

MATRIX POPULATION MODEL

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Мигель Х.Х. Матричная модель популяции. Дискретные структурированные модели взросления популяций интенсивно исследуются со времен новаторской работы Бернаделли, Льюиса и Лесли. Модели такого рода достаточно хорошо зарекомендовали себя как инструменты в биологии популяций. Настоящая статья состоит из двух частей. Первая из них посвящена матричным моделям популяций, основанным на работе Кэсулла [1]. Из-за дефицита структурированных данных иллюстративный материал, представленный в этой части, основан на искусственных данных. Во второй части статьи внимание сосредоточено на относительной скорости роста популяций креветок, совместно обитающих в районе отмели Софала в Мозамбике. Образцы обработаны при помощи технологий Matlab12 и Minitab12 Software.

1 WHAT IS POPULATION BIOLOGY?

A population is a group of individuals of the same species that have a high probability of interacting with each other. A simple example would be the shrimps in the ocean, trout in the lake, although in many cases the boundaries delineating a population is simply the study of population biology.

An understanding of the complex ecological communities with numerous species interacting with each other and the environment requires an understanding of the simpler ecological systems of one or two species first [2]. In present paper we will focus on population biology of single species for two reasons.

First, an understanding of the dynamics of a single species leads to the primary questions of population ecology. Second, this is the simplest system that can be studied from a population approach.

We will focus also on population size as the variable because it is possible, even likely, that small number of individuals may have effects, especially on population stability, out of proportion to their numbers.

Population biology is by its nature a science that focuses on numbers. Thus, we will be interested in understanding, explaining and predicting changes in the size of population.

2 MODELLING POPULATIONS BY LESLIE MATRICES

In this paper we will focus on model based on Leslie-Matrices. This kind of model is important in studying structural population dynamics. Studying the life cycle in demographic or population dynamic context requires a way to translate from the individual to the population level. Individual organisms are born, grow, mature reproduce and eventually die [1]. We assume that as females actually give birth, they are more essential to the propagation of a species than a male. This makes sense as one male can fertilize the eggs of several females and once this has been done each female will gestate for some period of time.

Obviously, the female will not be in position to be fertilized again until the gestation period has elapsed. So, the rate at which offspring are produced is determined by parameters that describe the female population.

Suppose that the maximum age of a female of the species is H . We shall divide the interval $[0;H]$ into n age classes,

$$\left[0; \frac{H}{n}\right), \left[\frac{H}{n}; \frac{2H}{n}\right), \dots, \left[\frac{(n-1)H}{n}; H\right]. \quad (1)$$

We are interested in the number of females in each age class and how this grows with time. Lets assume that the population in each of these age classes is measured at time intervals of H/n ; that is, at times

$$t_0 = 0, t_1 = \frac{H}{n}, \dots, t_k = \frac{kH}{n}. \quad (2)$$

Let $x_i^{(k)}$ be the population in the i^{th} age class C_i where

$$C_i = \left[\frac{(i-1)H}{n}, \frac{iH}{n}\right); \quad 1 \leq i \leq n,$$

as measured at $t_k = kH/n$.

Here we define two demographic parameters, which determine how these age specific populations changes:

- for $i = 1, 2, 3, \dots, n$, F_i will be the fraction of females (daughters) to a female in age class C_i .

- for $i = 1, 2, 3, \dots, n$, P_i will be the fraction of females in age class C_i expected to survive for the next H/n years (and hence class C_{i+1}).

One can see that it is obvious to consider $F_i \geq 0$ and $0 < P_i \leq 1$. If for any i we find that $F_i > 0$, we call the age class C_i fertile.

