NONLINEAR CONTINUOUS-TIME DISCRETE-AGE-SCALE POPULATION MODELS

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A general nonlinear continuous-time discrete-age-scale model in which birth and death rates are respectively monotonic decreasing and monotonic increasing functions of the total populations size, is considered. It is shown that whenever the corresponding linear model predicts exponential growth, the nonlinear model gives a stable equilibrium age-distribution. A method for discussing the stability of this equilibrium position is also given. A nonlinear delay model is also formulated and generalised to the case when both density dependence and delay effects are present.

1. Introduction

Let a population be divided into n age-groups and let $x_1(t)$, $x_2(t)$, ..., $x_n(t)$ be the population sizes of these n groups at time t. Let the first p groups be pre-reproductive, the next q groups be reproductive and let the last r groups be post-reproductive so that p+q+r=n. Let the death-rates in the n groups be $d_1, d_2, ..., d_n$ and let the birth-rates in the productive groups be $b_{p+1}, b_{p+2}, ..., b_{p+q}$. Let m_i be the rate at which members of the *i*th group migrate to (i+1)th group, on maturity and survival $(i=1, 2, ..., n-1; m_n=0)$. Kapur (1979a) has studied the following linear model

$$\frac{dx_1}{dt} = b_{p+1}x_{p+1} + \dots + b_{p+q}x_{p+q} - (d_1 + m_1)x_1
\frac{dx_i}{dt} = m_{i-1}x_{i-1} - (d_i + m_i)x_i, \quad i = 2, 3, ..., n$$
...(1)

Kapur (1979b, 1980) has also studied the nonlinear model

$$\frac{dx_1}{dt} = b_{p+1}x_{p+1} + \dots + b_{p+q}x_{p+q} - (d_1 + m_1)x_1 - k_1x_1(x_1 + x_2 + \dots + x_n)
\frac{dx_i}{dt} = m_{i-1}x_{i-1} - (d_i + m_i)x_i - k_ix_i(x_1 + x_2 + \dots + x_n), i = 2, 3, \dots, n.$$
...(2)

In the present paper we consider the more general model in which the birth-rates are monotonic decreasing functions of P(t) and death-rates are monotonic increasing functions of P(t), where P(t) is the total size of the population so that

$$P(t) = x_1(t) + x_2(t) + \dots + x_n(t), \qquad \dots (3)$$

so that our nonlinear model is

$$\frac{dx_1}{dt} = b_{p+1}(P) x_{p+1} + \dots + b_{p+q}(P) x_{p+q} - [d_1(P) + m_1] x_1
\frac{dx_i}{dt} = m_{i-1}x_{i-1} - [d_i(P) + m_i] x_i, \quad i = 2, 3, ..., n.$$

If

$$b_{p+i}(P) = b_{p+i} - c_{p+i}P \quad \text{when} \quad P \leqslant \frac{b_{p+i}}{c_{p+i}}$$

$$= 0 \qquad \text{when} \quad P \geqslant \frac{b_{p+i}}{c_{p+i}}$$

$$(j = 1, 2, ..., q) \qquad ...(5)$$

and

$$d_k(P) = d_k + e_k P \quad k = 1, 2, ..., n,$$
 ...(6)

then eqns. (4) become

$$\frac{dx_{1}}{dt} = b_{p+1}x_{p+1} + \dots + b_{p+q}x_{p+q} - (c_{p+1}x_{p+1} + \dots + c_{p+q}x_{p+q} + e_{1}x_{1}) P - (d_{1} + m_{1}) x_{1} + e_{1}x_{1} P - (d_{i} + m_{i}) x_{i} - e_{i}x_{i}P, \quad i = 2, 3, ..., n.$$

If

$$c_{p+1} = c_{p+2} = \dots = c_{p+q} = 0,$$
 ...(8)

the model represented by (7) is the same as the model represented by (2). Thus the model considered by Kapur (1979b) is a particular case of model (4) above when birth-rates are constants and death-rates increase linearly with population size P. The linear model (1) arises when both birth and death rates are constants.

