

Leslie Matrix Model in Population Dynamics

Mosimanegape Irvin Montshiwa (mosimanegape@aims.ac.za)
African Institute for Mathematical Sciences (AIMS)

Supervised by Prof. David Sherwell and Dr. Londiwe Masinga
University of Witwatersrand

June 7, 2007

Abstract

The Leslie Matrix Population Model is a fairly recent innovation in mathematics, and it has been found to be very useful in determining population growth. The model was discovered and named after P.H. Leslie in 1945. By using fertility rates, survival rates, and base population for a given species, this model can be used to calculate population growth. Ecologists find it useful in determining whether a species can survive when introduced into a new environment. Furthermore, the model can also be used to determine whether the population of a given species will increase or decrease over a certain period of time. We have gained an understanding of the construction and contents of the Leslie Matrix population model. We have also demonstrated with some simple examples that the Leslie Matrix population model is a reliable model for determining population growth.

Contents

Abstract	i
List of Figures	iii
1 Introduction	1
1.1 Historical background	1
1.2 Definition of the Leslie Matrix Population Model	1
1.3 Objective and organisation of this essay	3
2 Projections using the Leslie model and age stable population distribution	5
2.1 The birth-flow population	5
2.2 Birth-pulse populations	6
2.3 Dominating eigenvalue and the properties of the stable vector	7
2.4 Perturbation analysis : Sensitivity and Elasticity	8
3 Development over the years and the variation of the basic model	13
3.1 Development over the years	13
3.2 Variations of the model	15
3.2.1 Density Dependence in the Leslie model	15
3.2.2 Stochastic in the model	20
4 Vertical and Horizontal life table	24
4.1 Demographic Analysis	24
4.1.1 Life Table	24
5 Discussion and Conclusion	28
Bibliography	31

List of Figures

1.1	Discrete age class i and continuous age x	2
2.1	The trajectory of the salmon population over time.	10
2.2	The logscale of the trajectory of the salmon population.	10
2.3	The total number of population.	11
2.4	percentage at each iteration.	11
3.1	Schematic representation of the developments in the basic matrix model	13
3.2	Density dependence population projection.	18
3.3	Beverton-Holt model with $c = 2$	19
3.4	The total population after the Beverton-Holt model projection.	19
3.5	Beverton-Holt model for $c = 0.003$	20
3.6	Richer's model for $c = 0.003$	20
3.7	Three realization of the stochastic population model.	23
4.1	approximated value of r	27

1. Introduction

1.1 Historical background

Matrix population models have become increasingly important and useful in predicting population growth. Projections of population growth on the basis of survival and fertility assumptions date back to 1895 by Cannan. In the early 40's, Bernardelli (1941), Lewis (1942), and Leslie (1945) successfully formalised the matrix methods introduced by Whelpton in 1936 to project populations.

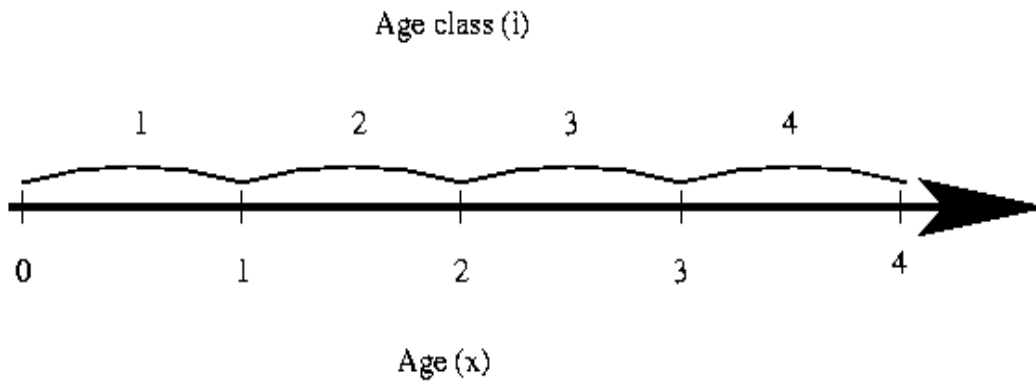
P. H. Leslie was born in 1900 and died in 1974. At the age of 21 he studied Physiology at Oxford and due to a health problem did not continue with his medical career, instead, he became an ecologist. By 1935 he was working at the Bureau of Animal Population (BAP) in Oxford, and did so until his retirement in 1968. In 1945 he wrote a paper that started by using the basic age-specific projection equations in a matrix form. He developed this tool after Elton, his director at BAP suggested to him that it would be useful if the mortality and fertility functions could be combined into a single expression [1, 2]. This tool was named after him as, "The Leslie Matrix Population Model".

In 1959 Leslie proposed a modified form of projection matrix to allow for the effect of the presence of other population members on population growth.

