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FOURTH AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(24 October - 11 November 1994)

"Discrete-Time Population Models with Age and Stage Structure II"

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These are preliminary lecture notes, intended only for distribution to participants.

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Discrete-Time Population Models with Age and Stage Structure II

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Fourth Autumn Course on Mathematical Ecology
International Center for Theoretical Physics
Trieste, Italy

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Outline of Talk

A. Nonautonomous Leslie Matrix

$$\vec{n}(t+1) = L(t)\,\vec{n}(t)$$

- Weak Ergodic Theorem
- Periodic Matrices

B. Autonomous Leslie Matrix

$$\vec{n}(t+1) = L(\vec{n}(t))\,\vec{n}(t)$$

- Review of some population models without structure
- Local Stability Analysis
- Applications:
  (1) Bacteria
  (2) Fish
  (3) Plants
- Strong Ergodic Theorem
- Leslie's Density-Dependent Matrix
- Density-Dependent Fertility Rates
- Application to Spatial Dynamics

C. Nonautonomous Leslie Matrix with Density-Dependence

$$\vec{n}(t+1) = L(t, \vec{n}(t))\,\vec{n}(t)$$

A. Nonautonomous Leslie Matrix

$$\vec{n}(t+1) = L(\vec{\text{[illegible]}}(t))\,\vec{n}(t)$$

- Weak Ergodic Theorem
- Periodic Matrices

Weak Ergodic Theorem

$$\vec{n}(t+1) = L(t)\,\vec{n}(t)$$

Two populations which are arbitrarily different in their age structure will tend to adopt the same age distribution as each other with passage of time if they are subject to the same regimes of fertility and mortality which may change in time.

Theorem WE Let the Leslie matrix sequence $\{L(t)\}$ be uniformly bounded by $M \le L(t) \le N$, where M is nonnegative and primitive and let $\{\vec{n}(t)\}$ and $\{\vec{n}'(t)\}$ be two population sequences,

$$L(t)\,\vec{n}(t) = \vec{n}(t+1) \quad \text{and} \quad L(t)\,\vec{n}'(t) = \vec{n}'(t+1),$$

where $\vec{n}(0)$ and $\vec{n}'(0)$ are positive. Then

$$\lim_{t \to \infty} \left(\frac{n_i(t)}{n_i'(t)} - \frac{n_j(t)}{n_j'(t)} \right) = 0$$

for any two indices $i, j = \{1, 2, \ldots, m\}$.

- Age classes eventually become proportional.
- Applies to any nonnegative primitive matrix.
- (Lopez, 1961; Pollard, 1973)

Periodic Matrices

If $L(t+k) = L(t)$, k positive integer, then the age distribution will also be periodic of period at most k.

Suppose $L(i)$, $i=1,\dots,k$ are nonnegative and primitive. Define

$$\mathbf{L}_i = L(k+i-1)\cdots L(i) \;,\; i=1,\dots,k$$

If Matrices $\mathbf{L}_i$ are nonnegative and primitive with dominant eigenvalue $\boldsymbol{\lambda}_i$ and associated positive right eigenvector $\vec{\mathbf{v}}_i$, $\|\vec{\mathbf{v}}_i\| = 1$.

Thus,

$$\mathbf{L}_i \vec{n}(i) = \vec{n}(i+k)$$

and

$$\lim_{t\to\infty} \frac{\vec{n}(tk+i)}{\|\vec{n}(tk+i)\|} = \vec{\mathbf{v}}_i .$$

A Simple Example with Period 2

Let

$$L(t+2) = L(t).$$

$$L(1) = \begin{pmatrix} f_1 & f_2 \\ p_1 & 0 \end{pmatrix} \quad \text{and} \quad L(2) = \begin{pmatrix} f_1' & f_2' \\ p_1' & 0 \end{pmatrix}$$

$$\mathbf{L}_1 = L(2)\,L(1)$$

$$= \begin{pmatrix} f_1' f_1 + f_2' p_1 & f_1' f_2 \\ p_1' f_1 & p_1' f_2 \end{pmatrix}$$

Eigenvalues:

$$\lambda_{1,2} = \tfrac{1}{2}(f_2' p_1 + f_2 p_1') + \tfrac{1}{2} f_1 f_1'$$
$$\pm \frac{1}{2}\sqrt{(f_2' p_1 - f_2 p_1')^2 + 2 f_1 f_1' (f_2 p_1' + f_2' p_1) + (f_1 f_1')^2}$$

The dominant eigenvalue increases with the largest possible difference between $f_2 p_1'$ and $f_2' p_1$.

Selection (for an increased population size or increased λ_1) favors periodicity. The years should alternate between high survival and low fertility and low survival and high fertility.

- MacArthur (1968)

B. Autonomous Leslie Matrix

$$\vec{n}(t+1) = L(\vec{n}(t))\,\vec{n}(t)$$

- Review of some population models without structure
- Local Stability Analysis
- Applications
  - (1) Bacteria
  - (2) Fish
  - (3) Plants
- Strong Ergodic Theorem
- Leslie's Density-Dependent Matrix
- Application to Spatial Dynamics

Some Discrete-Time Population Models

Logistic: $$N(t+1) = \frac{\lambda k N(t)}{k + (\lambda - 1)N(t)},$$

$$\lambda = e^r > 1 \quad \text{and} \quad N(0) > 0$$

$$\lim_{t \to \infty} N(t) = k$$

Approximate Logistic: $$N(t+1) = \lambda \exp\left(-\frac{rN(t)}{k}\right)$$

$$\lambda = e^r > 1 \quad \text{and} \quad N(0) > 0$$

If $0 < r \leq 2$, $\lim_{t \to \infty} N(t) = k$

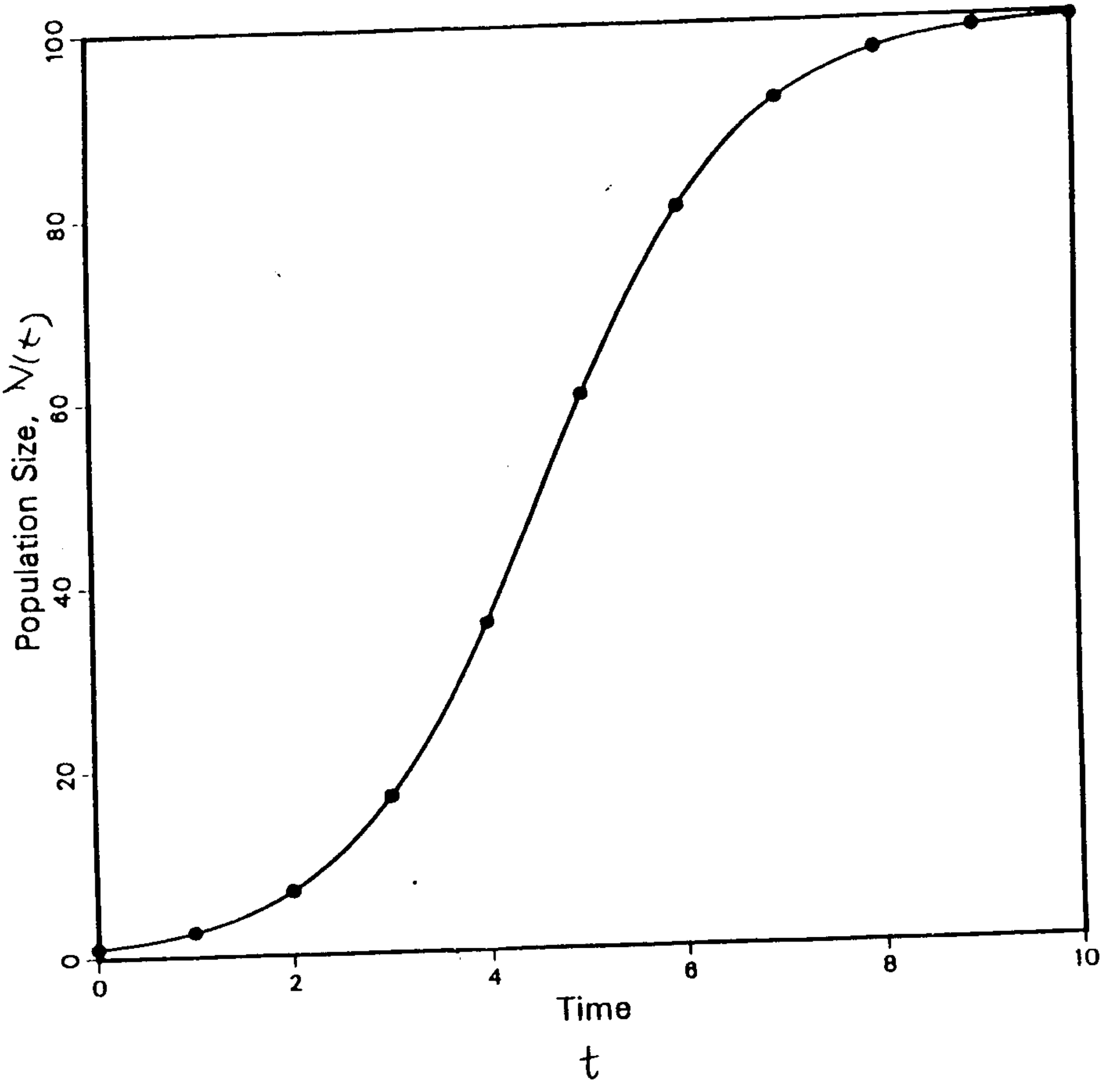
If $2 < r \leq 2.53$, $\lim_{t \to \infty} N(2t) = k_1$, $\lim_{t \to \infty} N(2t+1) = k_2$ two-point cycle

