S}\right)^{-3} \quad \text{...(47)}$$

and so on till as $k \to \infty$, the equilibrium is stable if

$$A < (1-S)\exp\left(\frac{1}{1-S}\right). \quad \text{...(48)}$$

In Fig. 1 the regions of stable equilibrium are below the corresponding curves for various values of k. As k increases, the region of stability goes on decreasing and the last region is obtained as $k \to \infty$ corresponding to Model III.

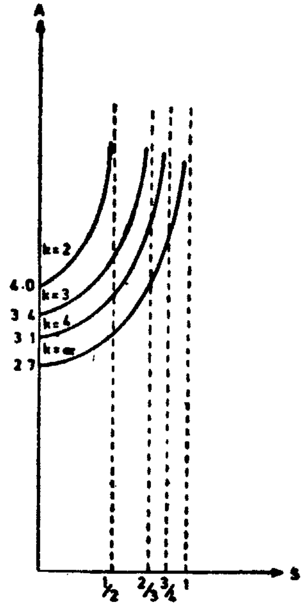

FIG. 1. Regions of stable equilibrium for $\theta = 0$, $r = 2$.

4. THE FIFTH MODEL

If we use Chapman's (1973) recruitment function, we get the model

$$N(t+1) = SN(t) + A(1 - \exp(-bN(t-\theta)). \qquad \text{...(49)}$$

The equilibrium value $\bar{N}$ is given by

$$\bar{N} = S\bar{N} + A(1 - \exp(-b\bar{N})) \qquad \text{...(50)}$$

$\bar{N}$ is obtained by finding the point of intersection of

$$y = \bar{N}\,\frac{1-S}{A} \quad \text{and} \quad y = 1 - \exp(-b\bar{N}). \qquad \text{...(51)}$$

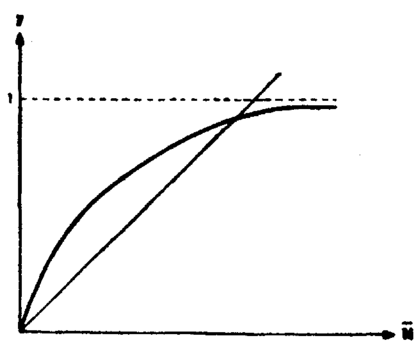

FIG. 2. Finding $\bar{N}$ for Chapman's model.

The slope of the first curve is constant and equal to $(1 - S)/A$, while the slope of the second curve is $be^{-b\bar{N}}$ and is maximum initially. There will exist a unique value of $\bar{N}$ only if

$$b > \frac{1-S}{A} \quad \text{or} \quad \frac{A}{1-S} > \frac{1}{b}. \qquad \ldots(52)$$

Also from (50)

$$A - \bar{N}(1-S) > 0 \quad \text{or} \quad \frac{A}{1-S} > \bar{N} \quad \text{or} \quad \bar{N} < \frac{A}{1-S}. \qquad \ldots(53)$$

The characteristic equation is given by

$$\lambda = S + \frac{A}{\lambda^n} be^{-b\bar{N}} \quad \text{or} \quad P(\lambda) = \lambda^n - \lambda^{n-1}S - A\,be^{-b\bar{N}} = 0 \qquad \ldots(54)$$

which is of the same form as (26), (27) with

$$M = -A\,be^{-b\bar{N}} < 0. \qquad \ldots(55)$$

Schur-Cohen conditions give the following:

$$P(1) > 0 \Rightarrow 1 - S - b\,[A - \bar{N}(1-S)] > 0 \Rightarrow \frac{A}{1-S} < \frac{1}{b} + \bar{N} = OA. \qquad \ldots(56)$$

For n even $P(-1) > 0 \Rightarrow 1 + S - b(A - \bar{N}(1-S)) > 0.$ ...(57)

Inequality (57) is automatically satisfied if (56) is satisfied.

For n odd, $P(-1) < 0 \Rightarrow -1 + S - b\,[A - \bar{N}(1-S)] < 0.$ ...(58)

Inequality (58) is satisfied in view of (53) and the fact that $S < 1$

$$|\,a_0\,| < a_n \Rightarrow b\,[A - \bar{N}(1-S)] < 1 \text{ or } \frac{A}{1-S} < \bar{N} + \frac{1}{b(1-S)} = OB \qquad \ldots(59)$$

$$|\,a_0^2 - a_n^2\,| > |\,a_0 a_{n-1} - a_1 a_n\,| \Rightarrow \frac{A}{1-S} < \bar{N} + \frac{1}{b} \times \frac{[S^2+4]^{1/2} - S}{2(1-S)} = OC. \qquad \ldots(60)$$

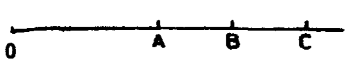

FIG. 3.

It can be shown that

$$S < \frac{[S^2 + 4]^{1/2} - S}{2(1 - S)} < \frac{1}{1 - S}. \quad \text{...(61)}$$

Thus for $\theta = 0$, we want $A/(1 - S)$ to be on the left of A; for $\theta = 1$, we want it to be on the left of A and B; for $\theta = 2$, we want it to be on the left of A, B, C.