Due to the importance of this deterministic model, J. H. Pollard developed a stochastic version of the basic model in 1966 by giving each complete point of time the mean and variance of the number of animals in each age group [3].

1.2 Definition of the Leslie Matrix Population Model

The Leslie matrix population model is a discrete (or finite, i.e time goes in steps as opposed to continuously) and age dependent model (construction of the model consider only age). This matrix population model is widely used in population ecology and demography in order to determine the growth of a population, as well as the age distribution within the population over time. The discretization of age classes and time (or continuous age) is shown in the diagram below, where age class i corresponds to ages $i - 1 \leq x \leq i$,

Figure 1.1: Discrete age class i and continuous age x

The model is written in compact form as

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t), \quad (1.1)$$

where $\mathbf{n}(t)$ is a population vector with elements $n_1(t), n_2(t), \dots$ representing the number of individuals in each age class at time t , $\mathbf{n}(t+1)$ is a population vector in the next year, and \mathbf{A} represents the $n \times n$ Leslie matrix, or “projection matrix”.

\mathbf{A} is defined as follows:

The entries of the first row of the matrix \mathbf{A} are given by the **fertility**, F_i and the sub-diagonal (the cells below the top-left to bottom right diagonal) is given by the **survival**, P_i and there are zeros elsewhere. Each element in the matrix represents a *transition*. The fertility and survival rates are generally referred to as **vital rates**. In a matrix form Eq. (1.1) is written as

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ n_w \end{pmatrix} (t+1) = \begin{pmatrix} F_1 & F_2 & F_3 & \dots & F_{w-1} & F_w \\ P_1 & & & & & \\ 0 & P_2 & & & & \\ \cdot & & P_3 & & & \\ \cdot & & & \ddots & & \\ \cdot & & & & \ddots & \\ 0 & \cdot & \cdot & \dots & P_{w-1} & 0 \end{pmatrix} \cdot \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ n_w \end{pmatrix} (t). \quad (1.2)$$

Now, considering only the females in a finite age scale, **fertility** and **survival** can be defined as,

Definition 1.1 Fertility is the number of offspring of a female of age i to $i+1$ in a unit of time t that will survive to the next age class [4] at time $t+1$.

Since the offspring are generated through reproduction, the first row of the projection matrix is expressed by the following equation

$$n_1(t+1) = \sum_{i=1}^w F_i n_i(t), \quad (1.3)$$

with w a constant that gives the number of age classes.

Obviously the reason why most assumptions do not include males is that they do not affect the survival and reproduction of females, except in insemination.

Definition 1.2 Survival is the likelihood or probability that an individual of age i at time t will survive to time $t + 1$, when her age will be $i + 1$.

Mathematically this can be written

$$n_i(t + 1) = P_{i-1}n_{i-1}(t), \quad i \geq 2, \dots, w \quad (1.4)$$

The projection matrix is non-negative, which implies the variables P_i and F_i are non-negative and mutually independent.

The most appealing property of Eq. (1.2) is that the number of equations we have in this model depends crucially on the mode of representation. For example, without using matrix algebra, we have w distinct equations. However, when we use matrix algebra, we have a single equation of population growth.

Most importantly, \mathbf{A} can either be a **constant** or a **variable**. The variability of \mathbf{A} can be *internally* generated (i.e Density-dependent or Frequency-dependent), *externally* generated (i.e Deterministic or Stochastic) or both internally and externally generated. All this leads to \mathbf{A} being a function of time or of a population vector [1].

Obviously, one can see that when Eq. (1.1) is used repeatedly for a given period of time, p , then the equation in a compact form becomes

$$\mathbf{n}(t + p) = \mathbf{A}^p \mathbf{n}(t) \quad (1.5)$$

In short, the model works as follows. At each time step, perhaps a month or a year depending on how you want to discretize your time steps, the total population is given as a vector with the number of individuals in each age class. This vector is premultiplied by the Leslie matrix to give a new vector with the number of individuals in each age class at the following time step. This multiplication put into action for an interval of one year of age-structured population growth or projection, and when this process is repeated, a projection of the population can be made.

1.3 Objective and organisation of this essay

This essay aims to provide the reader with an understanding of the application of the mathematical methods used to project age-structured populations, and to understand the dynamics that the Leslie matrix model describes.

We start in the second chapter by projecting the population using the Leslie matrix model. The significance of the age stable distribution of the projected model is investigated assuming there is a solution to the matrix that is given or constructed.

The third chapter explores the model by looking at specific factors that affect populations. For example, we examine the ways in which density or stochasticity become significant when modelling populations. We then discuss the development of the Leslie model over the years, and conclude whether it is a reliable model for use in the future or not. The fourth chapter investigates the relationship between demographic analysis and the Leslie model, since matrix population models have lately become standard tools for the demographic analysis of age-structured populations. In conclusion, we discuss the relevance and importance of the model, and summarise the results obtained.