If $r > 2.53$, period doubling and chaos

Exact Logistic

$$N(t+1) = \frac{e\,N(t)}{1 + \frac{e-1}{100} N(t)}$$

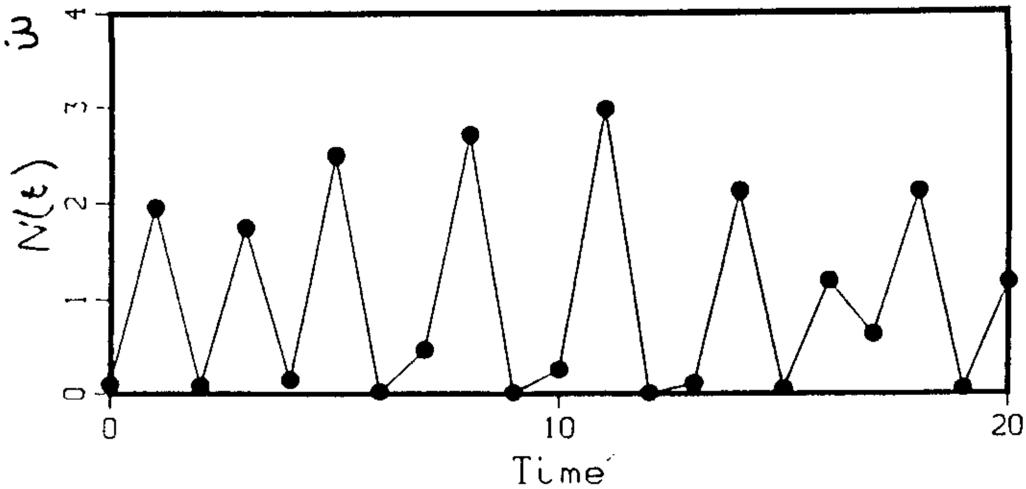
$k = 100$



$N(t+1) = N(t)\exp[r - rN(t)]$

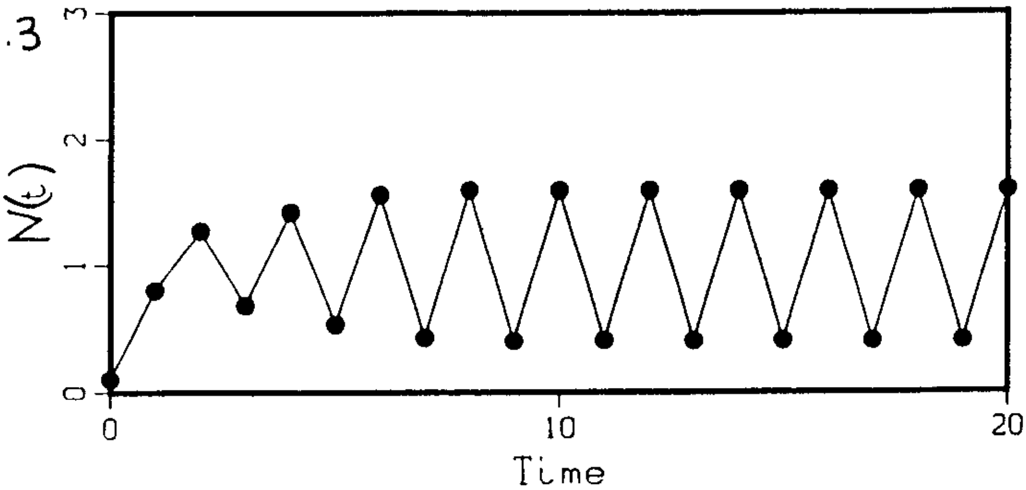
$k = 1$

$r = 3.3$



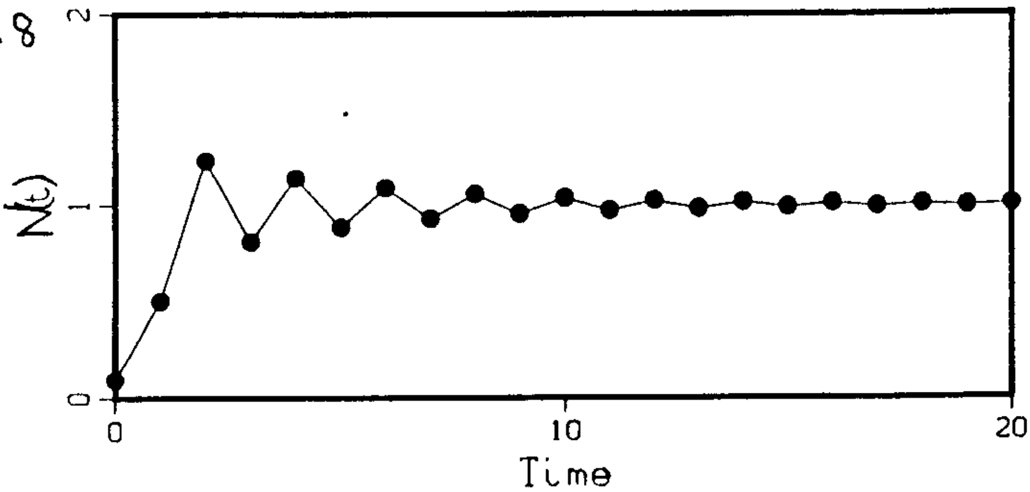
period = ?

$r = 2.3$



period 2

$r = 1.8$



$\lim_{t\to\infty} N(t) = 1$

Local Stability Analysis for $\vec{n}(t+1) = L(\vec{n}(t))\vec{n}(t)$

Let $\vec{n}_e = (n_{1e}, n_{2e}, \dots n_{me})^T$ be an equilibrium of the system:

$$\vec{n}_e = L(\vec{n}_e)\,\vec{n}_e$$

Suppose

$$L(\vec{n}(t)) = L(P) = \begin{pmatrix} f_1(P) & f_2(P) & \dots & f_m(P) \\ p_1(P) & & & \\ & p_2(P) & & \\ & & \ddots & \\ & & p_{m-1}(P) & 0 \end{pmatrix}$$

where $P \equiv P(t) = \sum_{i=1}^{m} k_i n_i(t)$, a weighted sum of age classes.

Assume $\vec{y}(t) = \vec{n}(t) - \vec{n}_e$. Then linearize $\vec{n}(t+1) = L(\vec{n}(t))\,\vec{n}(t)$ about $\vec{n}_e$.

Linearization Continued

Given $\quad \vec{n}(t+1) = L(\vec{n}(t))\,\vec{n}(t)$

$$\vec{n}_e + \vec{y}(t+1) \approx L(\vec{n}_e + \vec{y}(t))[\vec{n}_e + \vec{y}(t)]$$

$$\vec{n}_e + \vec{y}(t+1) \approx L(\vec{n}_e)[\vec{n}_e + \vec{y}(t)] + L'(\vec{n}_e)\,y(t)$$

But $\quad \vec{n}_e = L(\vec{n}_e)\vec{n}_e$, so

$$\underline{\vec{y}(t+1) \approx \left[L(\vec{n}_e) + L'(\vec{n}_e)\right]\vec{y}(t)},$$

where

$$L(\vec{n}_e) = \begin{pmatrix} f_1(P_e) & f_2(P_e) & \cdots & f_m(P_e) \\ p_1(P_e) & & & \\ & p_2(P_e) & & \\ & & \ddots & \\ & & p_{m-1}(P_e) & 0 \end{pmatrix}$$

$$L'(\vec{n}_e) = \begin{pmatrix} \sum_{i=1}^{m} \frac{\partial f_i}{\partial n_1} n_{ie} & \sum \frac{\partial f_i}{\partial n_2} n_{ie} & \cdots \\ \frac{\partial p_1}{\partial n_1} n_{1e} & \frac{\partial p_1}{\partial n_2} n_{1e} & \cdots \\ \frac{\partial p_2}{\partial n_1} n_{2e} & \frac{\partial p_2}{\partial n_2} n_{2e} & \cdots \\ \vdots & \vdots & \end{pmatrix}$$

The eigenvalues of $M = L(\vec{n}_e) + L'(\vec{n}_e)$ determine whether the equilibrium is locally stable. $|\lambda_i| < 1 \Rightarrow \vec{n}_e$ is locally stable.

A Density-Dependent Model

$$\vec{n}(t+1) = L(\vec{n}(t))\,\vec{n}(t)$$

- Beddington (1974)

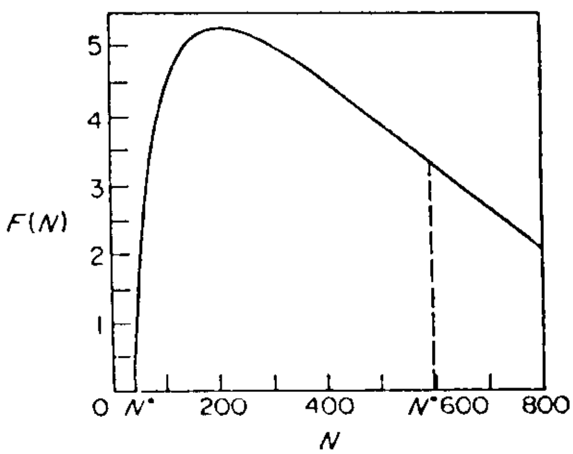
$$L(\vec{n}(t)) = \begin{pmatrix} 0 & 0 & f(N(t)) & f(N(t)) \\ p(N(t)) & 0 & 0 & 0 \\ 0 & p(N(t)) & 0 & 0 \\ 0 & 0 & p(N(t)) & 0 \end{pmatrix},$$

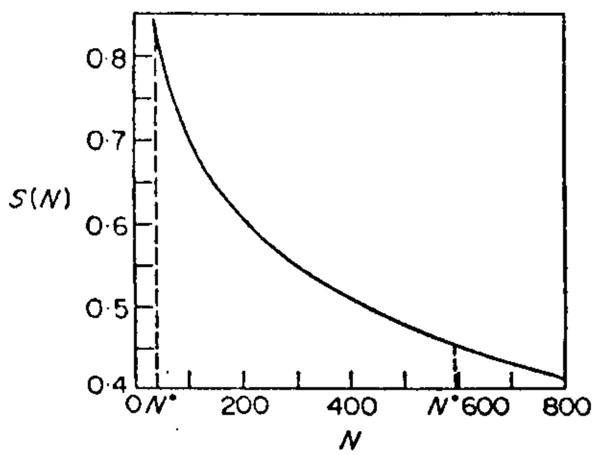
where $N(t) = \sum_{i=1}^{4} n_i(t)$, 4 weekly age classes.