The number of daughters born between successive population measurements at times t_{k-1} and t_k is

$$F_1 x_1^{(k-1)} + F_2 x_2^{(k-1)} + \dots + F_n x_n^{(k-1)} = \sum_{i=1}^n F_i x_i^{(k-1)} \quad (3)$$

and this quantity is exactly x_1^k , equating this we get

$$x_1^k = \sum_{i=1}^n F_i x_i^{(k-1)} \quad (4)$$

Also, for $i = 1, 2, 3, \dots, n-1$, we get

$$x_{i+1}^k = P_i x_i^{(k-1)}$$

writing this in matrix notation we find that,

$$\begin{bmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ \vdots \\ x_n^{(k)} \end{bmatrix} = \begin{bmatrix} F_1 & F_2 & \dots & F_{n-1} & F_n \\ P_1 & 0 & \dots & 0 & 0 \\ 0 & P_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & P_{n-1} & 0 \end{bmatrix} \begin{bmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \\ \vdots \\ x_n^{(k-1)} \end{bmatrix} \quad (5)$$

or indeed,

$$X^k = LX^{(k-1)} \quad (6)$$

where L is called the *Leslie Matrix*.

Let's define above-mentioned functions, F_i and P_i . Before doing this, we need some important definitions.

Survival

Survival is characterized by three functions of age:

a) the *survivorship function*. Let x be age, the survivorship function is defined as:

$$l(x) = P[\text{survival from birth to age } x].$$

It is assumed that this function is non increasing, with $l(0)=1$, (it is often rescaled so that $l(0)=10000$ or some other value and interpret as number of survivors out of an initial cohort of 10,000, rather than as a probability);

b) the *distribution of age at death*, $f(x)$ is the probability density function for the age at which individual die;

c) the *mortality rate or hazard function*, is

$$\mu(x) = \lim_{\Delta x \rightarrow 0} \frac{1}{\Delta x} P[\text{death in } [x, x+\Delta x] | \text{survival to } x] = \frac{f(x)}{l(x)}.$$

This last function can also be defined by the negative of the slope of the survivorship curve on a semi-logarithmic plot

$$\mu(x) = -\frac{d \ln l(x)}{dx}.$$

This formula is derived from the following result. The probability of surviving from age x to $x+\Delta x$ is given by

$l(x+\Delta x)/l(x)$. By Taylor expansion, leaving out terms power greater than one we get

$$l(x+\Delta x) = l(x) + \Delta x \frac{dl(x)}{dx}.$$

Thus, one minus the survival probability will give us the probability of death in the interval from x to $x+\Delta x$

$$1 - \frac{l(x+\Delta x)}{l(x)} = 1 - \frac{l(x) + \Delta x \frac{dl(x)}{dx}}{l(x)} = -\Delta x \frac{d \ln l(x)}{d(x)}.$$

Dividing both right and left hand sides of this equality and approaching Δx to zero we get

$$\mu(x) = -\frac{d \ln l(x)}{dx}.$$

All these three functions are interrelated [1]. Without details we will define reproduction as expected value of offspring per individual aged x per unit time

$$m(x) = E[\text{offspring per individual aged } x \text{ per unit time}].$$

Now we are in position to define the two functions in Leslie matrix, namely P_i and F_i .

In **birth-flow population** (in which the birth occur continuously over the projection interval) function P_i – (survival probability) is approximately found to be

$$P_i \approx \frac{l(i) + l(i+1)}{l(i-1) + l(i)} \quad (7)$$

and F_i – (fertility), as

$$F_i \approx \frac{l(0) + l(1)}{2} \left(\frac{m_i + P_{i+1}}{2} \right). \quad (8)$$

While in **birth-pulse populations** (in which reproduction is limited to a short breeding season within the interval), here the survival probability and the fertility coefficient are calculated as, [1]

$$P_i = P[\text{survival from age } i+p-1 \text{ to } i+p] = \frac{l(i+p)}{l(i+p-1)} \quad (9)$$

or

$$P_i = \begin{cases} \frac{l(i)}{l(i-1)} & \text{postbreeding } (p \rightarrow 0) \\ \frac{l(i+1)}{l(i)} & \text{prebreeding } (p \rightarrow 1) \end{cases} \quad (10)$$

while F_i , for birth-pulse is given by

$$F_i = l(p) P_i^{1-p} \begin{cases} P_i m_i & \text{postbreeding } (p \rightarrow 0) \\ l(1) m_i & \text{prebreeding } (p \rightarrow 1) \end{cases} \quad (11)$$

p stands for the fraction of a time unit needed by offspring to survive to the next generation ($n_1(t+1)$).