2. Projections using the Leslie model and age stable population distribution

To understand the dynamics of the population, we will proceed by projecting the population using the Leslie model. From the values projected, an interpretation of the age stable distribution and the dominating eigenvalue will be made. It is important to note that we always assume that a solution exists for any given or constructed matrix.

In order to project a matrix model (Leslie), a few necessary estimations will be made by considering the vital rates, which depend on the continuous survivorship and fertility functions.

Definition 2.1 The survivorship function is the chance of an individual surviving from birth to age x , and it can be rescaled to give a number of survivors from the initial cohort. It is mathematically denoted by $l(x)$.

There are two methods that can be used to determine $l(x)$: the **Cohort method** observing a set of individuals through time; and the **Static method**, assuming a stable age distribution.

Definition 2.2 The fertility function is the expected number of offspring (female offspring) per individual of age x at a unit time, and it is denoted by $m(x)$.

We start by distinguishing between two possible types of population that one might deal with when making projections.

2.1 The birth-flow population

The birth of offspring occurs continuously over the projection interval, as in the case for the human population.

Survival probabilities

The survival probability depends on the age of the individual from age x to $x + 1$, and is approximated by

$$P_i = \frac{l(i+1)}{l(i)} \quad (2.1)$$

where the age is assumed to be known [2], if the age is not known [1], then $l(x)$ can be approximated by taking its average within each age class over the interval $i - 1 \leq x \leq i$. Thus,

$$P_i \approx \frac{l(i) + l(i+1)}{l(i-1) + l(i)}. \quad (2.2)$$

Fertilities

Fertility depends on the distribution of births and deaths in the age class, given by,

$$F_i = P_i m_{i+1}, \quad (2.3)$$

which is the number of offspring born in the following year, multiplied by the survival probability.

2.2 Birth-pulse populations

Birth in this population is limited to a short breeding season within the interval and reproduction occurs on birthdays, thus leading to maternity function that is a discontinuous series of pulses, as for the age distribution. Therefore letting p ($0 < p < 1$) be the fraction of the time interval that elapses between the pulse of reproduction and counting.

During counting, the age distribution consists of a series of pulses of individual ages $p, 1 + p, 2 + p, \dots$

These are two cases relating to the counting:

- prebreeding implies the limit as p goes to 1.
- postbreeding implies the limit as p goes to 0.

Survival probabilities

Here every individual is identical and aged $i - 1 + p$. Therefore P_i is the probability of survival from age $i - 1 + p$ to $i + p$, given by

$$P_i = \frac{l(i + p)}{l(i - 1 + p)} \quad (2.4)$$

The survival probabilities are calculated using the formula below due to the two cases relevant to the counting.

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

Note that P_1 in postbreeding includes first-year mortality, while in prebreeding, this is not true; the missing mortality is incorporated into the fertility coefficients.

Fertilities

Since births occur during the next birthday of an individual, the probability of surviving for a fraction $1 - p$ is P_i^{1-p} . For the individual to be counted in $n_1(t + 1)$, it must survive a fraction p of a time unit, and that probability is determined by $l(p)$. The value of $l(p)$ can be estimated by interpolation.

Then the fertility of the birth-pulse population is calculated by using,

$$\begin{aligned}
 F_i &= l(p)P_i^{1-p}m_i \\
 &= \begin{cases} P_i m_i & \text{postbreeding } (p \rightarrow 0) \\ l(1)m_i & \text{prebreeding } (p \rightarrow 1) \end{cases} \quad (2.5)
 \end{aligned}$$

2.3 Dominating eigenvalue and the properties of the stable vector

Since the Leslie model is an $n \times n$ matrix, it can be concluded that there are n possible eigenvalues and eigenvectors which satisfy the equation

$$\mathbf{A}v = \lambda v, \quad (2.6)$$

where λ is any eigenvalue and v is an eigenvector corresponding to λ . Eigenvalues and eigenvectors are usually used to study the change in a population over time in a dynamical system and to give a meaningful biological interpretation. The aim is to determine the long term dynamics of the population, i.e. to demonstrate whether the population is increasing, decreasing or staying constant.

After computing the eigenvalues from a projected matrix using the analytical method (or any other suitable method), the eigenvalue of interest is the one which is more positive in comparison with the others. This eigenvalue is called the eigenvalue of greatest magnitude, or the dominating eigenvalue; in parts of the literature, it is referred to as a *latent root*. The reason λ is so important is that it defines the rate of population growth, or gives valuable information about the status of the population. The significance of the dominant eigenvalue is supported by the Perron-Frobenius theorem for non-negative and irreducible matrices, which has the following properties,

- There exists one eigenvalue that is greater than or equal to any of the others in magnitude, called the *dominant eigenvalue* of \mathbf{A} ,
- There exists an eigenvector such that its element are non-negative,
- λ is greater or equals to the smallest row sum of \mathbf{A} and less or equals to the largest row sum.