<u>Folsomia candida</u> L. grown at 10°C:

$f(N) = F(N) = 18.53 \ln N - 1.74 (\ln N)^2 - 44.04$

$p(N) = S(N) = 1.35 - 0.14 \ln N$





Local Stability Analysis

Linearized system:

$$\vec{y}(t+1) = M_\delta \, \vec{y}(t)$$

TABLE 1

Fecundity and survival values at equilibria

Equilibrium population size	$F(N)$	$S(N)$
41·129	0·7768	0·8301
596·453	3·3428	0·4563

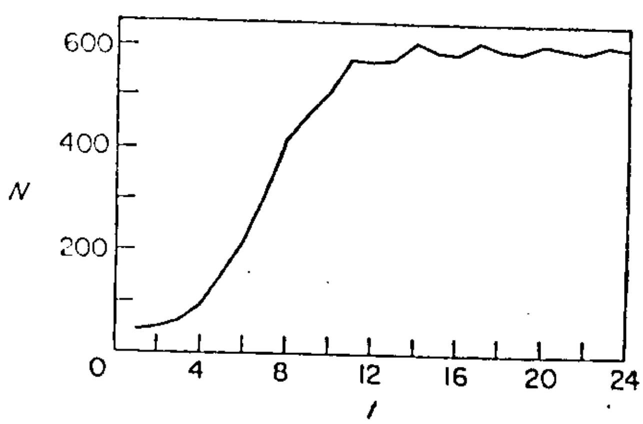
TABLE 2

Eigenvalues of $\mathbf{M}_\delta$ *at equilibria*

Equilibrium population size		Real part	Imaginary part	Modulus
Unstable	41·129	3·0305	0	3·0305
		−0·0573	0·8660	0·8679
		−·0573	−0·8660	0·8679
		−·7472	0	0·7472
Stable	596·453	·5226	0	0·5226
		−·4464	0·8000	0·9161
		−·4464	−0·8000	0·9161
		−·4017	0	0·4017

$|\lambda_i| < 1$

Model simulation: $\vec{n}(t+1) = M(\vec{n}(t))\, \vec{n}(t).$



Age-Structured Fishery Model

- Levin and Goodyear (1980)

Parameters:

k_i = average number of eggs per female of age class i.

p_i = density-independent probability of survival from egg to age 1, age i to $i+1$.

β = coefficient of density-independent mortality.

P = parental egg production.

$$P(t) = \sum_{i=1}^{m} k_i n_i(t)$$

$$n_1(t+1) = p_0 P(t) \exp(-\beta P(t))$$

$$n_i(t+1) = p_{i-1} n_{i-1}(t)$$

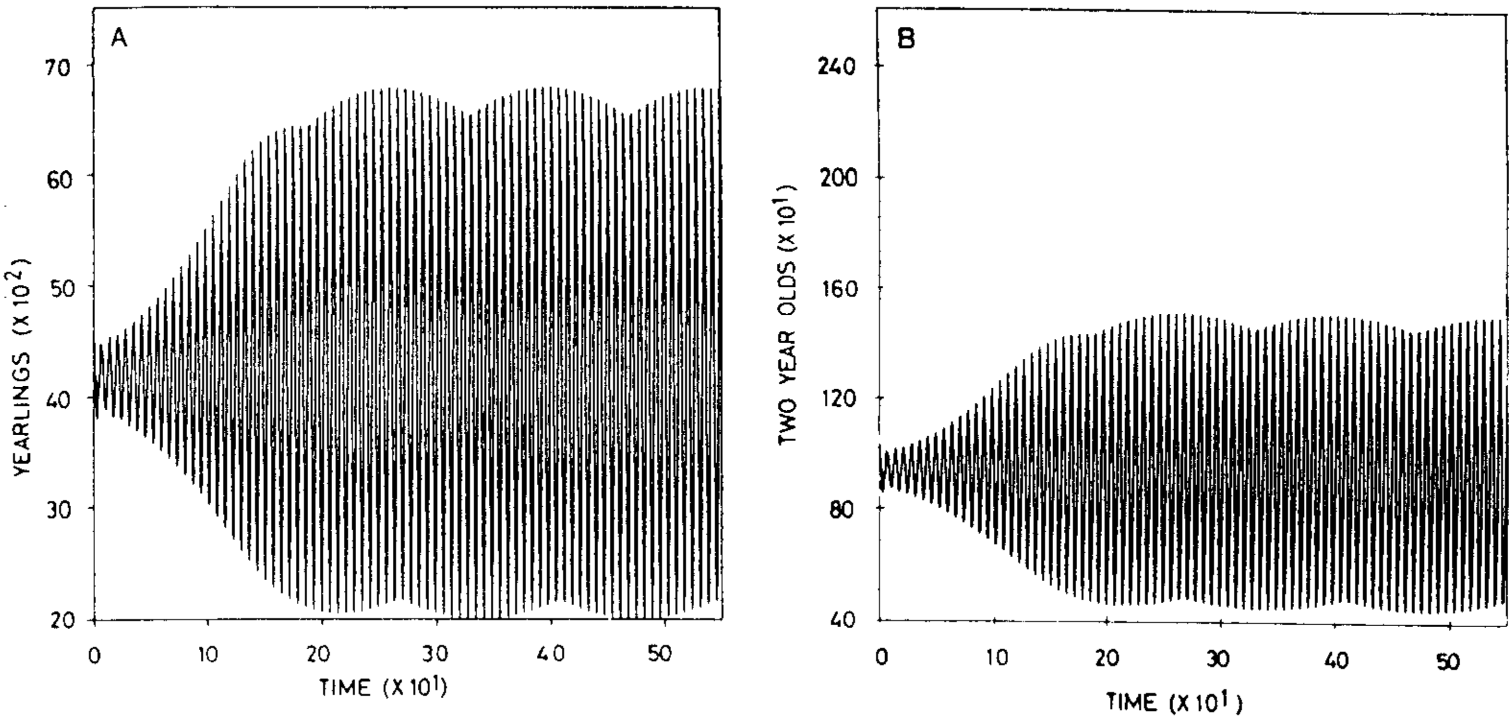
$$\vec{n}(t+1) = \begin{pmatrix} p_0 k_1 \exp(-\beta P) & \cdots & & p_0 k_m \exp(-\beta P) \\ p_1 & & & \\ & p_2 & & \\ & & \ddots & \\ & & p_{m-1} & 0 \end{pmatrix} \vec{n}(t)$$

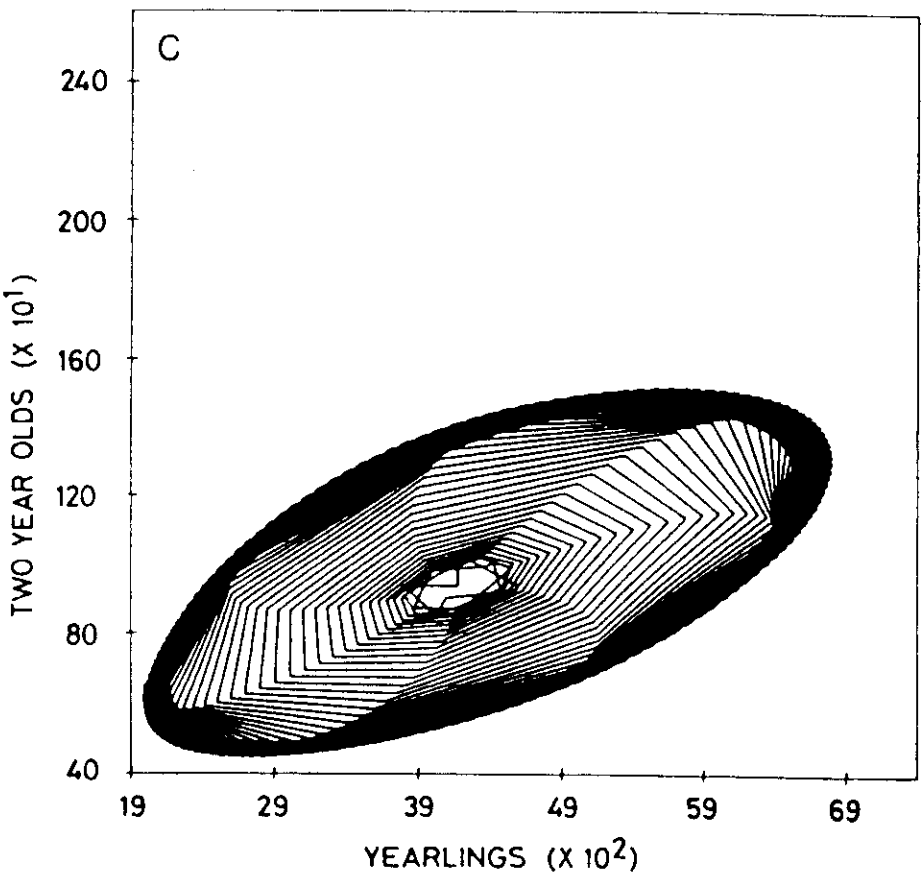
Equilibrium: $\overline{P} = (\ln\alpha)/\beta$, $\overline{n}_i = p_1 p_2 \cdots p_{i-1} \overline{n}_1$, $i = 2, \ldots, m$

$\alpha = R = p_0 k_1 + p_0 p_1 k_1 + \cdots + p_0 p_1 \cdots p_{m-1} k_m$.

Note: If $p_i = 0$ $i = 1, \ldots, m$, i.e., no age classes, then $\overline{P} = k_1 \overline{n}_1$ and $\overline{P}$ is stable if $0 < \ln\alpha \leq 2$.