2. Equilibrium Age-distribution for the General Model

If $\bar{x}_1, \bar{x}_2, ..., \bar{x}_n$ is the equilibrium age-distribution for the model (4) we have

$$b_{p+1}(\bar{P}) \, \bar{x}_{p+1} + \dots + b_{p+q}(\bar{P}) \, \bar{x}_{p+q} - [d_1(\bar{P}) + m_1] \, \bar{x}_1 = 0$$

$$m_{i-1}\bar{x}_{i-1} = [d_i(\bar{P}) + m_i] \, \bar{x}_i, \quad i = 2, 3, ..., n$$

where

$$\overline{P} = \overline{x}_1 + \overline{x}_2 + \dots \overline{x}_n. \tag{10}$$

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Eliminating $\bar{x}_1, \bar{x}_2, ..., \bar{x}_n$ from (9), we get

$$\phi(\bar{P}) \equiv \frac{b_{p+1}(\bar{P})}{(d_{1}(\bar{P}) + m_{1}) \dots (d_{p+1}(\bar{P}) + m_{p+1})} + \frac{b_{p+2}(\bar{P}) m_{p+1}}{(d_{1}(\bar{P}) + m_{1}) \dots (d_{p+2}(\bar{P}) + m_{p+2})} + \dots + \frac{b_{p+q}(\bar{P}) m_{p+1} \dots m_{p+q-1}}{(d_{1}(\bar{P}) + m_{1}) \dots (d_{p+q}(\bar{P}) + m_{p+q})} - \frac{1}{m_{1}m_{2} \dots m_{p}} = 0 \dots (11)$$

so that

$$\frac{d\phi}{d\bar{P}} = \frac{b'_{p+1}(P)}{(d_{1}(\bar{P}) + m_{1}) \dots (d_{p+1}(\bar{P}) + m_{p+1})} + \dots
+ \dots + \frac{b'_{p+1}(\bar{P}) m_{p+1} \dots m_{p+q-1}}{(d_{1}(\bar{P}) + m_{1}) \dots (d_{p+q}(\bar{P}) + m_{p+q})}
- \frac{b_{p+1}(\bar{P})}{(d_{1}(\bar{P}) + m_{1}) \dots (d_{p+1}(\bar{P}) + m_{p+1})} \sum_{k=1}^{p+1} \frac{d'_{k}(P)}{d_{k}(\bar{P}) + m_{k}} - \dots
- \frac{b_{p+q}(\bar{P}) m_{p+1} \dots m_{p+q-1}}{(d_{1}(\bar{P}) + m_{1}) \dots (d_{p+q}(\bar{P}) + m_{p+q})} \sum_{k=1}^{p+q} \frac{d'_{k}(\bar{P})}{d_{k}(\bar{P}) + m_{k}} \cdot \dots (12)$$

Since

$$b_{p+j}(\overline{P}) \geqslant 0, \ b'_{p+j}(\overline{P}) \leqslant 0 \quad \text{for } j = 1, 2, ..., q$$

$$d_{k}(\overline{P}) > 0, \ d'_{k}(\overline{P}) > 0 \quad \text{for } k = 1, 2, ..., n$$

$$...(13)$$

we find that

$$\frac{d\phi}{d\overline{P}} \leqslant 0 \qquad \qquad \dots (14)$$

so that $\phi(\overline{P})$ is a monotonic decreasing function of \overline{P} . In fact $\phi(\overline{P})$ is a strictly decreasing function of \overline{P} except when the population has become so large that all birth rates are zero. Let

$$\begin{cases}
b_{p+i}(0) = b_{p+i}, & j = 1, 2, ..., q \\
d_{k}(0) = d_{k}, & k = 1, 2, ..., n
\end{cases}$$
...(15)

and let

$$\frac{b_{p+1}}{(d_1+m_1)\dots(d_{p+1}+m_{p+1})}+\dots+\frac{b_{p+q}m_{p+1}\dots m_{p+q-1}}{(d_1+m_1)\dots(d_{p+q}+m_{p+q})}\\ -\frac{1}{m_1m_2\dots m_p}>0 \qquad \dots (16)$$

then

$$\phi(0) > 0$$
 ...(17)

As \overline{P} goes on increasing, $\phi(\overline{P})$ goes on decreasing till as \overline{P} tends to infinity $\phi(\overline{P})$ tends to negative value $-\frac{1}{m_1m_2\ldots m_p}$.