The above properties, especially the last one, does not always satisfy the **Markov theory** that says, given an $n \times n$ matrix A which is a transition matrix for an n -state Markov chain, if all entries in A are non-negative and the entries in each column sum up to 1 (unity). The reason why this theory does not sometimes hold here is that there is a possibility that the values of F_i of

the Leslie matrix may sometimes sum up to a value greater than 1, especially if you are dealing with a birth-pulse population [3].

After obtaining the eigenvalue by using the equations

$$|\mathbf{A} - \lambda I| = 0 \quad (2.7)$$

where I is the identity matrix, the values obtained represent:-

When $\lambda = 1$, the population is stationary, $\lambda > 1$, over-population is experienced.

When this is experienced, one may think of harvesting as an option in order to keep the population stable.

When $\lambda < 1$, the population is diminishing.

The annual rate of increase of the population is given by the logarithm of the dominant eigenvalue,

$$r = \log(\lambda)$$

The role of the eigenvector is to give the stable distribution of the population between age classes represented by the right and the left eigenvectors. The left eigenvector of a matrix is distinct from its right eigenvector, and to determine the stable vector (or the eigenvectors), we solve the equation

$$v^* \mathbf{A} = \lambda v^*$$

where the asterisk denotes the complex-conjugate transpose. If an eigenvector corresponding to the eigenvalue $\lambda = 1$ can be found, we can say that we have a **stable age distribution**.

Since the dominating eigenvalue is positive and real, one of the eigenvectors will also consist of real and positive elements [4]. The eigenvector is referred to as a stable age distribution for a specific population.

The eigenvector \mathbf{v} has components [1, 5],

$$v_i = P_i \lambda^{-i+1} \quad \text{where } i = 1, \dots, w. \quad (2.8)$$

This vector can be scaled arbitrarily so that v_1 equals to 1, and this gives the stable age distribution with abundance of each age class measured respectively to the abundance of the first[1].

2.4 Perturbation analysis : Sensitivity and Elasticity

We start from the general matrix population model:

$$\mathbf{A}\mathbf{v} = \lambda\mathbf{v}, \quad (2.9)$$

and when we do a perturbation analysis, we typically only change a single element of \mathbf{A} . Thus the basic formula for the sensitivity of the dominant eigenvalue to a small change in element a_{ij} is

$$S = \left(\frac{\partial \lambda}{\partial a_{ij}} \right) \quad (2.10)$$

Another measure of the change in a matrix, given a small change in an underlying element, is the eigenvalue elasticity.

The elasticity of λ with respect to a_{ij} is given by:

$$\begin{aligned} e_{ij} &= \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \\ &= \frac{\partial \log \lambda}{\partial \log a_{ij}}. \end{aligned} \quad (2.11)$$

Elasticities are proportional sensitivities, they measure the linear change on a log scale (the slope of $\log \lambda$ plotted against $\log a_{ij}$). An important property of elasticities is that they sum to one

$$\sum_{i,j} e_{ij} = 1. \quad (2.12)$$

An alternative way of finding the elasticity is given by:

$$\begin{aligned} E &= \left(\frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \right) \\ &= \frac{1}{\lambda} \mathbf{S} \circ \mathbf{A} \end{aligned} \quad (2.13)$$

where \mathbf{S} is the sensitivity matrix and \circ denotes the Hadamard product (or the entrywise product). Only non-zero matrix elements have elasticities since they measure proportional change in λ .

Illustrative example

Suppose a particular species of salmon population has three age classes and the survival rate of these salmon in their first and second age classes is 53 percent and 22 percent, respectively. Also assume that each female in the second age class produces 4 female offspring and 5 offspring in the third age class. The other age class produce no offspring and 12 female salmon in each of the three age classes are introduced into the system.