2.1 Eigenvalues and long-term behaviour

It is natural to ask what the *long-term* population distribution will be. And to find this, we need eigenvalues and eigenvectors. We have found that the population distribution in the k^{th} time period can be found from the population distribution in the $(k-1)^{\text{th}}$ time period using the formula (6), and one can relate population distribution in k^{th} time period to the initial population distribution by using the formula

$$X^{(k)} = L_k X(0). \tag{12}$$

So, to understand what happens in the long run, we need to be able to find L_k for suitable large k , and the easiest way to do this is to use *diagonalization*.

Consequently, assuming that the Leslie L matrix is diagonalizable, we can find an invertible matrix P that

$$P = \begin{bmatrix} | & | & \dots & | \\ v_1 & v_2 & \dots & v_n \\ | & | & \dots & | \end{bmatrix} \tag{13}$$

where the vectors v_1, v_2, \dots, v_n are the eigenvectors corresponding to the eigenvalues $\lambda_1, \lambda_2, \dots, \lambda_n$ with multiplicity of L and

$$P^{-1}LP = D = \text{diag} [\lambda_1, \lambda_2, \dots, \lambda_n]. \tag{14}$$

On re-arranging we find that $L = PDP^{-1}$, and so if we multiply L by itself k times we would find that

$$L^k = (PDP^{-1})^k = \underbrace{(PDP^{-1}) \dots (PDP^{-1})}_{k \text{ times}} = PD^k P^{-1}. \tag{15}$$

Now we can rewrite L_k matrix as follows

$$L^k = P \text{diag} [\lambda_1^k, \lambda_2^k, \dots, \lambda_n^k] \tag{16}$$

provided matrix D diagonal. This result simplifies the task of finding the population distribution in the k^{th} time period. However, if we are concerned with suitably values of k we can further simplify the problem.

Result 1. The characteristic polynomial for the matrix L is given by

$$p(\lambda) = \|L - \lambda I\| = (-1)(\lambda^n - F_1 \lambda^{n-1} - F_2 P_1 \lambda^{n-2} - \dots - F_{n-1} P_1 P_2 \dots P_n - 2\lambda - F_n P_1 P_2 \dots P_{n-1}). \tag{17}$$

Solutions of (17) are the eigenvalues of the Leslie matrix, given this fact it can be seen that

$$p(\lambda) = 0 \Leftrightarrow q(\lambda) = 1,$$

where $q(\lambda)$ is found by isolating λ^n in $p(\lambda) = 0$ and dividing both sides by λ^n

$$q(\lambda) = \frac{F_1}{\lambda} + \frac{F_2 P_1}{\lambda^2} + \dots + \frac{F_n P_1 P_2 \dots P_{n-1}}{\lambda^n} = \sum_{i=1}^n \left(\prod_{j=1}^{i-1} P_j \right) F_i \lambda^{-i}. \tag{18}$$

The function $q(\lambda)$ has the following properties

- $q(\lambda)$ is a decreasing function for $\lambda > 0$,
- as $\lambda \rightarrow 0^+$, $q(\lambda) \rightarrow \infty$,
- as $\lambda \rightarrow \infty$, $q(\lambda) \rightarrow 0$.

As conclusion we can say that there is a unique positive real solution of equation $q(\lambda) = 1$. That is, L has a unique positive real eigenvalue, and we shall call this by λ_1 . Further, an eigenvector corresponding to this eigenvalue is given by

$$v_1 = \begin{bmatrix} 1 \\ P_1/\lambda_1 \\ P_1 P_2/\lambda_1^2 \\ \vdots \\ P_1 P_2 \dots P_{n-1}/\lambda_1^{n-1} \end{bmatrix} \tag{19}$$

and all the entries in this vector are positive. Vector v_1 is an eigenvector of L corresponding to λ_1 .

Result 2. The contribution of all eigenvalues can be summarized as follows:

- If λ_i is positive, λ_i^k produces exponential growth if $\lambda > 1$ positive and exponential decay if $\lambda < 1$ negative,
- If $-1 < \lambda_i < 0$, then λ_i^k produces damped (convergent) oscillations with period equal to 2,
- If $\lambda_i < -1$ then λ_i^k produces diverging oscillations with period equal to 2.
- Complex eigenvalues $\lambda = a + ib$ produce oscillations. Lets define complex λ in polar form $\lambda = [a^2 + b^2 (\cos \theta + i \sin \theta)]^{1/2}$, where $\theta = \arctan(b/a)$, $\lambda^k = |\lambda|^k (\cos k\theta + i \sin k\theta)$.

