

Linear Algebra in Prediction of Population Biology

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Abstract—Linear algebra is a strong and useful tool to solve problems in real-world. In this article, linear algebra is applied to studying the development of species' population which is much more complicate than species like bacteria because their key factors influencing population change with their age. Through building model with linear algebra, track of changes in age-structured population is well described.

I. PROBLEM SETUP AND ASSUMPTIONS

Different from species having exponential and simple growth, species studied in this paper have different stages and show different growth characteristics correspondingly. Thus we need to treat them in an age-structured manner which requires linear algebra.

A. Assumptions

In order to simplify the model, we use discrete age and make two assumptions as following [1]:

1. Male to female ration is 50:50.
2. The number of offspring per year depends primarily on the number of females.

B. Notation

3. All parameters related to time are defined as years.
4. Lifespan of species is w

Before building the model, we need to provide definitions and notation used in subsequent analysis[1]:

$n_i(t)$ = number of females of age i in year t
 p_i = probability that a female of age i will survive to age $i+1$
 f_i = number of offspring surviving to age 1

C. Model setup

1) The number of individuals in age i at $t+1$ depends on number survival rate of individuals in the age $i-1$ at t :

$$n_i(t+1) = \begin{cases} p_{i-1}n_{i-1}(t) & i \neq 1 \\ \sum_{k=1}^w f_k n_k(t) & i = 1 \end{cases} \quad (1)$$

Based on all $n_i(t)$, we can build population vector $n(t)$:

$$n(t) = \begin{bmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_w(t) \end{bmatrix} \quad (2)$$

2) Leslie matrix is a matrix containing information of fertility and survival rate according to different age. So as mentioned in [2], we can have Leslie matrix,

$$L = \begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_{w-1} & f_w \\ p_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & 0 & \cdots & 0 & 0 \\ 0 & 0 & p_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{w-1} & 0 \end{bmatrix} \quad (3)$$

3) Based on the above discussion, we can calculate population growth by matrix multiplication with L and $n(t)$:

$$Ln(t) = \begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_{w-1} & f_w \\ p_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & 0 & \cdots & 0 & 0 \\ 0 & 0 & p_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{w-1} & 0 \end{bmatrix} \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ \vdots \\ n_w(t) \end{bmatrix} \quad (4)$$

$$= \begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ \vdots \\ n_w(t+1) \end{bmatrix}$$

From this, we can see that

$$n(t+1) = Ln(t) \quad (5)$$

Then, we have

$$n(t+T) = L^T n(t), \quad T \in [0, w] \quad (6)$$

We now get the equation (6) with which we can calculate the population at different stage in different time.

II. ANALYSIS AND BASIC RESULTS

A. Spectral Decomposition

Matrix A can be decomposed as:

$$A = \sum_{k=1}^w \lambda_k T_k \quad (7)$$

Where $T_k = e_k \otimes \varepsilon_k$ is outer product of the right eigenvalues and left eigenvalues.

To prove it, let's create matrix R, L whose columns are the right eigenvectors and left eigenvalues for matrix A respectively:

$$Ae = \lambda e, \quad \varepsilon A = \varepsilon \lambda \quad (8)$$

And scale ε to make $\langle e_i, \varepsilon_i \rangle = 1$, then we have:

$$\langle e_i, \varepsilon_j \rangle = \delta_{ij}, \quad (0 \text{ if } i \neq j, 1 \text{ if } i = j) \quad (9)$$

$$RL = I \quad (10)$$

Then we have:

$$AR = [Ae_1 | Ae_2 | \dots | Ae_w] = [\lambda_1 e_1 | \lambda_2 e_2 | \dots | \lambda_w e_w] \quad (11)$$

And construct matrix D:

$$D = \begin{bmatrix} \lambda_1 & 0 & \dots & 0 \\ 0 & \lambda_2 & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \dots & 0 & \lambda_w \end{bmatrix} \quad (12)$$

Then we have:

$$\begin{aligned} RD &= [e_1 \ e_2 \ \dots \ e_w] \begin{bmatrix} \lambda_1 & 0 & \dots & 0 \\ 0 & \lambda_2 & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \dots & 0 & \lambda_w \end{bmatrix} \\ &= [\lambda_1 e_1 | \lambda_2 e_2 | \dots | \lambda_w e_w] \end{aligned} \quad (13)$$

Thus,

$$\begin{aligned} AR &= RD \\ ARR^{-1} &= RDR^{-1} \end{aligned} \quad (14)$$

$$A = RDL = \sum_{k=1}^w \lambda_k e_k \otimes \varepsilon_k = \sum_{k=1}^w \lambda_k T_k$$