Example: Hudson River Striped Bass



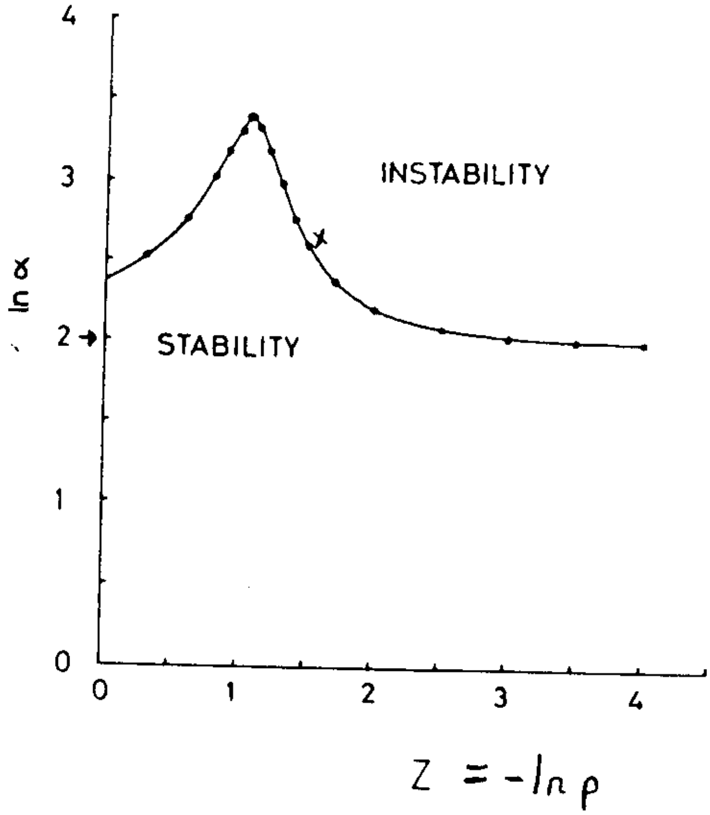


Age i	Fecundity $K_i \times 10^{-3}$
1	0
2	0
3	26
4	46
5	110
6	307
7	798
8	1166
9	1570
10	1760
11	1980
12	2090
13	2130
14	2190
15	2590

$\ln \alpha = 2.708 \qquad p_i = .2231, \; i = 1, \ldots, 15.$

Example: Hudson River Striped Bass

Stability Boundary as a function of $\ln\alpha$ and $z = -\ln p$, $p_i = p$, $i = 1, \ldots, 15$



Why does the stability boundary appear as above?

(i) Initial period of no or very small fecundity.

(ii) Middle period in which fecundity increases with age.

(iii) Leveling off and truncation of reproduction when maximum reproductive age is reached.

Example: Reproduction parameters increase, then level off

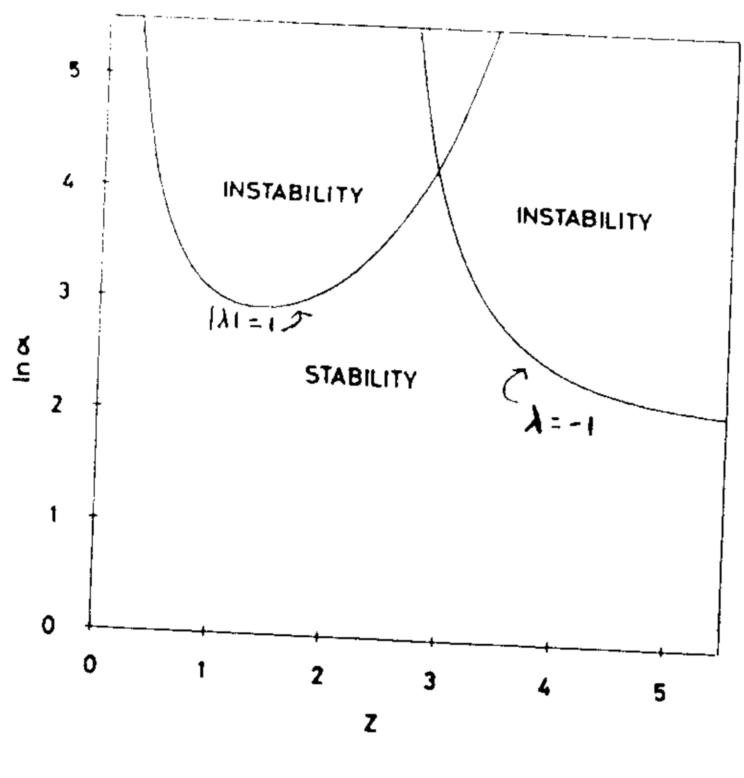
$$M = \begin{pmatrix} p_0 \exp(-\beta P) & p_0 k \exp(-\beta P) & \cdots & \\ p & & & \\ & p & & \\ & & \ddots & \end{pmatrix}$$

$m \to \infty$, $k_i = k$, $i > 1$, $k_1 = 1$.

Age classes ≥ 2 can be lumped in n_2, then model behaves like

$$n(t+1) = p_0 P \exp(-\beta P)$$
$$n_2(t+1) = p n_1(t) + p n_2(t)$$

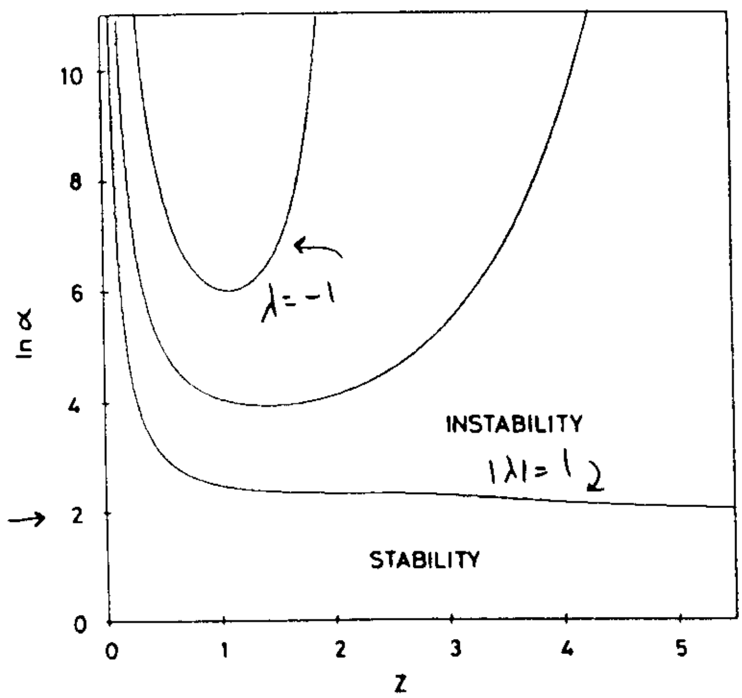
Stability Boundary, $k = 10$



Example : Delaying Reproduction

$$M = \begin{pmatrix} 0 & p_0 \exp(-\beta P) & p_0 k \exp(-\beta P) & \cdots \\ p & & & \\ & p & & \\ & & p & \\ & & & \ddots \end{pmatrix}$$

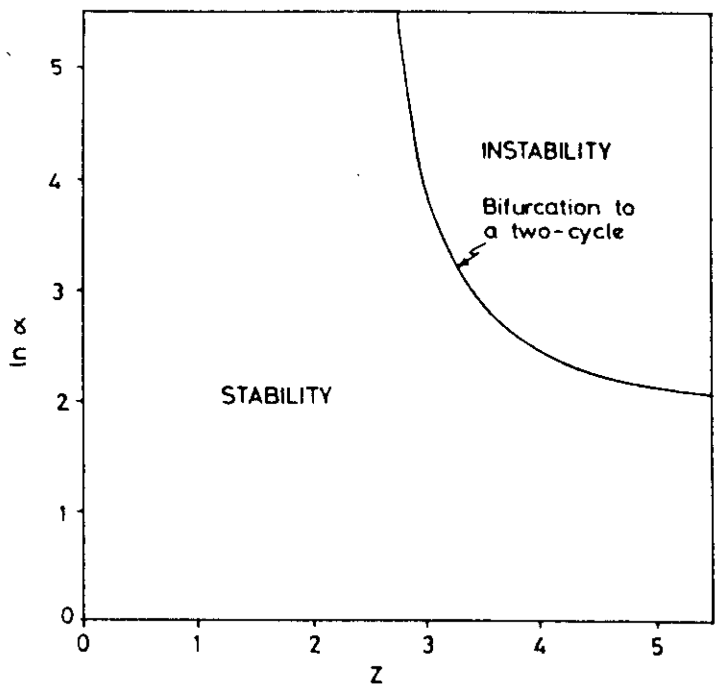
$m \to \infty$, $k_1 = 0$, $k_2 = 1$, $k_i = k$, $i > 2$.



$k_i = 10 \quad i > 2$

Example Exponential Increase in Fecundity

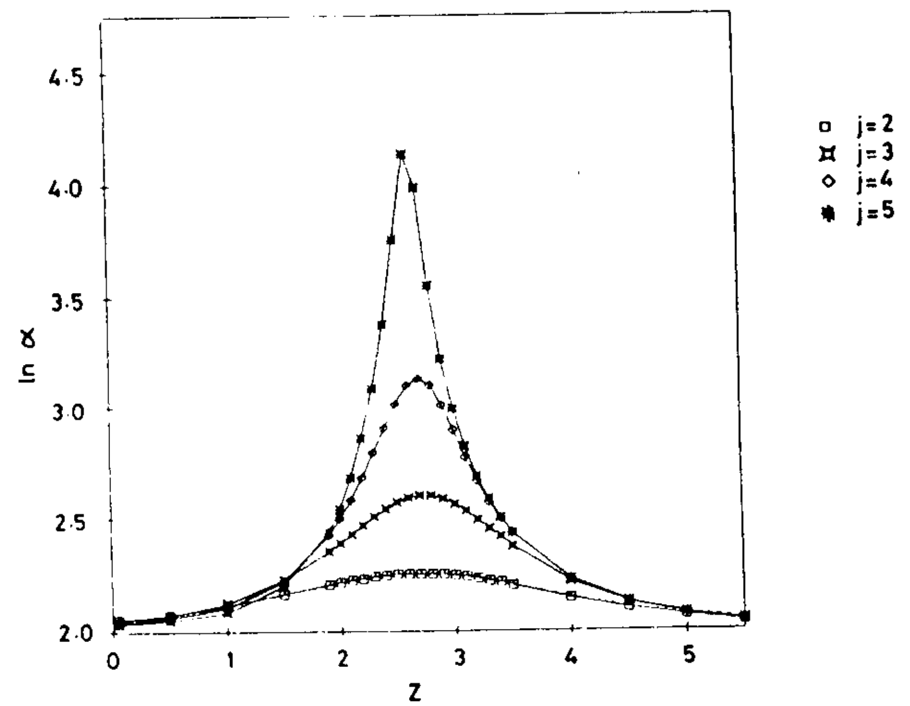
$m \to \infty \quad K_1 = 1, \; K_2 = K, \; K_3 = K^2, \ldots, K_i = K^{i-1}, \ldots$



$K_i = 10^{i-1}, \quad i = 2, \ldots$

Example Reproduction Delay and Truncation

Reproduction is delayed one step, $K_1=0$
Reproduction ends after $j+1$ years.
There are j reproductive years.