The Leslie matrix is given as:

$$\mathbf{A} = \begin{pmatrix} 0 & 4 & 5 \\ 0.53 & 0 & 0 \\ 0 & 0.22 & 0 \end{pmatrix}$$

and the population vector at the beginning is

$$\mathbf{n}(1) = \begin{pmatrix} n_1(1) \\ n_2(1) \\ n_3(1) \end{pmatrix} = \begin{pmatrix} 12 \\ 12 \\ 12 \end{pmatrix}.$$

and $N_1 = 36$. Now we want to see what happens to the population in the next year, therefore

$$\begin{aligned} n(2) &= A * n(1) \\ &= \begin{pmatrix} 108.000 \\ 6.3600 \\ 2.6400 \end{pmatrix} \end{aligned} \tag{2.14}$$

and $N_2 = 117$ and one can continue until p times. If $p = 16$, then the population of salmon after 15 years is given by

$$n(16) = \begin{pmatrix} 3.9034e + 04 \\ 1.1833e + 04 \\ 1.8678e + 04 \end{pmatrix}, \tag{2.15}$$

with $N_{16} = 5.27348e + 04$ (or 52734.8). The trajectory of this population is shown on the graph below

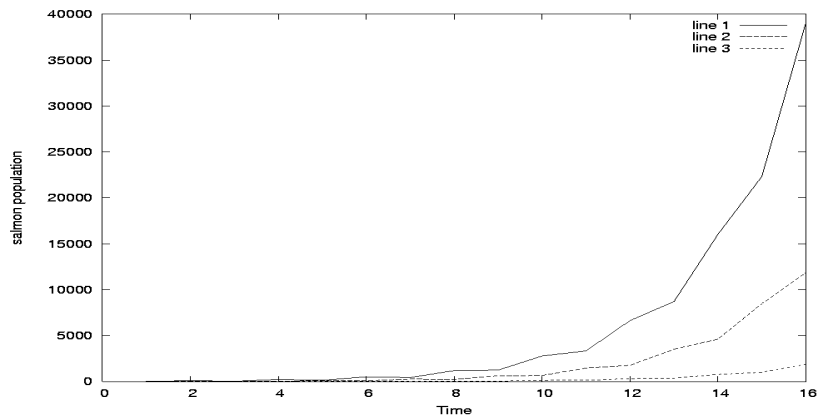


Figure 2.1: The trajectory of the salmon population over time.

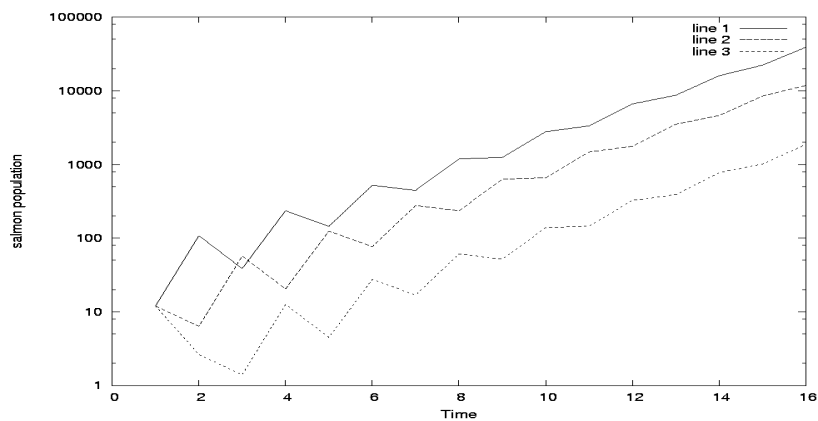


Figure 2.2: The logscale of the trajectory of the salmon population.

Each line on the graph represent an age class, the solid line represent the first age class, the dash line represent the second age class and the dotted line represent the third age class, and the total population is given by the graph below after projecting the population for 16 time steps.

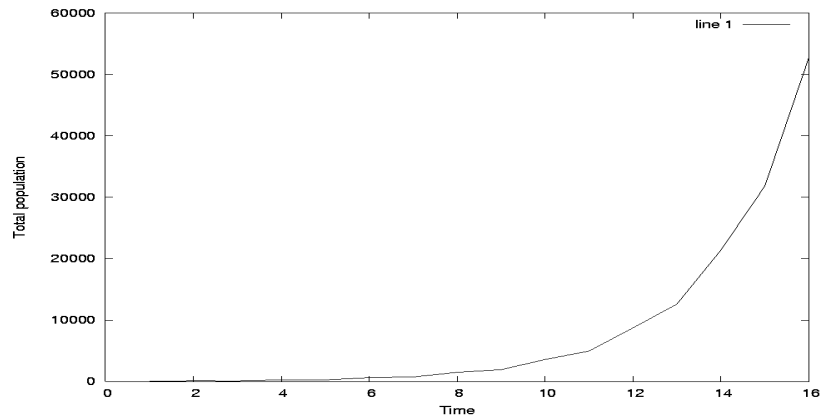


Figure 2.3: The total number of population.

If one consider only the analysis from the graph, it is clear that the population is growing exponentially and there is a bit of fluctuation being experienced due to the seasonal changes.

Taking a look at the percentage of the organisms after a long period of time, it is clear that the population in the first age class approaches 72 percent, second age class approaches 24 percent and their age class approaches 4 percent. All this can be seen in the graph below.