Thus if (16) is satisfied, then the equation

$$\phi(\overline{P}) = 0 \qquad ...(18)$$

has a unique positive solution P_0 and an equilibrium age-distribution exists. On using (4), this is given by

$$\frac{\overline{x}_{1}}{(d_{2}(P_{0}) + m_{2}) \dots (d_{n}(P_{0}) + m_{2})} = \frac{\overline{x}_{2}}{m_{1}(d_{3}(P_{0}) + m_{3}) \dots (d_{n}(P_{0}) + m_{n})}$$

$$= \dots \dots$$

$$= \frac{\overline{x}_{n}}{m_{1}m_{2} \dots m_{n-1}} \dots (19)$$

along with

$$\bar{x}_1 + \bar{x}_2 + ... + \bar{x}_n = P_0.$$
 ...(20)

We now proceed to interpret (16).

For the linear model (1), let a solution be given by

$$x_i = B_i e^{\lambda t}$$
 $(i = 1, 2, ..., n)$(21)

Substituting in (1) we get

$$B_{1}\lambda = b_{p+1}B_{p+1} + ... + b_{p+q}B_{p+q} - (d_{1} + m_{1}) B_{1}$$

$$B_{i}\lambda = m_{i-1}B_{i-1} - (d_{i} + m_{i}) B_{i}; \quad i = 2, 3, ..., n.$$

$$...(22)$$

Eliminating $B_1, B_2, ..., B_n$, we get

$$\psi(\lambda) \equiv \frac{b_{p+1}}{(d_1 + m_1 + \lambda) \dots (d_{p+1} + m_{p+1} + \lambda)} + \dots + \frac{b_{p+q}m_{p+1} \dots m_{p+q-1}}{(d_1 + m_1 + \lambda) \dots (d_{p+q} + m_{p+q} + \lambda)} - \frac{1}{m_1m_2 \dots m_p} = 0.$$
...(23)

 $\psi(\lambda)$ is a monotonic decreasing function of λ which decreases from

$$\frac{b_{p+1}}{(d_1+m_1)\dots(d_{p+1}+m_{p+1})}+\dots+\frac{b_{p+q}m_{p+1}\dots m_{p+q-1}}{(d_1+m_1)\dots(d_{p+q}+m_{p+q})}\\-\frac{1}{m_1m_2\dots m_p}$$

to $-\frac{1}{m_1 \dots m_p}$ as λ varies from 0 to ∞ . If (16) is satisfied $\psi(\lambda) = 0$ has a unique positive root λ_0 . In this case, using (21) and the linearity of (1), we find that the populations of all age-groups grow exponentially.

Thus in the case when for the corresponding linear model, all populations grow exponentially, the nonlinear model has an equilibrium age distribution given by (19) and (20).

In the special case when birth rates are constant and death rates increase linearly with P, (11) gives

$$\frac{b_{p+1}}{(d_1 + m_1 + e_1 P_0) \dots (d_{p+1} + m_{p+1} + e_{p+1} P_0)} + \dots
+ \frac{b_{p+q} m_{p+1} \dots m_{p+q-1}}{(d_1 + m_1 + e_1 P_0) \dots (d_1 + m_1 + e_{p+q} P_0)}
= \frac{1}{m_1 m_2 \dots m_p} \cdot \dots (24)$$

Comparing (24) with

$$\frac{b_{p+1}}{(d_1 + m_1 + \lambda_0) \dots (d_{p+1} + m_{p+1} + \lambda_0)} + \dots
+ \frac{b_{p+q} m_{p+1} \dots m_{p+q-1}}{(d_1 + m_1 + \lambda_0) \dots (d_{p+q} + m_{p+q} + \lambda_0)}$$

$$= \frac{1}{m_1 m_2 \dots m_p}, \dots (25)$$

we easily find that P_0 lies between the greatest and least values of (λ_0/e_i) for i varying from 1 to p+q.