$j=2 \quad K_1=0,\ K_2=1,\ K_3=10,\ K_i=0 \quad i\geq 4.$

$j=3 \quad K_1=0 \quad K_2=1,\ K_i=10^{i-2},\ i=3,4,\ K_i=0 \quad i\geq 5.$

$j=4 \quad K_1=0 \quad K_2=1 \quad K_i=10^{i-2},\ i=3,4,5,\ K_i=0 \quad i\geq 6.$

$j=5 \quad K_1=0 \quad K_2=1 \quad K_i=10^{i-2},\ i=3,4,5,6,\ K_i=0 \quad i\geq 7.$

Density-Dependent Structured Model for Monocarpic and Polycarpic Perennial Plants

$$M = \begin{array}{cc} \begin{pmatrix} 0 & 0 & f p_0(N) \\ p_{JS} & p_{JJ} & V \\ 0 & p_{FJ} & p_{FF} \end{pmatrix} & \begin{array}{l} \text{Seedlings (S)} \\ \text{Juveniles (J)} \\ \text{Flowering (F)} \end{array} \\ \begin{array}{ccc} S & J & F \end{array} & \end{array}$$

f = number of seeds per plant

$p_0(N)$ = emergence rate of seeds $(p_0'(N) < 0)$

N = total population size

p_{ij} = transition probability from stage j to stage i.

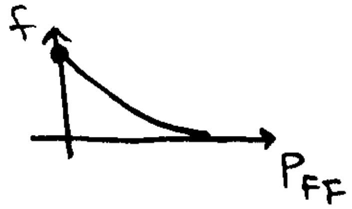
V = average number of vegetatives per flowering plant

Monocarpic if $P_{FF} = 0$.

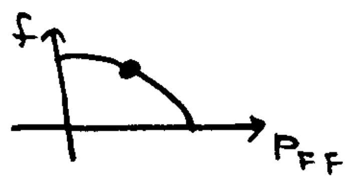
Polycarpic if $P_{FF} > 0$.

$f = g(P_{FF})$ – seed production causes increases in mortality risks $g'(p_{FF}) < 0$.

Which strategy (monocarpic, polycarpic) will be favored (Increase in λ_1)?



monocarpic



monocarpic or polycarpic

- Takada and Nakajima (1992)

Strong Ergodic Theorem for Density Dependent Matrices

$$\vec{n}(t+1) = M(\vec{n}(t))\vec{n}(t)$$

Every term in the matrix depends on the same density-dependent factor:

$$M(\vec{n}(t)) \equiv h(\vec{n}(t))M,$$

where h is a scalar function.

Theorem SE2: Let M be nonnegative and primitive. Suppose that $h: \mathbb{R}^n \longrightarrow (0,1]$, $h(\vec{0})=1$. Let $\vec{n}(t)$ be a solution of

$$\vec{n}(t+1) = h(\vec{n}(t))\, M\vec{n}(t),$$

where $\vec{n}(0) \geq 0$ and $\|\vec{n}(0)\| > 0$. Then

$$\lim_{t\to\infty} \frac{\vec{n}(t)}{\|\vec{n}(t)\|} = \vec{v}_1$$

where $\vec{v}_1$ is the positive eigenvector of M associated with λ_1 satisfying $\|\vec{v}_1\| = 1$. Also, the total population size satisfies the scalar difference equation

$$N(t+1) = \left\| \frac{M\vec{n}(t)}{\|\vec{n}(t)\|} \right\| h(\vec{n}(t))N(t).$$

(Cushing, 1989).

Under centain conditions the total population size may satisfy:

$$\underline{N(t+1) = \lambda\, h(\vec{n}(t))\, N(t)}$$

Sketch of Proof of SE 1

$$\vec{n}(t+1) = h(\vec{n}(t))\, M \vec{n}(t)$$

$$\frac{\vec{n}(t+1)}{\|\vec{n}(t+1)\|} = \frac{h(\vec{n}(t))\, M \vec{n}(t)}{\|\vec{n}(t+1)\|}$$

$$= \frac{h(\vec{n}(t))\, M \vec{n}(t)}{h(\vec{n}(t))\, \|M \vec{n}(t)\|}$$

Thus, let $\vec{u}(t) = \dfrac{\vec{n}(t)}{\|\vec{n}(t)\|}$. Then

$$\vec{u}(t+1) = \frac{M\, \vec{u}(t)}{\|M\, \vec{u}(t)\|}$$

If $\vec{x}(t+1) = M\vec{x}(t)$ and $\vec{x}(0) = \vec{n}(0)$, then $\vec{u}(t) = \dfrac{\vec{x}(t)}{\|\vec{x}(t)\|}$. Since

$$\lim_{t \to \infty} \frac{\vec{x}(t)}{\|\vec{x}(t)\|} = \vec{V}_1$$

it follows that

$$\lim_{t \to \infty} \frac{\vec{n}(t)}{\|\vec{n}(t)\|} = \vec{V}_1$$

Example 1 $\quad h(N) = \exp\left(-\frac{r}{K} N\right)$

$$M = \begin{pmatrix} 0 & 6 & 2\frac{2}{3} \\ .25 & 0 & 0 \\ 0 & .75 & 0 \end{pmatrix}$$

Total Population: $N(t+1) = \lambda_1 N(t) \exp\left(-\frac{r}{K} N(t)\right)$

$\lambda_1 \approx 1.366$, $r = \ln \lambda_1 = .3119 = K$, $\vec{v}_1^{\,T} = (.779, .143, .0782)$

$0 < r < 2 \Rightarrow \lim_{t \to \infty} N(t) = K$

Time t	Components of the Normalized Age Distribution			Total population $p(t)$
0	3.33 E-01	3.33 E-01	3.33 E-01	3.00 E 00
1	8.97 E-01	2.57 E-02	7.76 E-01	4.81 E-01
2	5.98 E-01	3.70 E-01	3.20 E-02	1.80 E-01
3	8.44 E-01	5.47 E-02	1.02 E-01	4.11 E-01
4	7.04 E-01	2.48 E-01	4.82 E-02	2.31 E-01
5	8.17 E-01	8.90 E-02	9.40 E-02	3.64 E-01
:				:
:				:
95	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
96	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
97	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
98	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
99	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01
100	7.79 E-01	1.43 E-01	7.83 E-02	3.11 E-01

Cushing (1989)

Example 2 $h(N) = \exp\left(-\frac{r}{K}N\right)$

$$M = \begin{pmatrix} 0 & 300 & 133\frac{1}{3} \\ .25 & 0 & 0 \\ 0 & .75 & 0 \end{pmatrix}$$

Total Population: $N(t+1) = \lambda_1 N(t) \exp\left(-\frac{r}{K} N(t)\right)$

$\lambda_1 = 8.822 \quad r = \ln \lambda_1 = 2.177 = K, \vec{v}_1^{\,T} = (.970, .0275, .00234)$

$$2 < r < 2.53 \Rightarrow \begin{cases} \lim\limits_{t\to\infty} N(2t) = K_1 \\ \lim\limits_{t\to\infty} N(2t+1) = K_2 \end{cases}$$ Two-point cycles

Time i	Components of the Normalized Age Distribution			Total population $p(i)$
0	8.33 E-01	1.67 E-01	0.00 E 00	1.20 E 00
1	0.93 E-01	4.14 E-03	2.48 E-03	1.82 E-01
2	8.62 E-01	1.36 E-01	1.70 E-03	4.17 E-07
3	9.92 E-01	5.20 E-03	2.47 E-03	1.73 E-05
4	8.82 E-01	1.16 E-01	1.82 E-03	3.70 E-05
5	9.91 E-01	6.25 E-03	2.46 E-03	1.30 E-03
:				:
:				:
195	9.70 E-01	2.75 E-02	2.34 E-03	3.22 E 00
196	9.70 E-01	2.75 E-02	2.34 E-03	1.13 E 00
197	9.70 E-01	2.75 E-02	2.34 E-03	3.22 E 00
198	9.70 E-01	2.75 E-02	2.34 E-03	1.13 E 00
199	9.70 E-01	2.75 E-02	2.34 E-03	3.22 E 00
200	9.70 E-01	2.75 E-02	2.34 E-03	1.13 E 00

• Cushing (1989)

Example 3 $h(N) = \exp\left(-\frac{r}{K}N\right)$

$$M = \begin{pmatrix} 0 & 1200 & 533\frac{1}{3} \\ .25 & 0 & 0 \\ 0 & .75 & 0 \end{pmatrix}$$

Total Population: $N(t+1) = \lambda_1 N(t) \exp\left(-\frac{r}{K}N(t)\right)$

$\lambda_1 = 17.485$, $r = \ln\lambda_1 = 2.861 = K$, $\vec{v}_1^{\,T} = (.985, .0141, .000604)$