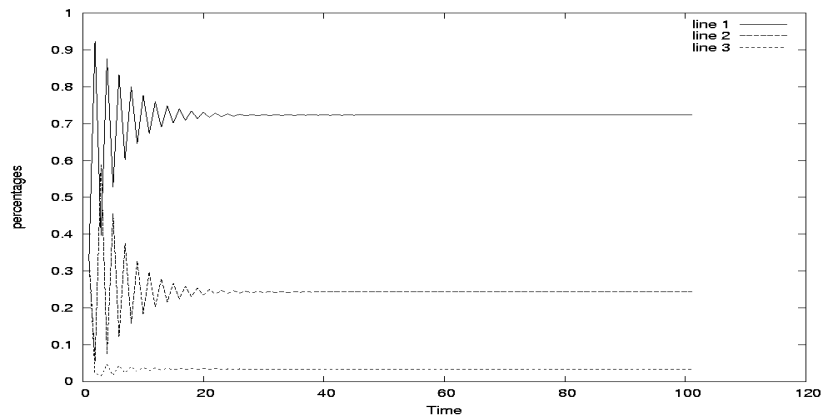


Figure 2.4: percentage at each iteration.

The rate of the population growth.

$$\lambda = \{1.5778, -1.2918, -0.28604\}$$

and the dominating eigenvalue is given by $\lambda = 1.5778$. This implies a 57.781 percent increase per year in the population size. The corresponding stable age distribution is

$$\mathbf{v} = \{0.947016, 0.318110, 0.044355\}$$

The annual rate of change for this population is

$$\begin{aligned} r &= \log(\lambda) \\ &= \log(1.57781) = 0.45604, \end{aligned} \tag{2.16}$$

this indicates that the population is increasing. In general, salmon experience a period of rapid growth mostly in summer and a slower growth in winter. They spend one to five years in the open seas where they become matured sexually, then return to the natal streams to spawn. Salmon are born in the fresh water, after development they migrate to the seas and then return at a later stage to reproduce.

Since, $\lambda = 1.5778$, if one perturb λ by subtracting about 0.1 from a_{12} making it 3.9. Then $\lambda = 1.56212$ and the change experienced is 0.0157. Again taking away 0.1 from a_{21} making it 0.43, then $\lambda = 1.43190$ with a change of 0.14591. Now, this shows that the growth rate of the salmon is more sensitive to changes in P_1 than in F_2 . This shows the importance of the survivorship rates which are more important stages in the life history.

The sensitivity and elasticity are given in the table below,

Elements	Sensitivity	Elasticity
a_{12}	0.15690	0.39777
a_{13}	0.02180	0.069083
a_{21}	1.45910	0.49012
a_{32}	0.51900	0.072366

and the value of $\sum_{i,j} e_{ij} = 1.0293 \approx 1$.

3. Development over the years and the variation of the basic model

3.1 Development over the years

Several studies have been done on the basic Leslie matrix model, which has been used continuously since its early development. The sketch below[3] indicates the major contributors to the development, and eventual sophistication of the model.