The complex solution always comes with its conjugate $\lambda = a - bi$, the solution to the projection equation will then contain terms of the form

$$\lambda^k + \lambda^{-k} = |\lambda|^k 2 \cos k\theta.$$

As complex eigenvalue is raised to higher powers, its magnitude $|\lambda|^k$ increases or decreases exponentially, depending on whether $|\lambda|$ is greater or less than one. Its angle in the complex plane increases by θ each time step, completing an oscillation with period of $2\pi/\theta$.

Remark. Regardless of whether λ_i is real or complex, the boundaries between population increase and population decrease comes at $|\lambda| = 1$.

L e m m a 1. *If two successive entries of matrix L are positive (say F_i and F_{i+1}) are both non-zero, then for any eigenvalue, of L other than λ_1 ,*

$$|\lambda| < \lambda_1.$$

In other words, if there are two successive fertile classes, then the eigenvalue λ_1 is dominant.

Proof: Let's consider two successive fertile classes and that L diagonalizable.

We let λ_1 to be dominant eigenvalue and v_1 as given above to be the corresponding eigenvector. Let's define the other eigenvalues and eigenvectors of L by $\lambda_2, \lambda_3, \dots, \lambda_n$ and v_2, v_3, \dots, v_n respectively. Now, recalling (16), (13) and (12), we can write

$$X^{(k)} = P \text{diag} [\lambda_1^k, \lambda_2^k, \dots, \lambda_n^k] P^{-1} X^{(0)}, \quad (20)$$

and by dividing both sides by λ_1^k we get

$$\frac{X^{(k)}}{\lambda_1^k} = P \text{diag} \left[1, \left(\frac{\lambda_2}{\lambda_1} \right)^k, \dots, \left(\frac{\lambda_n}{\lambda_1} \right)^k \right] P^{-1} X^{(0)} \quad (21)$$

as we are considering λ_1 to be dominant, we find that $|\lambda_i/\lambda_1| < 1$ for $i = 2, 3, \dots, n$, and this implies that the diagonal entries of the form $(\lambda_i/\lambda_1)^k \rightarrow 0$ as $k \rightarrow +\infty$ consequently, we find that

$$\begin{aligned} c v_1 &= \lim_{k \rightarrow \infty} \frac{X^{(k)}}{\lambda_1^k} = \\ &= \lim_{k \rightarrow \infty} P \text{diag} \left[1, \left(\frac{\lambda_2}{\lambda_1} \right)^k, \dots, \left(\frac{\lambda_n}{\lambda_1} \right)^k \right] P^{-1} X^{(0)} \end{aligned} \quad (22)$$

where the constant c is the first entry of the vector given by $P^{-1} X^{(0)}$. Thus, for large values of k we can have approximately

$$X^{(k)} \approx c \lambda_1^k v_1,$$

and this result tells us the *proportion* of the population lying in each age class is, in the long run, constant. We can also deduce that

$$X^{(k)} \approx \lambda_1 X^{(k-1)}.$$

This tells us that the population in each age class grows by factor of λ_1 every time period (i. e. every H/n).

2.2 Density – Dependent Models

Hypotheses for population regulation

The ecosystems do not regulate consciously by themselves. Instead, the role that different organism plays in the ecosystem impact other organisms through the flow of energy and nutrients. These impacts regulate the production of other organisms, and hence the flow of energy or nutrients through the entire ecosystem. Many hypotheses have been proposed for the causes of regulation of population:

- Populations are limited by density-independent factors such as changes in the weather.
- Populations are limited by their food supply.
- Populations regulate themselves through mechanisms such as territoriality of cannibalism.
- Populations are limited through competition.
- Populations are regulated by predators.
- Populations are regulated by parasites or diseases.