We may also note here that if (16) is not satisfied and $\lambda_0 < 0$, then the only equilibrium age distribution is

$$\bar{x}_1 = \bar{x}_2 = \dots = \bar{x}_n = 0 \qquad \qquad \dots (26)$$

3. STABILITY OF THE EQUILIBRIUM AGE-DISTRIBUTION

Let

$$x_i = \bar{x}_i + u_i, \ P = \bar{P} + p, \quad i = 1, 2, ..., n,$$
 ...(27)

Substituting in (4), neglecting squares, products and higher powers of u's and simplifying we get

$$\frac{du_{1}}{dt} = b_{p+1}(\overline{P}) u_{p+1} + \dots + b_{p+q}(\overline{P}) u_{p+q} - (d_{1}(\overline{P}) + m_{1}) u_{1}
+ (u_{1} + u_{2} + \dots + u_{n}) [b'_{p+1}(\overline{P}) \overline{x}_{p+1} + \dots
+ b'_{p+q}(\overline{P}) \overline{x}_{p+q} - d'_{1}(\overline{P}) \overline{x}_{1}]
+ (u_{1} + u_{2} + \dots + u_{n}) u_{i}
- (u_{1} + u_{2} + \dots + u_{n}) d'_{i}(\overline{P}) \overline{x}_{i}; (i = 2, 3, ..., n).$$

We try the solution

$$u_i = c_i e^{\mu t}, \quad i = 1, 2, ..., n$$
 ...(29)

$$(d_{1}(\overline{P}) + m_{1} + \mu) c_{1} = (b_{p+1}(\overline{P}) c_{p+1} + \dots + b_{p+q}(\overline{P}) c_{p+q}) - (c_{1} + c_{2} + \dots + c_{n}) M_{1}$$

$$(d_{i}(\overline{P}) + m_{2} + \mu) c_{i} = m_{i-1}c_{i-1} - M_{i}(c_{1} + c_{2} + \dots + c_{n})$$

$$\dots (30)$$

where $M_1, M_2, ..., M_n$ are positive quantities.

Eliminating $c_1, c_2, ..., c_n$ from (30), we get

where A is matrix with diagonal elements $-(d(P) + m_i + \mu)$, main subdiagonal elements as m_i and (p + 1)th to (p + q)th elements of the first row as

$$b_{p+1}(\bar{P}), ..., b_{p+q}(\bar{P})$$

and the rest of its elements as zero whereas B is the matrix with all the elements of ith row as $-M_i$.

If the real parts of all the roots of (31) are negative, the equilibrium age-distribution is stable.

4. A Nonlinear Delay Model

Here (Cushing 1977) the birth and death rates are monotonic functions not of P(t), but of

$$Q(t) = \int_{-\infty}^{t} K(t-s) P(s) ds = \int_{0}^{\infty} K(u) P(t-u) du, \qquad ...(32)$$

with

$$\int_{0}^{\infty} K(u) du = 1 \qquad ...(33)$$

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i.e. we assume that the birth and death rates do not depend just on the population P(t) at time t, but on the cumulative effects of populations at all earlier times. Our model then becomes

$$\frac{dx_1}{dt} = b_{p+1}(Q) x_{p+1} + \dots + b_{p+q}(Q) x_{p+q} - (d_1(Q) + m_1) x_1$$

$$\frac{dx_i}{dt} = m_{i-1}x_{i-1} - (d_1(Q) + m_i) x_i; \quad (i = 2, 3, ..., n)$$

so that for equilibrium age distribution

$$b_{p+1}(Q_0) \, \overline{x}_{p+1} + \dots + b_{p+q}(Q_0) \, \overline{x}_{p+q} - (d_1(Q_0) + m_1) \, \overline{x}_1 = 0$$

$$m_{i-1} \overline{x}_{i-1} - (d_i(Q_0) + m_i) \, \overline{x}_i = 0 \quad (i = 2, 3, ..., n).$$

If

$$\bar{x}_1 + \bar{x}_2 + ... + \bar{x}_n = P_0$$
 ...(36)

then

$$Q_0 = \int_0^\infty K(u) P_0 du = P_0$$

and we get the same equation as before for determining the equilibrium age distribution, so that equilibrium age distribution exists for this case also and is the same as for the earlier model.