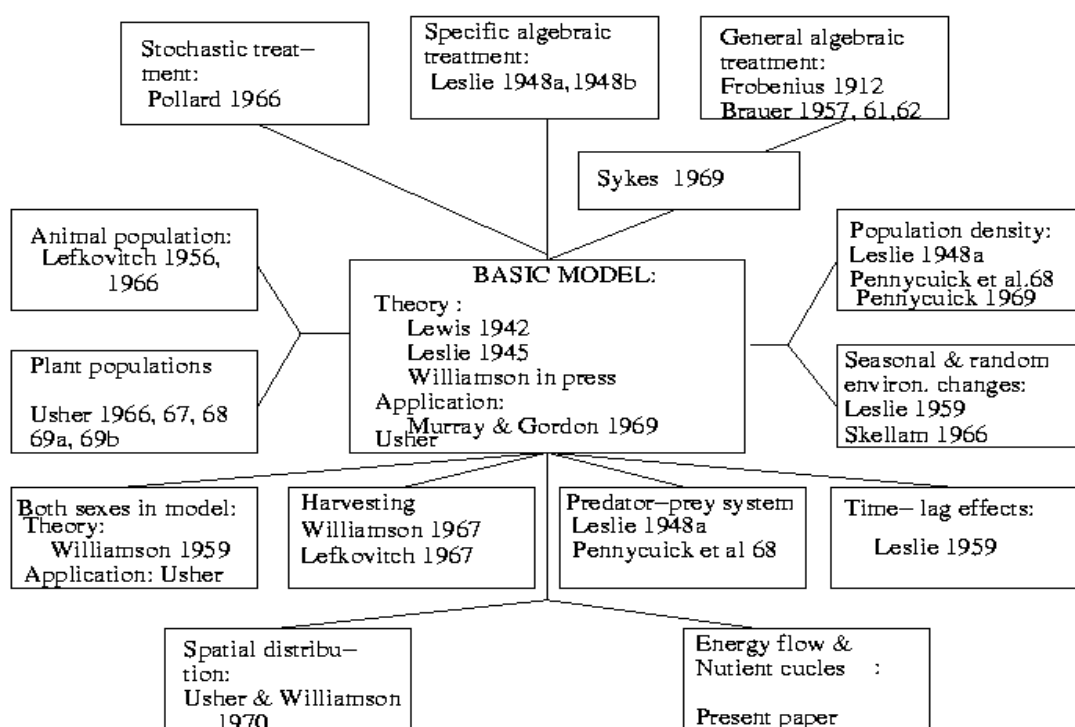


Figure 3.1: Schematic representation of the developments in the basic matrix model

Considering the above schematic representation, the first three box above the middle one deals with the theoretical development of the basic model. Whereby,

- Pollard dealt with the stochastic treatment in 1966 by looking at the randomly variation of the vital rates over time, thus allowing \mathbf{A} to be a function of time ($\mathbf{A} \rightarrow \mathbf{A}_t$), multiplying the vital rates by a function of time say $g(t)$ which is a stochastic process function.
- Leslie (1948a) showed that the basic model was similar to the exponential growth equation

$$N(t) = N(0)e^{rt}, \tag{3.1}$$

whereby the population approaches the equilibrium size K and their growth can be approximated by a sigmoid growth equation

$$N = \frac{K}{1 + Ce^{rt}} \quad (3.2)$$

where C is an arbitrary constant and r is the growth rate.

- Sykes showed in 1969 that the Leslie matrix is irreducible, and so is Brauer in 1962 and he called it an unreduced matrix.

The eight boxes surrounding the middle one dealt with the size grouping and variability effects corresponding to the application of the model in dynamical systems.

- Willamson looked at including both sexes in the model in 1959. The model was structured such that the first row elements of \mathbf{A} is the fertility of females and the second row element consists of male fertility except the element a_{11} and a_{21} which are zero elements; then the entries regarding the survival rates were constructed in a way that the subdiagonal's first entry correspond to the elements of the first row and the second entry correspond to the second row and so is the population vector.
- In 1966 Usher developed further the Leslie model using *size* instead of *age* for forests trees.
- Lefkovitch(1965, 1966, 1967) was concerned about the insects pests of stored product and he structured the stage matrix model using four stages:

$$eggs \longrightarrow larvae \longrightarrow pupae \longrightarrow adult \quad (3.3)$$

and later in 1967 he investigated the effect of *harvesting* in the development structure of the population i.e if a population is increasing, one might be interested in harvesting a portion of the population for some purpose. An issue of major interest in this case was how much of the population might be harvested while maintaining the population at a constant level.

- Leslie looked at time-lag in the model and he discovered that it showed oscillatory solution, so is the predator-prey systems and also the inclusion of functional elements in the matrix.

The last two boxes at the bottom refer to the application of the model and which does not cater for age and time structure.

- Usher(1966) and Goodman(1969) together showed that the Leslie basic model can be written as

$$\mathbf{A} = \mathbf{F} + \mathbf{P}, \quad (3.4)$$

or in a matrix form

$$\mathbf{A} = \begin{pmatrix} F_1 & F_2 & \cdots & F_w \\ 0 & \cdots & & 0 \\ \vdots & & & \vdots \\ 0 & \cdots & & 0 \end{pmatrix} + \begin{pmatrix} 0 & \cdots & 0 & 0 \\ P_1 & \cdots & 0 & 0 \\ 0 & \ddots & 0 & \vdots \\ 0 & \cdots & P_{w-1} & 0 \end{pmatrix}, \quad (3.5)$$

and later this formulation was used in analysing the energy flow and the nutrients cycles in an ecosystem [3], where \mathbf{F} represent the energy input or nutrients into the ecosystem and \mathbf{P} represent the transfer of energy or nutrients. This method was considered by Smith in 1970.

3.2 Variations of the model

The effect of population fluctuation is mostly affected by density dependency and stochasticity (environmental and demographic), and in 1959 P. H. Leslie put forward a proposal of projection matrix model to allow for the effect on the growth of population the presence of other population members (i.e including density-dependency in the model) and J. H. Pollard looked at the stochastic treatment of the model in 1966.