$r > 2.53 \Rightarrow$ periodic

Time i	Components of the Normalized Age Distribution			Total population $p(i)$
0	9.81 E-01	9.71 E-03	9.71 E-03	1.03 E 00
1	9.85 E-01	1.44 E-02	4.26 E-04	2.08 E-01
2	9.85 E-01	1.39 E-02	6.08 E-04	2.29 E 00
3	9.85 E-01	1.43 E-02	6.04 E-04	2.91 E 00
4	9.85 E-01	1.39 E-02	6.05 E-04	2.79 E 00
5	9.85 E-01	1.43 E-02	6.04 E-04	2.97 E 00
6	9.85 E-01	1.39 E-02	6.05 E-04	2.70 E 00
7	9.85 E-01	1.43 E-02	6.04 E-04	3.14 E 00
8	9.85 E-01	1.39 E-02	6.05 E-04	2.41 E 00
9	9.85 E-01	1.42 E-02	6.04 E-04	3.75 E 00
10	9.85 E-01	1.39 E-02	6.05 E-04	1.55 E 00
⋮				⋮
⋮				⋮
190	9.85 E-01	1.41 E-02	6.04 E-04	3.24 E 00
191	9.85 E-01	1.41 E-02	6.04 E-04	2.22 E 00
192	9.85 E-01	1.41 E-02	6.04 E-04	4.22 E 00
193	9.85 E-01	1.41 E-02	6.04 E-04	1.08 E 00
194	9.85 E-01	1.41 E-02	6.04 E-04	6.43 E 00
195	9.85 E-01	1.41 E-02	6.04 E-04	1.81 E 00
196	9.85 E-01	1.41 E-02	6.04 E-04	2.65 E 00
197	9.85 E-01	1.41 E-02	6.04 E-04	3.26 E 00
198	9.85 E-01	1.41 E-02	6.04 E-04	2.19 E 00
199	9.85 E-01	1.41 E-02	6.04 E-04	4.28 E 00
200	9.85 E-01	1.41 E-02	6.04 E-04	1.04 E 00

Cushing (1989)

Leslie's Density-Dependent Matrix

- Leslie (1948)
- Allen (1989)

$$L(\vec{n}(t)) = \frac{K}{K + (\lambda_1 - 1)N(t)} L_1,$$

where $\lambda_1 > 1$ is the dominant eigenvalue of L_1

Total population size is

$$N(t+1) = \frac{K \lambda_1 N(t)}{K + (\lambda_1 - 1) N(t)},$$

logistic growth: $\boxed{\lim_{t \to \infty} N(t) = K}$ if L_1 is primitive.

Example 1: (primitive) $\quad L_1 = \begin{pmatrix} 0 & 6 & 12 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix} \quad \begin{matrix} \lambda_1 = 2 \\ \lambda_{2,3} = -1 \end{matrix}$

Example 2: (imprimitive) $\quad L_2 = \begin{pmatrix} 0 & 0 & 48 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix} \quad \begin{matrix} \lambda_1 = 2 \\ \lambda_{2,3} = 1 \pm i\sqrt{3} \end{matrix}$

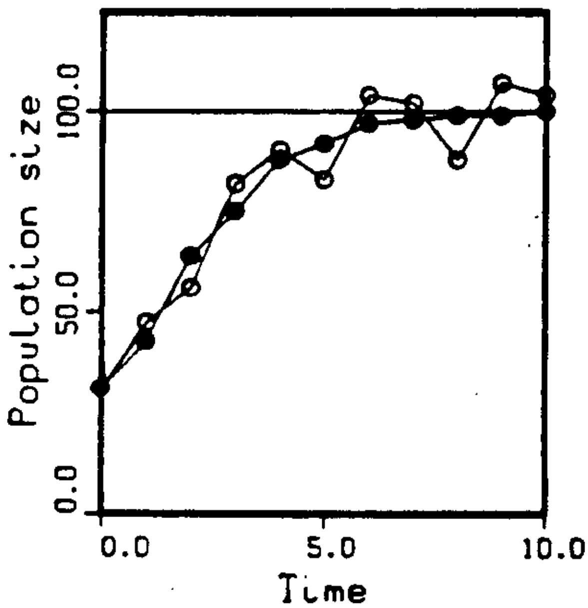
Examples of Leslie's Density - Dependent Matrix

$$\vec{n}(t+1) = L(\vec{n}(t))\vec{n}(t) = \frac{K}{K+(\lambda_1-1)N(t)} L_i \vec{n}(t)$$

$$L_1 = \begin{pmatrix} 0 & 6 & 12 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}$$

$K = 100, \lambda_1 = 2$

primitive

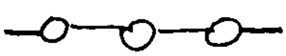


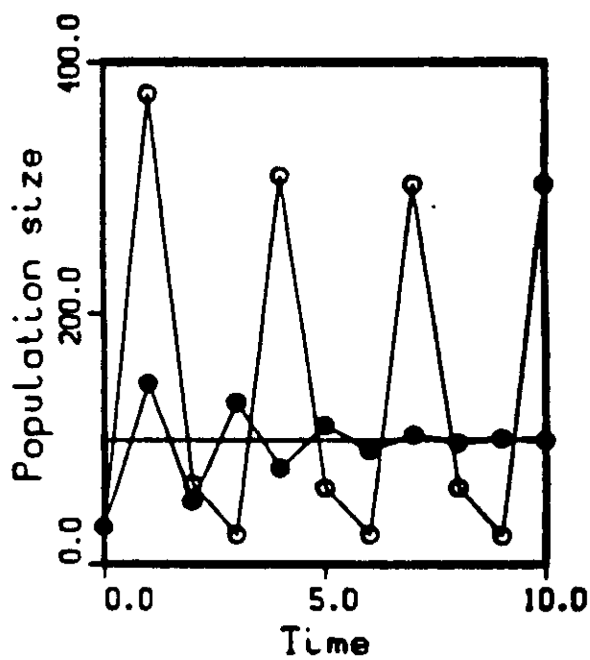
$\vec{n}(0) = (25, 5, 1)^T$

$$L_2 = \begin{pmatrix} 0 & 0 & 48 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}$$

$K = 100, \lambda_1 = 2$

imprimitive





$\vec{n}(0) = (10, 10, 10)^T$

Density-Dependent Fertility Rates

- Silva and Hallam (1992)

Let $P(t) = \sum_{i=1}^{m} k_i n_i(t)$ and $f_i(P) = f_i\, g(P)$.

(i) $g : [0,\infty) \to (0,1]$, $g' < 0$

(ii) $g(0) = 1$, $\lim_{x\to\infty} g(x) = 0$

(iii) $h : [0,\infty) \longrightarrow (0,1]$, $h(x) = x\,g(x) \le M$.

(iv) $\phi : [0,\infty) \to (0,\infty)$, $\phi(x) = -\dfrac{x\,g'(x)}{g(x)}$,
$\phi' > 0$

Examples of g: $e^{-\beta P}$, $\dfrac{1}{1+P}$

$$n_1(t+1) = p_0\, g(P(t)) \sum_{i=1}^{m} f_i n_i(t)$$
$$n_2(t+1) = p_1 n_1(t)$$
$$\vdots$$
$$n_m(t+1) = p_{m-1} n_{m-1}(t)$$

$$R = p_0 f_1 + p_0 p_1 f_2 + \cdots + p_0 p_1 \cdots p_{m-1} f_m$$

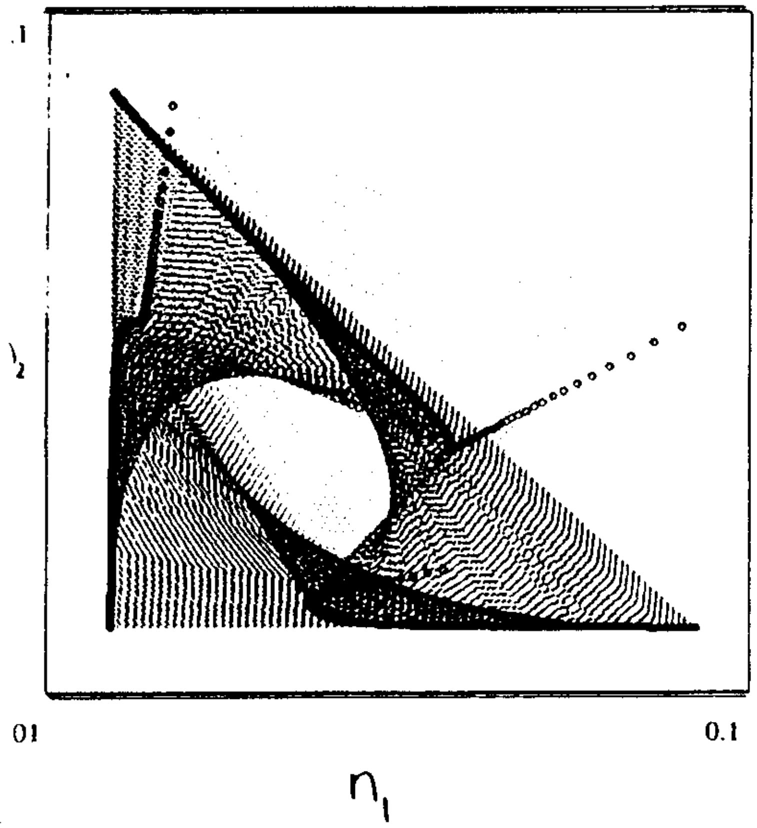
The zero equilibrium is stable if and only if $R < 1$.