Model construction

Lets define density-dependent model as

$$\mathbf{n}(t+1) = \mathbf{A}_n \mathbf{n}(t) \quad (23)$$

where the subscript indicates that all the entries $a_{ij}(\mathbf{n})$ depend on the population vector \mathbf{n} . Each stage in the life cycle may contribute differently to "density". We will write entries a_{ij} as function of a weighted sum of stage density:

$$N(t) = \sum_{i=1}^n c_i n_i(t); \quad c_i \geq 0 \quad (24)$$

where c_i measures the contribution of n_i to resource, or whatever other interactions is responsible for the dependence. This includes as a special case, the total population size

$$N(t) = \sum_{i=1}^n n_i(t)$$

and density of a single stage, $N(t) = n_i(t)$ for some i .

The entries should satisfy $a_{ij}(\mathbf{n}) \geq 0$ for all i, j and $\mathbf{n} \geq 0$. Lets call

$$\mathbf{A}_n = \mathbf{T}_n + \mathbf{F}_n \quad (25)$$

projection matrix, where \mathbf{T}_n is the transition matrix and \mathbf{F}_n is the reproduction matrix. \mathbf{T}_n should be substochastic; that is the entries should satisfy $0 \leq a_{ij}(\mathbf{n}) \leq 1$ for all i, j and $\mathbf{n} \geq 0$.

$$\sum_{i=1}^n t_{ij}(n) \leq 1$$

for all i, j and $\mathbf{n} \geq 0$.

In one-dimensional maps for unstructured populations we have

$$N(t+1) = f(N(t)) = g(N(t))N(t) \quad (26)$$

where $g(N)$ is the per-capita growth rate. If

$$\frac{dg(N)}{dN} > 0 \quad (27)$$

for some $N > 0$, then $g(\cdot)$ is said to exhibit *depensation*, i. e., the increase in the per-capita rate with density is exactly compensated by the increase in density, so that the net growth rate is asymptotically constant.

2.3 Local stability of equilibria

A set $\hat{\mathbf{e}}$ is equilibrium state of (23), and it satisfies the condition

$$\hat{\mathbf{e}} = \mathbf{A}_e \hat{\mathbf{e}}.$$

By definition, an equilibrium state \mathbf{n} is said to be stable if for any $\varepsilon > 0$, there exist a $\delta > 0$ such that $\|\mathbf{n}(0) - \hat{\mathbf{e}}\| < \delta$, then $\|\mathbf{n}(t) - \hat{\mathbf{e}}\| < \varepsilon$ for all $t = 1, 2, 3, \dots$, where $\|\cdot\|$ denotes any vector norm. Saying that an equilibrium point $\hat{\mathbf{e}}$ is stable, means that if we start somewhere very closer to this point, $\hat{\mathbf{e}}$, the solution will stay closer to $\hat{\mathbf{e}}$ for long time.

If $\|\mathbf{n}(t) - \hat{\mathbf{e}}\|$ tends to zero as t tends to infinity, then the equilibrium state is called asymptotically stable. In this case the solution will actually converge to $\hat{\mathbf{e}}$. Lets define the difference between vector \mathbf{n} and the equilibrium $\hat{\mathbf{e}}$ by

$$\mathbf{x}(t) = \mathbf{n}(t) - \hat{\mathbf{e}} \quad (28)$$

which gives $\mathbf{n}(t) = \mathbf{x}(t) + \hat{\mathbf{e}}$. Then we can find our linearized model to be

$$\mathbf{x}(t+1) = \left(\mathbf{A}_n + \sum_{i=1}^m \frac{\partial \mathbf{A}}{\partial n_i} \Big|_{\hat{\mathbf{e}}} \mathbf{H}_i \right) \mathbf{x}(t) = \mathbf{B} \mathbf{x}(t) \quad (29)$$

where the set of matrices \mathbf{H}_i has $\hat{\mathbf{e}}$ in column i and zeros elsewhere.

$$\mathbf{B} = \mathbf{A}_n + \begin{pmatrix} \frac{\partial \mathbf{A}}{\partial n_1} \Big|_{\hat{\mathbf{e}}} \hat{\mathbf{e}} & \frac{\partial \mathbf{A}}{\partial n_2} \Big|_{\hat{\mathbf{e}}} \hat{\mathbf{e}} & \dots \end{pmatrix}. \quad (30)$$

for detail see [1]. For stability analysis of (23) is enough to study the stability of linearized system (29). As the final

form of the linearized model is

$$\mathbf{x}(t+1) = \mathbf{B} \mathbf{x}(t)$$

it is reasonable to discuss the magnitude of the eigenvalues of matrix \mathbf{B} .