For discussing the stability of this position, let

$$x_i = \bar{x}_i + u_i, \ P(s) = P_0 + p(s), \ Q(t) = Q_0 + q(t)$$
 ...(37)

so that

$$q(t) = \int_{-\alpha}^{t} K(t-s) p(s) ds = \int_{-\alpha}^{t} K(t-s) [u_{1}(s) + ... + u_{n}(s)] ds ...(38)$$

$$\frac{du_{1}}{dt} = b_{p+1}(Q_{0}) u_{p+1} + ... + b_{p+q}(Q_{0}) u_{p+q} + q[b'_{p+1}(Q_{0}) \overline{x}_{p+1} + ... + b'_{p+q}(Q_{0}) \overline{x}_{p+q}]$$

$$- [d_{1}(Q_{0}) + m_{1}] u_{1} - qd'_{1}(Q_{0}) \overline{x}_{1}$$

$$\frac{du_{i}}{dt} = m_{i-1}u_{i-1} - (d_{i}(Q_{0}) + m_{i}) u_{i} - qd'_{i}(Q_{0}) \overline{x}_{i},$$

$$i - 2 \cdot 3 \qquad n$$

Let

$$u_i = D_i e^{vt} \quad (i = 1, 2, ..., n)$$
 ...(40)

i = 2, 3, ..., n

then

$$q(t) = \int_{-\alpha}^{t} K(t-s) [D_{1} + D_{2} + ... + D_{n}] e^{vt} ds$$

$$= \int_{0}^{\infty} K(v) (D_{1} + ... + D_{n}) e^{v(t-\sigma)} dv$$

$$= (D_{1} + ... + D_{n}) e^{vt} K^{*}(v) \qquad ...(41)$$

$$D_{1}^{v} = b_{p+1}(Q_{0}) D_{p+1} + ... + b_{p+q}(Q_{0}) D_{p+q} - [d_{1}(Q_{0}) + m_{1}] D_{1}$$

$$+ (D_{1} + ... + D_{n}) K^{*}(v) [b_{p+1}(Q_{0}) \overline{x}_{p+1} + ...$$

$$+ b_{p+q}(Q_{0}) \overline{x}_{p+q} - d'_{1}(Q_{0}) \overline{x}_{1}]$$

$$D_{i}^{v} = m_{i-1} D_{i-1} - [d_{i}(Q_{0}) + m_{i}] D_{i} - [D_{1} + D_{2} + ...$$

$$+ D_{n}] K^{*}(v) d'_{i} (Q_{0}) \overline{x}_{i}; \quad (i = 2, 3, ..., n)$$

Eliminating $D_1, D_2, ..., D_n$, we get the characteristic equation as

$$|A+B'|=0 \qquad ...(43)$$

where all the elements of the *i*th row of B' are $-M_iK^*(v)$. If the real parts of all the roots of this equation are negative, the equilibrium age-distributions would be stable.

5. A MORE GENERAL DELAY MODEL

In this case birth and death rates are functions of both P(t) and Q(t) so that (34) becomes

$$\frac{dx_1}{dt} = b_{p+1}(P, Q)x_{p+1} + \dots + b_{p+q}(P, Q)x_{p+q} - (d_1(P, Q) + m_1)x_1
\frac{dx_i}{dt} = m_{i-1}x_{i-1} - (d_i(P, Q) + m_i)x_i \quad (i = 2, 3, ..., n).$$

The equilibrium age-distribution is given by

$$b_{p+1}(P_0, P_0) \, \overline{x}_{p+1} + \dots + b_{p+q}(P_0, P_0) \, \overline{x}_{p+q} - [d_1(P_0, P_0) + m_1] \, \overline{x}_1 = 0$$

$$m_{i-1} \, \overline{x}_{i-1} - [d_i(P_0, P_0) + m_i] \, \overline{x}_i = 0 \quad (i = 2, 3, ..., n)$$

$$\overline{x}_1 + \overline{x}_2 + \dots + \overline{x}_n = P_0.$$

$$(45)$$

It is easily seen that if $\lambda_0 > 0$, (45) always gives a positive equilibrium value for P_0 and if birth and death rates are monotonic functions, then this value is unique.

The stability of this position can be discussed as before.

As a special case, let birth rates be constant and let

$$d_i(P, Q) = d_i + k_{i1}P + k_{i2}Q \qquad ...(46)$$

then (44) gives

$$\frac{dx_{1}}{dt} = b_{p+1}x_{p+1} + \dots + b_{p+q}x_{p+q} - (d_{1} + m_{1})x_{1} - k_{11}x_{1}(x_{1} + \dots + x_{n}(s)) ds + \dots + x_{n}(s) ds$$

$$+ x_{n} - k_{12}x_{1} \int_{-\infty}^{t} K(t - s) [x_{1}(s) + \dots + x_{n}(s)] ds$$