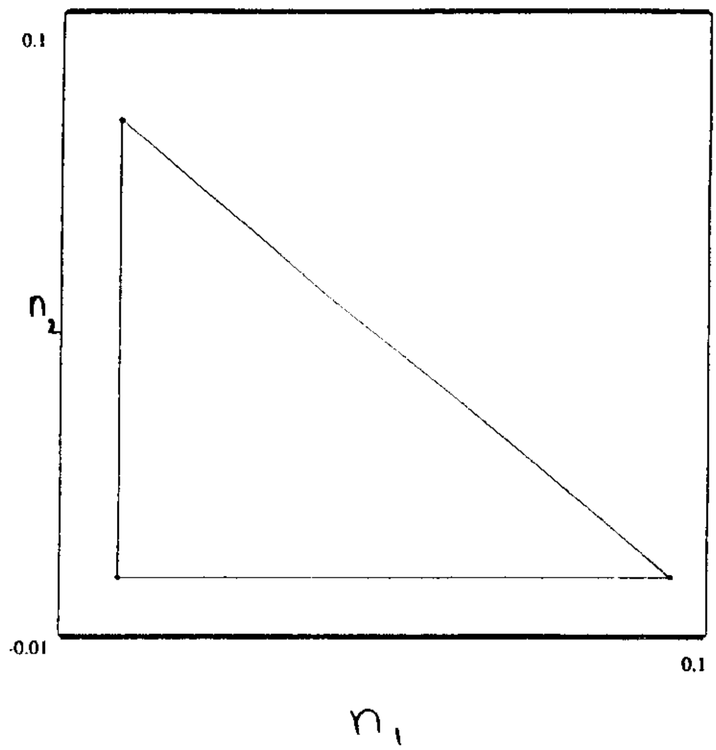
Example 1

Let $g(P) = \dfrac{1}{1+P}$ $\quad P(t) = N(t) = \sum_{i=1}^{3} n_i(t)$

$$L(\vec{n}(t)) = \begin{pmatrix} 0 & 0 & \dfrac{f_3}{1+N(t)} \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{pmatrix}$$

$f_3 = 1.2$, $p_1 = p_2 = .95$, $R = 1.083$



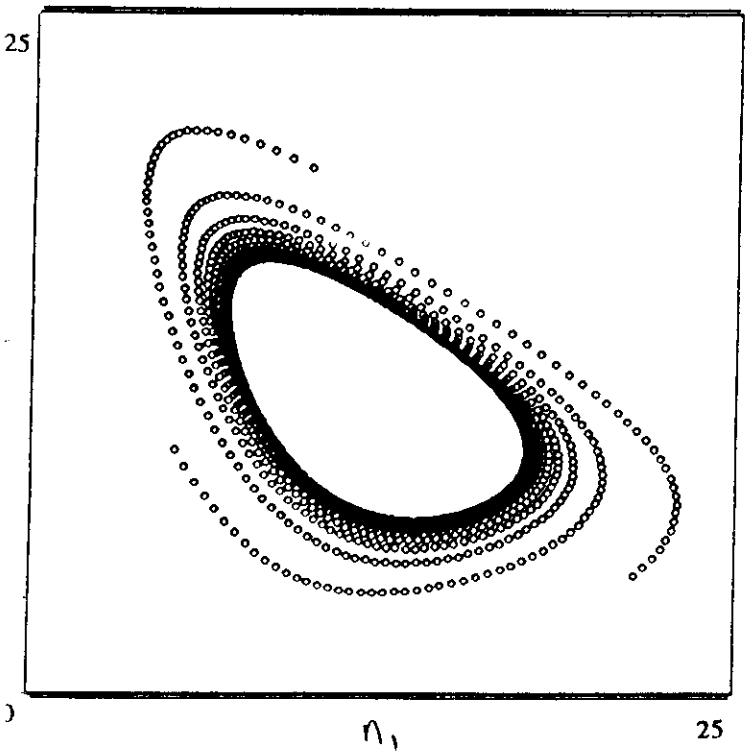


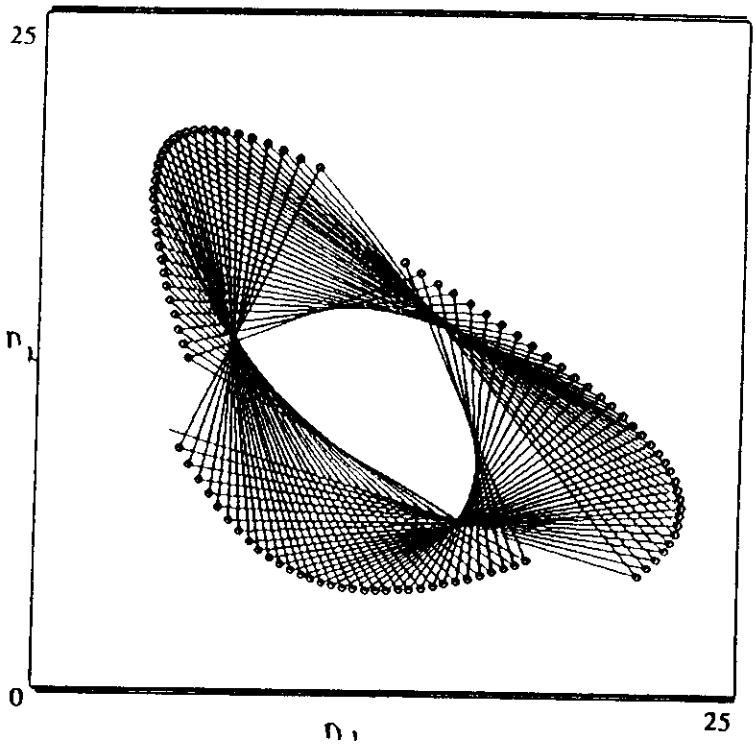
Example 2

Let $g(P) = \dfrac{1}{1+P}$, $P(t) = N(t) = \sum_{i=1}^{3} n_i(t)$

$$L(\tilde{n}(t)) = \begin{pmatrix} 0 & \dfrac{f_2}{1+N(t)} & \dfrac{f_3}{1+N(t)} \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{pmatrix}$$

$f_2 = 1$, $f_3 = 40$ $p_1 = p_2 = .9$ $R = 33.3$





Density-Dependent Model with Applications to Spatial Dynamics

$$\vec{n}(t+1) = M(\vec{n}(t))\,\vec{n}(t)$$

- Allen, Moulton, Rose (1990)

Def: Population persistence means $\limsup_{t\to\infty} \vec{n}(t) \geq \vec{0}$ $(\neq \vec{0})$ for all $\vec{n}(0) \geq \vec{0}$ $(\neq \vec{0})$. Population extinction means $\lim_{t\to\infty} \vec{n}(t) = \vec{0}$ for all $\vec{n}(0) \geq \vec{0}$ $(\neq \vec{0})$.

Theorem: Let A be a nonnegative and primitive matrix with dominant eigenvalue λ.

(i) If $M(\vec{n})$ satisfies $\lim_{\vec{n}\to\vec{0}^+} M(\vec{n}) = A$ and $\lambda > 1$, then the population is persistent.

(ii) If $M(\vec{n}) \leq A$ for $t \geq t_1 \geq 0$, and $\lambda < 1$, then the population becomes extinct.

Suppose

$$A = L \otimes D^k,$$

where L is a Leslie matrix $(m\times m)$ and D is a diffusion matrix $(N \times N)$. There is movement between N regions. Matrix A has a dominant eigenvalue $\underline{\lambda = \lambda_1 \lambda_D^k}$, where λ_1 is the dominant eigenvalue of L and λ_D is the dominant eigenvalue of D.

Example: Island Model

Suppose

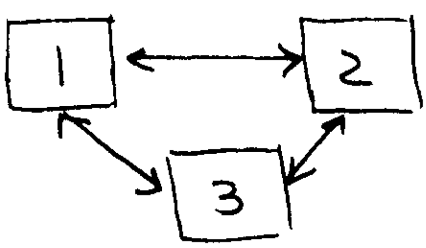
(i) $M(\vec{n})$ is a continuous and decreasing function of the components of $\vec{n}$.

(ii) $\lim_{\vec{n}\to\vec{0}} M(\vec{n}) = L \otimes D^k$, where

$$D = \begin{pmatrix} 1-(N-1)d_1 & d_2 & \cdots & d_2 \\ d_2 & 1-(N-1)d_1 & & d_2 \\ \vdots & \vdots & & \vdots \\ d_2 & d_2 & & 1-(N-1)d_1 \end{pmatrix}$$

and L is a primitive Leslie matrix with $\lambda_1 > 1$. Also, $\lambda_D = 1+(N-1)(d_2-d_1)$.

$N=3$



If $d_2 < d_1$, then the number of regions is critical for persistence. Solve $\lambda_1 \lambda_D^{k} = 1$ for N:

$$N_c = [\![\, 1 + \frac{(1-\lambda_1^{-\frac{1}{k}})}{d_1 - d_2} \,]\!]$$

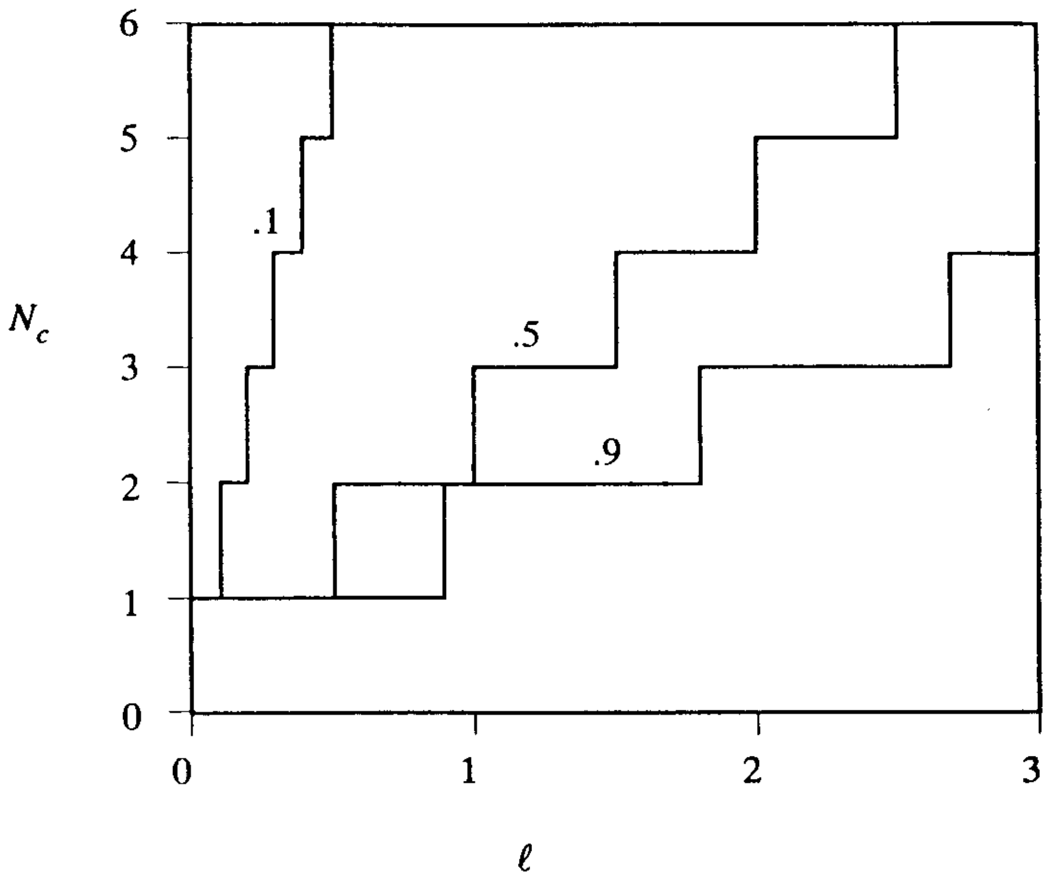
If $N < N_c$, then the population persists.
If $N > N_c$, the the population becomes extinct.