B. Growth and Equilibrium

We can notice an important property of the matrix $T_k T_j$,

when $k = j$:

$$\begin{aligned} T_k T_k &= e_k \otimes \varepsilon_k \cdot e_k \otimes \varepsilon_k \\ &= e_k (\varepsilon_k)^T e_k (\varepsilon_k)^T \\ &= e_k \langle e_k, \varepsilon_k \rangle (\varepsilon_k)^T \\ &= e_k (\varepsilon_k)^T = e_k \otimes \varepsilon_k = T_k \end{aligned} \quad (15)$$

Similarly, when $k \neq j$:

$$T_k T_j = 0 \quad (16)$$

Let's apply spectral decomposition to the Leslie matrix, we can get:

$$L^n = \sum_{k=1}^w \lambda_k^n T_k \quad (17)$$

For a Leslie matrix, there is one and only one real, positive eigenvalues, which is the dominant eigenvalue [3]. Let's consider $\det(A) = \det(L - \lambda I)$:

$$\begin{aligned} \det(A) &= \begin{vmatrix} f_1 - \lambda & f_2 & f_3 & \dots & f_{w-1} & f_w \\ p_1 & -\lambda & 0 & \dots & 0 & 0 \\ 0 & p_2 & -\lambda & \dots & 0 & 0 \\ 0 & 0 & p_3 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & p_{w-1} & -\lambda \end{vmatrix} \\ &= (-1)^2 a_{11} M_{11} + (-1)^2 a_{12} M_{12} + \dots + (-1)^{1+w} a_{1w} M_{1w} \\ &= 0 \end{aligned} \quad (18)$$

Where M_{1i} is the matrix A eliminating column and row of a_{1i} .

And take M_{13} as an example:

$$M_{13} = \begin{bmatrix} p_1 & -\lambda & 0 & \dots & 0 & 0 \\ 0 & p_2 & 0 & \dots & 0 & 0 \\ 0 & 0 & -\lambda & \dots & 0 & 0 \\ 0 & 0 & p_4 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & p_{w-1} & -\lambda \end{bmatrix} \quad (19)$$

So $|M_{13}| = p_1 p_2 (-\lambda)^{w-3}$

Then

$$\begin{aligned} \det(A) &= (f_1 - \lambda)(-\lambda)^{w-1} - p_1 f_2 (-\lambda)^{w-2} + \dots \\ &\quad + (-1)^{1+w} p_1 p_2 \dots p_{w-1} f_w \\ &= (-1)^w (\lambda^w - l_1 f_1 \lambda^{w-1} - l_2 f_2 \lambda^{w-2} - \dots - l_w f_w) = 0 \end{aligned} \quad (20)$$

Where $l_j = \prod_{i=1}^{j-1} p_i$, $l_1 = 1$

Then we have:

$$\sum_{i=1}^w \lambda^{-i} l_i f_i - 1 = 0 \quad (21)$$

It is easy to find out that if we treat this equation as $Q(\lambda)$, $Q(\lambda)$ is decreasing when $\lambda > 0$. So there is only one unique positive real root λ_1

C. Basic Results

This eigenvalue λ_1 would give the asymptotical growth rate for the population [1] which means the ratio of individuals in different age will not change and absolute number will increase by λ_1 each year [1].

Meanwhile, it can also be noticed that the right eigenvalues and left eigenvalues with respect to λ_1 have vital biological meanings. The right eigenvalues gives the percentage of the population in each age at equilibrium if we scale it to $\|e_1\|_1 = 1$. And the left eigenvalues gives the reproductive ratio of each age.

III. SIMULATIONS

Based on the analysis and results proved above, the utility of the Leslie matrix is tested by an example from the marine shore zone fish, the cunner [4] in this section. This species ranges from Newfoundland to the Chesapeake Bay. All required information is obtained from Williams et al (1973), Serchuk (1972), and Dew (1970) in Table 1.

So the Leslie matrix is:

$$L = \begin{bmatrix} 8 & 6 & 2 & \cdots & 8 & 11 \\ 0.625 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0.625 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0.625 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0.625 & 0 \end{bmatrix}$$

Tbale.1. Estimation of age specific fertility and survival for the cunner, 1977

Age(years)	Fertility f_i	Survival probability p_i
1	8	0.625
2	6	0.625
3	2	0.625
4	3	0.625
5	6	0.625
6	8	0.625
7	11	0

And the population vector in 1977 is:

$$n(1977) = \begin{bmatrix} n_1(1977) \\ n_2(1977) \\ n_3(1977) \\ n_4(1977) \\ n_5(1977) \\ n_6(1977) \\ n_7(1977) \end{bmatrix} = \begin{bmatrix} 71 \\ 26 \\ 35 \\ 31 \\ 22 \\ 3 \\ 1 \end{bmatrix}$$

Then population growth of each age class can be computed by high matrix powers, and its prediction is in Figure 1.