Clearly, if $|\lambda_i|$ is the largest eigenvalue of \mathbf{B} , then one can draw the following conclusions:

- $|\lambda_1| > 1 \Rightarrow$ equilibrium state $\hat{\mathbf{e}}$ is unstable;
- $|\lambda_1| < 1 \Rightarrow$ equilibrium state $\hat{\mathbf{e}}$ is asymptotically stable;
- $|\lambda_1| = 1 \Rightarrow$ linear approximation by Taylor series

does not provide sufficient information about stability. In this case stability depends on higher order terms.

In Caswell's book the Jury criterion for stability is presented only for 2×2 matrixes. It could be of interest to extend the criteria for stability of discrete models with $n \times n$ matrices, $n > 2$. It will allow us to identify exactly the total number of roots in and outside the unit disc, respectively.

If we write the characteristic polynomial of \mathbf{B} in the form

$$p(\mu) = \alpha_0 \mu^n + \alpha_1 \mu^{n-1} + \dots + \alpha_n \quad (31)$$

then $p(\mu)$ is also termed convergent if all its roots have modulus less than a unity. A convenient scheme to determine whether $p(\mu)$ is convergent is follows:

Theorem 1 (Jury-Marden) [3]: *A necessary and sufficient condition for $p(\mu)$ to be convergent polynomial is that*

$$d_{21} > 0, \quad d_{i1} < 0, \quad i = 3, 4, \dots, n+1 \quad (32)$$

where the d_{i1} are first column elements in the array of Jury-Murray table, see [3].

$$\begin{array}{cccccccc} \alpha_0 & \alpha_1 & \cdot & \cdot & \cdot & \alpha_{n-1} & \alpha_n & \\ \alpha_n & \alpha_{n-1} & \cdot & \cdot & \cdot & \alpha_1 & \alpha_0 & \\ c_{21} & c_{22} & \cdot & \cdot & \cdot & c_{2n} & & \\ d_{21} & d_{22} & \cdot & \cdot & \cdot & d_{2n} & & \\ c_{31} & c_{32} & \cdot & \cdot & \cdot & c_{3,n-1} & & \\ d_{31} & d_{32} & \cdot & \cdot & \cdot & d_{3,n-1} & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & & & \\ c_{i-1,1} & \cdot & \cdot & c_{i-1,j+1} & \cdot & c_{i-1,n-i+3} & & \\ d_{i-1,1} & \cdot & \cdot & d_{i-1,j+1} & \cdot & d_{i-1,n-i+3} & & \\ \cdot & \cdot & c_{ij} & c_{i,j+1} & \cdot & & & \\ \cdot & \cdot & d_{ij} & d_{i,j+1} & \cdot & & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & & & \end{array} \quad (33)$$

and

$$c_{ij} = \begin{vmatrix} c_{ij} & c_{i-1,j+1} \\ d_{i-1,j} & d_{i-1,j+1} \end{vmatrix}, \quad i = 1, 2, \dots, n + 1$$

$$d_{ij} = c_{i,n-j-i+3}$$

with

$$c_{1j} = \alpha_{j-1}, \quad j = 1, 2, \dots, n + 1.$$

Here is also possible to find the exact number of zeros of polynomial $p(\mu)$ outside and inside a unity disc $|\mu| < 1$ (excluding the boundary). If there is no $d_n = 0$, and let

$$Q_k = (-1)^k d_{21} d_{31} d_{41} \dots d_{k+1,1}, \quad k = 1, 2, \dots, n \quad (34)$$

then the number of roots of $p(\mu)$ inside and outside the unity disc is N and $n - N$, respectively where N is the number of negative products Q_k defined in (34).

3 SUSTAINABLE HARVESTING POLICY

In many cases, the harvesting process is done, without considering whether the harvesting rate will maintain the population in stable level or it will drive it to extinction.