In every case, we want it to be on the left of A.

5. Clark's Condition

According to Clark (1976), the region of stability for the fourth model, includes the region given by

$$\left|(1 - S)\left(1 - \ln\left(\frac{A}{1 - S}\right)^r\right)\right| < (1 - S)$$

or

$$\frac{A}{1 - S} < \exp(2/r) \Rightarrow A < (1 - S)\exp(2/r). \quad \text{...(62)}$$

This gives a much smaller region than given by our detailed consideration (Tables I).

For the fifth model, this condition gives

$$Abe^{-b\bar{N}} < 1 \quad \text{or} \quad \frac{A}{1 - S} < \bar{N} + \frac{1}{b}. \quad \text{...(63)}$$

6. Two-Period Fixed Points

(a) *Third Model, No delay*

Eliminating $N(t + 1)$ between

$$N(t + 1) = SN(t) + AN(t)\exp[-BN^r(t)] \quad \text{...(64)}$$

and

$$N(t + 2) = SN(t + 1) + AN(t + 1)\exp[-BN^r(t + 1)] \quad \text{...(65)}$$

we get

$$N(t + 2) = N(t)[S + A\exp(-BN^r(t)]$$
$$\times [S + A\exp(-BN^r(t)(S + A\exp(-BN^r(t))^r)]. \quad \text{...(66)}$$

If $N(t + 2) = N(t) = N_0$ satisfies (66), then we get

$$[S + A\exp(-BN_0^r)]^{-1} = S + A\exp[-BN_0^r(S + A\exp(-BN_0^r))]. \quad \text{...(67)}$$

Substituting

$$S + A\exp(-BN_0^r) = u \quad \text{...(68)}$$

we get

$$f(u) = \frac{1}{u} - S - A\left(\frac{u-S}{A}\right)^{u^r} = 0 \qquad \ldots(69)$$

$u = 1$ satisfies (69) which shows that one-period fixed point is also a two-period fixed point. Now

$$f(S) = \frac{1}{S} - S > 0,\ f(1) = 0,\ f\left(\frac{1}{S}\right) = -\left(\frac{1-S^2}{AS}\right)^{1/Sr} < 0,$$

$$f(\infty) < 0 \qquad \ldots(70)$$

$$f'(u) = -\frac{1}{u^2} - A\left(\frac{u-S}{A}\right)^{u^r}\left[ru^r \ln \frac{u-S}{A} + \frac{u^r}{u-S}\right] \qquad \ldots(71)$$

$$f'(1) = -2 - r(1-S)\ \ln \frac{1-S}{A}. \qquad \ldots(72)$$

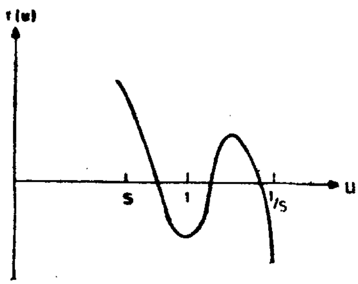

FIG. 4. A typical graph for $f(u)$.

If $f'(1) > 0$, there is a pair of fixed points corresponding to two values of λ, one lying between S and 1 and the other lying between 1 and $1/S$. Thus the condition for the existence of a pair of two-period fixed points is

$$A > (1-S)\left(\exp \frac{2}{1-S}\right)^{1/r} = A^*. \qquad \ldots(73)$$

If $A > A^*$, a pair of two-period fixed points exists and the equilibrium is unstable. If $A < A^*$, this pair does not exist and the equilibrium is unstable.

(b) *Third Model, Unit Delay*

In this case

$$N(t+1) = SN(t) + AN(t-1)\exp(-BN^r(t-1)) \qquad \ldots(74)$$

$$N(t+2) = SN(t+1) + AN(t)\exp(-BN^r(t)). \qquad \ldots(75)$$

Let

$$N(t-1) = N(t+1) = N_1;\ N(t) = N(t+2) = N_2 \qquad \ldots(76)$$

so that

$$N_1 = SN_2 + AN_1 \exp(-BN_1^r) \qquad \text{...(77)}$$

$$N_2 = SN_1 + AN_2 \exp(-BN_2^r). \qquad \text{...(78)}$$

Eliminating N_2, we get

$$\frac{1 - A\exp(-BN_1^r)}{S}\left[1 - A\exp\left(-BN_1^r\,\frac{(1-\exp(-BN_1^r))^r}{S^r}\right)\right] = S. \qquad \text{...(79)}$$

Let

$$\frac{1 - A\exp(-BN_1^r)}{S} = v \qquad \text{...(80)}$$

so that

$$g(v) \equiv \frac{S}{v} - 1 + A\left(\frac{1-vS}{A}\right)^{v^r} = 0;\ v \leqslant 1/S \qquad \text{...(81)}$$

$$g(0) > 0,\quad g(S) > 0,\quad g(1) = 0,\quad g(1/S) < 0. \qquad \text{...(82)}$$

$$g'(1) = -\,2S - r(1-S)\ln\frac{A}{1-S} < 0. \qquad \text{...(83)}$$

As expected $v = 1$ is a solution of (81)

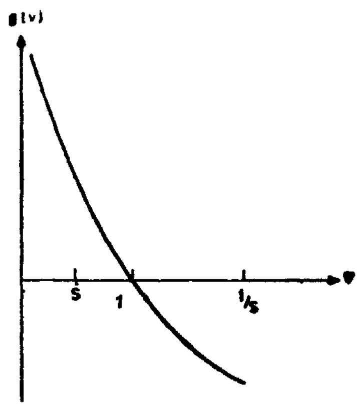

FIG. 5. Typical graph for $g(v)$.