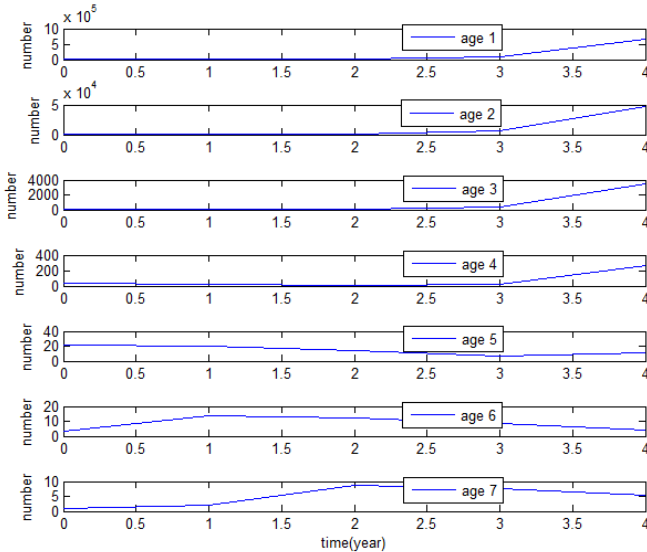


Figure 1. Predict of Population growth of each age class in 4 years.

The dominant eigenvalue of matrix L is:

$$\lambda_1 = 8.4558$$

It represents the asymptotic growth rate for the population, i.e. the proportions of individuals in each age class will come to a constant finally and the total number of

the population will increase by λ_1 times each year after each the equilibrium. The population of the cunner will increase by 8.4558 times each year in Figure 2.

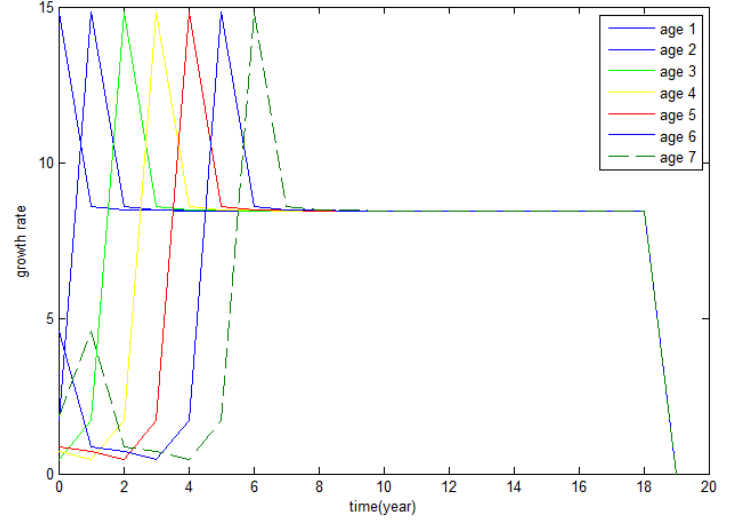


Figure 2. Results of analysis of eigenvalues model of cunner

Besides, right eigenvector and left eigenvector work well in real model too.

The right eigenvector and left eigenvector are:

$$e_1 = \begin{bmatrix} 0.9973 \\ 0.0737 \\ 0.0054 \\ 4.0270 \cdot 10^{-4} \\ 2.9765 \cdot 10^{-5} \\ 2.2000 \cdot 10^{-6} \\ 1.6261 \cdot 10^{-7} \end{bmatrix}, \quad \varepsilon_1 = \begin{bmatrix} 0.4398 \\ 0.3207 \\ 0.1174 \\ 0.1816 \\ 0.3459 \\ 0.4583 \\ 0.5721 \end{bmatrix}$$

After 20 years developing, the population of cunner in each class is

$$n(1997) = \begin{bmatrix} 5.2368 \cdot 10^{19} \\ 3.8707 \cdot 10^{18} \\ 2.8610 \cdot 10^{17} \\ 2.1147 \cdot 10^{16} \\ 1.5630 \cdot 10^{15} \\ 1.1553 \cdot 10^{14} \\ 8.5392 \cdot 10^{12} \end{bmatrix}$$

The age distribution in 1977 is almost the same as it indicted in right eigenvector e_1 .

IV. APPLICATION

The example talked about shows the usefulness of the eigenvalues analysis of the Leslie matrix of population biology. And this technique can be applied to any environmental effect which is manifested as a change in the age specific fertility and/or survivorship [4]. Although the Leslie works well, it still has some limitation. Take semelparous species as an example, in which the females produce only at specific ages. So there exists some common

denominator for all ages. And different cohorts are considered distinct. Because of this, there is no intrinsic rate or equilibrium. In a world, all cohort will be isolated population and reproductively independent.

Matrices not only provide a practical way to predict the development of population of age-structured populations, but also indict some useful biologically characteristics.

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