Example: Island Model

Let $\gamma d = d_1 - d_2$, $\gamma = .1, .5, .9$, then

$$N_c = [\![1 + \frac{\ell}{\gamma}]\!],$$

where $\ell = (1 - \lambda_1^{-\frac{1}{k}})/d$. As d increases the persistence regions decrease since there is a greater loss due to diffusion $d_2 < d_1$.



Example 2: Stepping Stone Model

Suppose

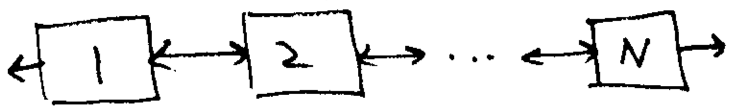
(i) $M(\vec{n})$ is a continuous decreasing function of the components of $\vec{n}$.

(ii) $\lim_{\vec{n} \to \vec{0}^+} M(\vec{n}) = L \otimes D^k$, where

$$D = \begin{pmatrix} 1-2d & d & d & \cdots & 0 \\ d & 1-2d & d & \cdots & 0 \\ \vdots & & \ddots & \ddots & d \\ 0 & & d & & 1-2d \end{pmatrix},$$

and L is a primitive Leslie matrix with dominant eigenvalue $\lambda_1 > 1$. Also,

$\lambda_D = 1 - 2d - 2d\cos\left(\frac{\pi N}{N+1}\right)$, $\quad 0 < d < 0.5$.



If $1 - \lambda_1^{-\frac{1}{k}} \le 2d$, then the number of regions N is critical for persistence,

$$N_c = \left[\!\left[\frac{\mathrm{Arccos}([1-\alpha]/2d - 1)}{\pi - \mathrm{Arccos}([1-\alpha]/2d - 1)} \right]\!\right] + 1$$

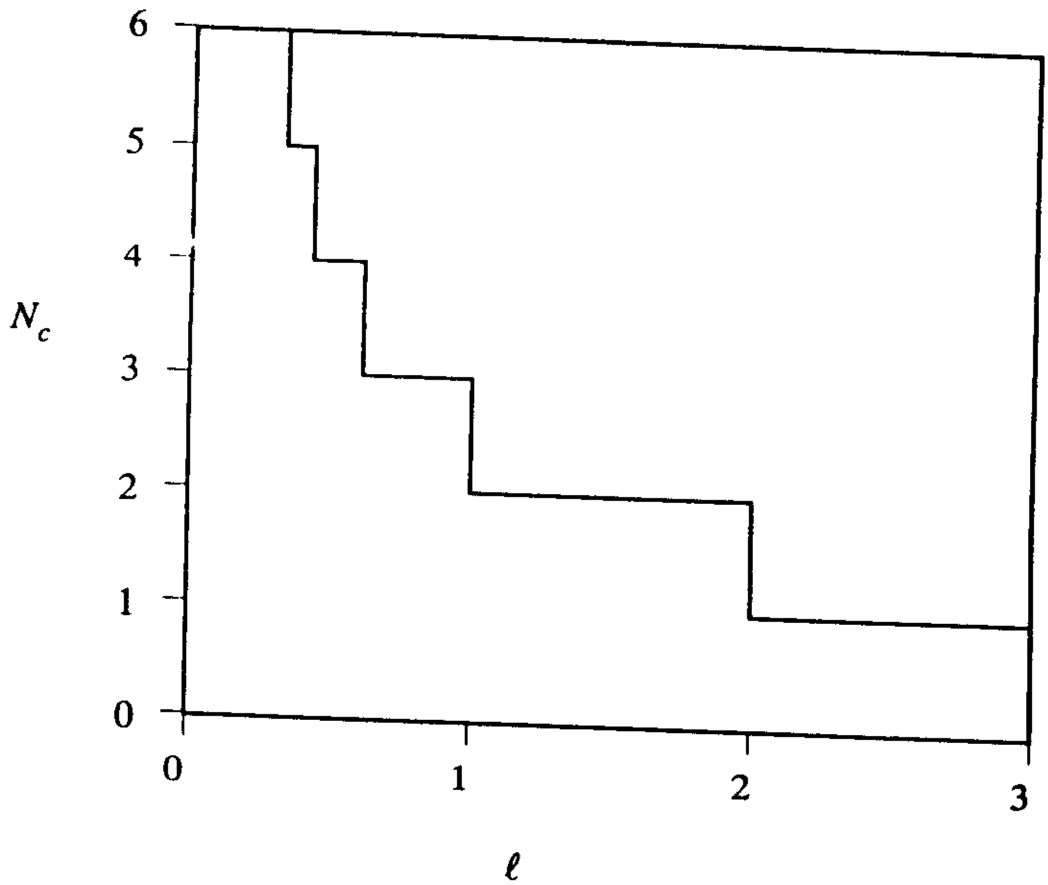
If $N > N_c$, then the population persists.
If $N < N_c$, then the population becomes extinct.

Example: Stepping Stone Model

Let $\ell = (1 - \lambda_1^{-1/n})/d$, then

$$N_c = \left[\!\left[\frac{\mathrm{Arccos}(\ell/2 - 1)}{\pi - \mathrm{Arccos}(\ell/2 - 1)} \right]\!\right] + 1.$$

As ℓ increases (λ_1 increases or d decreases) the minimum number of regions required for persistence decreases.



C. Nonautonomous Leslie Matrix with Density-Dependence

$$\vec{n}(t+1) = L(t, \vec{n}(t))\, \vec{n}(t)$$

Density-Dependent Nonautonomous Matrix Model

$$\vec{n}(t+1) = M(t, \vec{n}(t))\,\vec{n}(t)$$

- Li (1988)

$$\begin{aligned} x(t+1) &= y(t)\left[\alpha(t) - f(y(t))\right]^{+} \quad \text{Juveniles} \\ y(t+1) &= x(t)\left[\beta(t) - g(y(t))\right]^{+} \quad \text{Adults} \end{aligned}$$

$$\vec{n}(t+1) = \begin{pmatrix} x(t+1) \\ y(t+1) \end{pmatrix} = \begin{pmatrix} 0 & \alpha(t) - f(y(t)) \\ [\beta(t) - g(y(t))]^{+} & 0 \end{pmatrix} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix}$$

$$\vec{n}(t+1) = M(t, \vec{n}(t))\,\vec{n}(t)$$

<u>Def</u>: A population is <u>strongly persistent</u> if $x_n > 0$ and $y_n > 0$ for each $n = 0, 1, \ldots$ and $\limsup_{n\to\infty} x_n > 0$ and $\limsup_{n\to\infty} y_n > 0$.

<u>Def</u>: A population <u>goes to extinction at time N</u> provided $x_n > 0$, $y_n > 0$ for $n = 0, 1, \ldots, N-2$, $x_{N-1} \geq 0$, $y_{N-1} \geq 0$, $x_{N-1} + y_{N-1} > 0$ but $x_N \leq 0$, $y_N \leq 0$.

Example:
$$x(t+1) = y(t)\,(\alpha(t) - y(t))^+$$
$$y(t+1) = x(t)\,(\beta(t) - y(t))^+$$

$$\begin{pmatrix} x(t+1) \\ y(t+1) \end{pmatrix} = \begin{pmatrix} 0 & \alpha(t) - y(t) \\ (\beta(t) - y(t))^+ & 0 \end{pmatrix} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix}$$

Parameters

t	$\alpha(t)$	$\beta(t)$
0	2.2	0.9
1	1.5	0.95
2	1.05	0.9
3	3.0	0.9
4	0.23	0.21

TABLE I

Time	0	1	2	3	4	5
x	0.7200	0.3075	0.5184	0.1165	1.0426	0.0100
y	0.1500	0.5400	0.1261	0.4012	0.0581	0.1584

Time	0	1	2	3	4	5
x	0.0100	0.9291	0.0049	0.1499	0.0003	0.0128
y	0.5700	0.0033	0.8796	0.0001	0.1349	0.0000

Time	0	1	2	3	4	5
x	0.0200	0.5539	0.0182	0.2756	0.0207	−0.0040
y	0.2900	0.0122	0.5194	0.0069	0.2461	−0.0010

Summary of Talk

A. Nonautonomous Leslie Matrix

$$\vec{n}(t+1) = L(t)\vec{n}(t)$$

- Weak Ergodic Theorem (Lopez, 1961; Pollard, 1973)
- Periodic Matrices (MacArthur, 1968)

B. Autonomous Leslie Matrix

$$\vec{n}(t+1) = L(\vec{n}(t))\vec{n}(t)$$

- Review of some population models without structure
- Local Stability Analysis
- Applications
  (1) Bacteria (Beddington, 1974)
  (2) Fish (Levin and Goodyear, 1980)
  (3) Plants (Takada and Nakajima, 1992)

- Strong Ergodic Theorem (Cushing, 1989)
- Leslie's Density-Dependent Matrix (Leslie, 1948; Allen, 1989)
- Density-dependent Fertility Rates (Silva and Hallam, 1992)
- Application to Spatial Dynamics (Allen, Moulton, and Rose, 1990)

C. Nonautonomous Leslie Matrix with Density-Dependence

$$\vec{n}(t+1) = L(t, \vec{n}(t))\vec{n}(t)$$

(Li, 1988)