Sustainable harvest is a plan for harvesting on a regular schedule in such a way that the harvest is always the same and the state of the population after harvesting is always the same. Suppose we let h_i be the fraction of the i^{th} age group that will be harvested at the end of each growth period, and we let H be the diagonal matrix, whose entries are the h_j 's.

If we start a growth period with a age-distribution state x , then the state after growth will be Lx . The harvest after growth will be HLx , and that will reduce the population to $Lx - HLx$, or $(I - H)Lx$. To be sustainable, the population state after harvest must match the starting state, i. e., $(I - H)Lx = x$. That, is x must be an eigenvector for eigenvalue 1 (λ_1) in the matrix $(I - H)L$.

Let's explore some of the implications of this definition:

1. We enter the Leslie matrix L in symbolic form and compute $(I - H)L$, after that one can see that $(I - H)L$ is another Leslie matrix. It differ from L in that i^{th} row of L is now multiplied by $(1 - h_i)$.

2. We had defined characteristic polynomial p for Leslie matrix and his auxiliary function q (which depends on p), (see section 2.2). Recall that λ is an eigenvalue of L if and only if $p(\lambda) = 0$, and $p(\lambda) = 0$ if and only if $q(\lambda) = 1$. We defined λ_1 to be dominant eigenvalue of Leslie matrix and it is unique positive solution of $q(\lambda) = 1$. To get zero population growth, we must have $q(1) = 1$, so that the largest eigenvalue (and only positive one) turns to be 1. Substitute $\lambda = 1$ in the definition of q to get an explicit condition on birth and survival rates for having zero growth. In conclusion if all this conditions are placed, in our new matrix one finds that there are infinitely many ways to construct a sustainable harvesting policy.

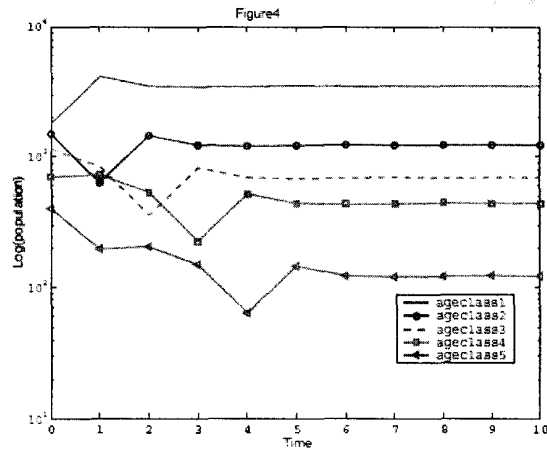


Fig. 1.

3. It is important to recompute the dominant eigenvalue λ_1 .

4. A *uniform* harvesting policy is one in which the same fraction h is harvested from each age group. In this case, we must have $(1 - h)Lx = x$. This means that h must satisfy $\lambda_1 = 1/(1 - h)$, so $h = 1 - 1/(\lambda_1)$.

Using this observation one can find the fraction of the population that can be harvested every year and leave the population distribution the same as at the start of each year.

Suppose that the population is harvested with harvest rate h , in all age groups. The Leslie matrix in this case is:

$$(I - H)L = (1 - h) \begin{bmatrix} 0,4 & 1,5 & 1,7 & 1,2 & 0,3 \\ 0,5 & 0 & 0 & 0 & 0 \\ 0 & 0,8 & 0 & 0 & 0 \\ 0 & 0 & 0,9 & 0 & 0 \\ 0 & 0 & 0 & 0,4 & 0 \end{bmatrix}$$

Considering the same initial population, the total female population after n years is given by,

$$T = [11111] L^n X_0.$$

As we found in example 5, the dominant eigenvalue is $\lambda_1 = 1,4232$, before rounding. We can use this value to calculate the harvest fraction h , in this case $h = 1 - 1/\lambda_1 = 0,297$. That is with this fraction the population can be harvested without risk of driving it to extinction. Now the dominant eigenvalue of the new Leslie matrix is as required for uniform harvesting policy, approximately 1, i. e., $\lambda_1 = 1,0005$, computed in Matlab. One can find that using this fraction h , the total population over years is not very different. The next figure shows that in long run the population will have stable growth rate in spite of that the same population have been harvested.