Thus a pair of two-period fixed points does not exist. Thus in the case of non-zero delay, stability is not connected with the existence of two-period fixed points (Kapur 1980, Oster 1975).

(c) *Model IV, No Delay*

Proceeding in the same way for Model IV as in Case I and putting

$$N(t + 2) = N(t) = N_0$$

we get

$$h(w) = \frac{1}{w} - S - \frac{A}{\left[1 + w^r\left(\frac{A}{w - s}\right)^{1/k} - w^r\right]^k}, \; w \geqslant S \qquad ...(84)$$

where

$$w = S + \frac{A}{(1 + Bk^{-1}N_0^r)^k} \qquad ...(85)$$

$$h(S) < 0, \quad h(1) = 0, \quad h(S + A) < 0 \qquad ...(86)$$

$$h'(1) = -2 + rk(1 - S) - k_r(1 - S)\left(\frac{1 - S}{A}\right)^{1/k} \qquad ...(87)$$

$$h'(1) > 0 \text{ if } \left(\frac{A}{1 - S}\right)^{1/k} > \left(1 - \frac{2}{hr(1 - S)}\right)^{-1}. \qquad ...(88)$$

Thus if the equilibrium is unstable, a pair of two-period fixed points exists and vice-versa.

(d) *Model IV, Unit Delay*

In this case, it can be shown as before that a pair of two-period fixed points does not exist.

(e) *A General Model, No Delay*

We consider the general model with no delay

$$N(t + 1) = SN(t) + N(t)\, G\,[N(t)]. \qquad ...(89)$$

Eliminating $N(t + 1)$, between (89) and

$$N(t + 2) = SN(t + 1) + N(t + 1)\, G(N(t + 1)) \qquad ...(90)$$

we get

$$N(t + 2) = [SN(t) + N(t)\, G(N(t))]\, [S + G(SN(t) + N(t) G(N(t))] \qquad ...(91)$$

so that if $N(t + 2) = N(t) = N_0$, we get

$$\frac{1}{S + G(N_0)} = S + G\,[SN_0 + N_0G(N_0)]. \qquad ...(92)$$

Substituting

$$S + G(N_0) = z \qquad ...(93)$$

$$\phi(z) \equiv \frac{1}{z} - S - G(N_0 z) = 0. \qquad ...(94)$$

In (94), we have to regard N_0 as a function of z defined by (93), then it is easily seen that $z = 1$ satisfies (94).

$$\phi'(z) = \frac{1}{z^2} - G'(N_0 z)\left[N_0 + z\frac{dN_0}{dz}\right], \; G'(N_0)\frac{dN_0}{dz} = 1 \qquad ...(95)$$

$$\phi'(1) = -2 - N_0 G'(N_0), \; G(N_0) = 1 - S. \qquad ...(96)$$

For a pair of two-period fixed points to exist, we require

$$-N_0 G'(N_0) > 2, \quad G(N_0) = 1 - S. \qquad ...(97)$$

For Model III $G(N) = A \exp(-BN^r)$, eqn. (97) gives

$$\frac{A}{1-S} > \exp\frac{2}{r(1-S)} \qquad ...(98)$$

which is the same as (22).

For Model IV $G(N) = \frac{A}{(1 + Bk^{-1}N^r)^k}$ and (67) gives

$$\left(\frac{A}{1-S}\right)^{-1/k} < 1 - \frac{2}{rk}\frac{1}{1-S} \qquad ...(99)$$

which gives the same result as (42).

For Model V $G(N) = \frac{A(1 - \exp(-BN))}{N}$ and (97) gives

$$\frac{A}{1-S} < N_0 - \frac{1}{b}\frac{1+S}{1-S} \qquad ...(100)$$

which is different from (6).

(f) *General Discussion*

We find that for Models I, II, III and IV, in the case of no delay, the existence of two-period fixed points implies the instability of the equilibrium position and vice-versa. This does not happen in the case of Model V. The reason lies in the different shapes of the graphs of the recruitment function $F(x)$. While in the first four models, the graph of $F(x)$ starts at the origin, then rises to a maximum and falls to zero steadily afterwards, for model V, the graph starts at the origin and then continues to increase and approaches $v = A$ as $x \to \infty$. It is explained elsewhere (Oster 1975) why we should expect a relation between instability and existence of two-period fixed points for functions of the first type.

When there is a non-zero delay, there is no such simple relationship between the two concepts.

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