$$\frac{dx_{i}}{dt} = m_{i-1}x_{i-1} - (d_{i} + m_{i})x_{i} - k_{i1}x_{i}(x_{1} + \dots + x_{n})$$

$$- k_{i2}x_{i} \int_{-\infty}^{t} K(t - s) [x_{1}(s) + \dots + x_{n}(s)] ds$$

$$(i = 2, 3, ..., n).$$

The equilibrium age distribution is given by

$$b_{p+1}\overline{x}_{p+1} + \dots + b_{p+q}\overline{x}_{p+q} - (d_1 + m_1)\overline{x}_1 - (k_{11} + k_{12})\overline{x}_1P = 0 m_{i-1}\overline{x}_{i-1} - (d_i + m_i)\overline{x}_i - (k_{i1} + k_{i2})\overline{x}_iP = 0, \quad i = 2, 3, ..., n$$
 ...(48)

Eliminating $\overline{x}_1, \overline{x}_2, ..., \overline{x}_n$, we get

$$\frac{b_{p+1}}{[d_1 + m_1 + (k_{11} + k_{12}) P] \dots [d_{p+1} + m_{p+1} + (k_{p+1,1} + k_{p+1,2}) P]} + \dots
+ \frac{b_{p+q} m_{p+1} \dots m_{p+q-1}}{[d_1 + m_1 + (k_{11} + k_{12}) P] \dots [d_{p+q} + m_{p+q} + (k_{p+q,1} + k_{p+q,2}) P]}
= \frac{1}{m_1 m_2 \dots m_p} \cdot \dots (49)$$

If $\lambda_0 > 0$, this has a unique solution lying between the least and greatest value of $\frac{\lambda_0}{k_{i1} + k_{i2}}$ for *i* varying from 1 to p + q.

6. CONCLUDING REMARKS

(i) Let

$$f(\overline{P}) = \frac{p_{p+1}(\overline{P})}{(d_1(\overline{P}) + m_1) \dots (d_{p+1}(\overline{P}) + m_{p+1})} + \dots + \frac{b_{p+q}(\overline{P}) m_{p+1} \dots m_{p+q-1}}{(d_1(\overline{P}) + m_1) \dots (d_{p+q}(P) + m_{p+q})} \qquad \dots (50)$$

$$g(\bar{P}) = \frac{b_{p+1}}{(d_1(\bar{P}) + m_1) \dots (d_{p+1}(\bar{P}) + m_{p+1})} + \dots + \frac{b_{p+q}m_{p+1} \dots m_{p+q-1}}{(d_1(\bar{P}) + m_1) \dots (d_{p+q}(\bar{P}) + m_{p+q})} \dots (51)$$

$$h(\overline{P}) = \frac{b_{p+1}(\overline{P})}{(d_1 + m_1) \dots (d_{p+1} + m_{p+1})} + \dots + \frac{b_{p+q}(\overline{P}) m_{p+1} \dots m_{p+q-1}}{(d_1 + m_1) \dots (d_{p+q} + m_{p+q})} \dots (52)$$

All these three $f(\overline{P})$, $g(\overline{P})$, $h(\overline{P})$ are monotonic decreasing functions of \overline{P} and

$$f(\overline{P}) \leqslant g(\overline{P}); \ f(\overline{P}) \leqslant h(\overline{P})$$
 ...(53)

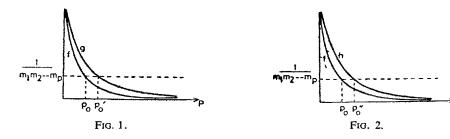


Figure 1 shows that the equilibrium population size P_0 when the birth rates are constant is greater than the equilibrium population size P_0 when birth rates are monotonic decreasing function of P.

Similarly Fig. 2 shows that the equilibrium population size P_0 when the death rates are constant is greater than the equilibrium population size P_0 when death rates are monotonic increasing functions.

- (ii) We have assumed the birth and death rates to be continuous monotonic function. Even if they are just continuous function but the birth rates are always bounded and the death rates tend to infinity as \overline{P} tends to infinity, we find that if $\lambda_0 > 0$, $\phi(0) > 0$ and $\phi(\infty) < 0$ and therefore a positive equilibrium value for P_0 always exists.
- (iii) Gurtin and Maccamy (1974) have discussed the corresponding problem for continuous-time continuous-age-scale model.

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