4 STATISTICAL ANALYZE OF SHRIMP DATA

Fishery industry being one of the most contributors to the Mozambican economy, is of great importance to study

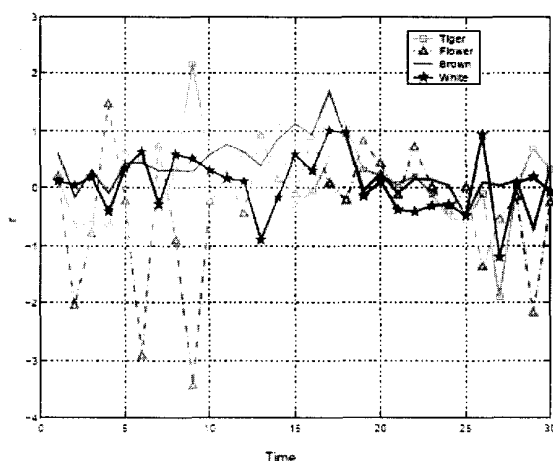


Fig. 2.

the dynamics of the exploited species in order to determine stock size for the decision makers.

It is well known that when population is exploited by culling or harvesting it is much easier to say what we want to avoid than what we precisely might wish to achieve. We of course want to avoid over exploitation, where too many individuals are removed and the population is driven to biological jeopardy, or economical insignificance or perhaps even to extinction. On the other hand we want to avoid under exploitation where very fewer individuals are removed than the population can bear.

Because of the nature of the available data, it is not possible to make use of matrix model, the data were collected for other type of model that I used in my thesis [4] (using Delay Differential Equations). However, would be of interest to understand the growth rate of shrimps using cross-correlation.

From this view point, we will study the growth rate of the four species of shrimps cohabiting in the Sofala Bank, one of the reacherest regions in shrimps in Mozambique: *peneaus indicus*, *metapeneaus monoceros*, *peneaus japonicus* and *peneaus monodom*, respectively white, brown, tiger and flower prawns.

Many facts may have influence in the dynamics of the population size for example, temperature, seasonal fluctuation of biomass and recruitment of new individuals.

The following model will be used to find the relative growth rate for each species:

$$\frac{1}{N} \frac{dN(t)}{dt} = \ln \frac{N(t)}{N(t-1)} = r \quad (35)$$

where $N(t)$ stands for the population size at time t and $dN(t)/Ndt$ denotes the relative growth rate. The correlation coefficients were found. The time interval is assumed to be equal to 30 units during the year, because the catch period is of 10 days giving a total of 300 days of fishing per year.

There is no fishing during January and February; this period is assumed by policy makers as maturation and recruitment season. The correlation coefficients of pair wise species are given below^{1a} (36). The flower species is negatively correlated to the white and tiger species, respectively. The overall relative growth rates also show that the flower species has decreased from 1997 to 1998 (37).

$$\begin{aligned} \rho_{bt} &= 0,29, & \rho_{bf} &= 0,21, & \rho_{bw} &= 0,49, \\ \rho_{wt} &= 0,57, & \rho_{wf} &= -0,40, & \rho_{ft} &= -0,35; \end{aligned} \quad (36)$$

$$\begin{aligned} r_b &= 0,396, & r_w &= 0,141, \\ r_t &= 0,085, & r_f &= -0,132. \end{aligned} \quad (37)$$

The statistical analysis of the data was performed, a clustering of the (4) variables was done in Minitab Package to find the species that have tendency to grow at same rate. As result, was possible to identified that brown, tiger and white species form one cluster while flower species forms each own cluster, (Appendix.I). A plot of relative growth against time, for all species over the year are given the next figure 2.

4.1 Conclusions

This study, although with very few data, has showed that the total stock of the shrimp population in Sofala bank region is dominated by brown and 3The subscripts are initials of the species white species on the one hand and, tiger and flower in small quantities on the other hand.

From result in (37), one can see that some significant increase of population was verified in brown and white species whereas flower has decreased from 1997 to 1998. This result may suggest that there should be a good harvesting strategy, (see section 2.4), in other to avoid over exploitation of the species.

The different scenarios shall then be analysed and a final decision can be made, when the study is conducted with more data, which is more detailed that can enable us to use matrix models including also other knowledge not represented in this brief analysis.

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^a The subscripts are initials of the species.