3.2.1 Density Dependence in the Leslie model

Leslie in his papers (1945, 1948, 1959) treated the density as a sum of all individuals in the population, regardless of their age. The population size being given by

$$N(t) = \sum n_i(t). \quad (3.6)$$

Considering the fact that \mathbf{A} is non-singular and taking its dominating eigenvalue to be λ . Now to include the density dependency we focus on the column that gives the fertility and survival rates of the i th column [6]. He incorporated density-dependent feedback by postulating that the population density at each time affects survival of the different age group. He defined the quantity

$$q(t) = 1 + aN(t), \quad (3.7)$$

where a is the density parameter (which is the strength of the density dependence) given by

$$a = \frac{\lambda - 1}{K}.$$

If $a = 0$ then there will be no population density whereas if a is less than 0 then we end up with negative entries in our model and that will invalidate the suggestion which was made when projecting the model i.e F_i and P_i are greater or equals to 0, therefore a must be greater than 0 and take the same value for all age classes also the value of $q(t)$ must be greater than 1, and K is the steady state size of the population after the population become stationary i.e the age

distribution will be stable and the total size of the population remain constant. Note that q is time dependent since N is and we divide the projection matrix by this quantity. Sometimes not all vital rates are affected by density, then one need to specify which ones are affected, their functional form and their parameter values. The $q(t)$ values are the diagonal elements of a matrix Q

$$Q(t) = \begin{pmatrix} q_1(t) & 0 & \cdots & 0 \\ 0 & q_2(t) & \cdots & 0 \\ \vdots & & \ddots & \vdots \\ 0 & 0 & \cdots & q_w(t) \end{pmatrix}. \quad (3.8)$$

Now the number of individuals in the different age groups at time t can now be mapped to time $t + 1$ as

$$\mathbf{n}(t + 1) = \mathbf{A}Q^{-1}\mathbf{n}(t). \quad (3.9)$$

In 1959 he also introduced time-lag into the basic model. If the lags are taken to be the number of relevant age groups in the population for each age class i one has

$$q_i(t) = 1 + aN(t - i - 1) + bN(t), \quad (3.10)$$

where b is the effect of density at birth on the probability survival [7] at a later stage. Both a and b are > 0 , and their relative magnitude

$$\frac{b}{b + a}, \quad (3.11)$$

which determines how strong the impact of the cohort effect is on the density dependence feedback in the equation above. The elements in the projection matrix will be divided by a number depending on

- the size of the current population at time t , and
- the size of the population at time $t - i - 1$, which is the beginning of the time interval where individuals were currently born of age i .

After a certain number of projections the population will reach stability say at time τ ("residence time or steady state time"), then for the stationary state [4], $q(t) = \lambda \forall i$ hence

$$\mathbf{A}(\tau) = \mathbf{A}Q^{-1}(\tau) \quad (3.12)$$

$$= \lambda^{-1}\mathbf{A}, \quad (3.13)$$

therefore the matrix become

$$\begin{pmatrix} \frac{F_1}{\lambda} & \frac{F_2}{\lambda} & \frac{F_3}{\lambda} & \cdots & \frac{F_{w-1}}{\lambda} & \frac{F_w}{\lambda} \\ \frac{P_1}{\lambda} & 0 & \cdots & & & 0 \\ 0 & \frac{P_2}{\lambda} & & & & \\ \cdot & & \frac{P_3}{\lambda} & & & \\ \cdot & & & & & \vdots \\ \cdot & & & \ddots & & 0 \\ 0 & \cdot & \cdot & \cdots & \frac{P_{w-1}}{\lambda} & 0 \end{pmatrix}. \quad (3.14)$$

Any incorporation of density-dependence in population dynamics is thought to decrease the vital rates [1] due to competition, and other factors that might affect population growth. In matrix models, the entry elements of the density-dependence matrix are either depensatory, compensatory, or overcompensatory. The classification of the entry elements can be determined from the result of unstructured populations:

$$N(t + 1) = f(N) \quad (3.15)$$

$$= g(N)N, \quad (3.16)$$

and the function $g(N)$ is the growth rate per-capita and $f(N)$ is the *recruitment* function [1]. The total population is given by $N = \mathbf{n}(t)$ or $\sum n_i(t)$.

When N is greater than 0,

$$\frac{dg(N)}{dN} > 0. \quad (3.17)$$

Therefore $g(N)$ is said to produce depensation, and if

$$\frac{dg(N)}{dN} \leq 0, \quad (3.18)$$

$$\frac{df(N)}{dN} \geq 0 \text{ and} \quad (3.19)$$

$$\lim_{N \rightarrow \infty} f(N) = C > 0, \quad (3.20)$$

then $g(N)$ is compensatory. Now if

$$\lim_{N \rightarrow \infty} f(N) = 0, \quad (3.21)$$

then $g(N)$ displays overcompensation.

We here introduce two of the most famous *recruitment* functions in ecology [1],

- The Beverton-Holt model is characterised by recruitment that approaches an asymptote as the parental stock size increases. This model was introduced by Beverton and Holt (1956, 1957).
- The Ricker model was developed by Ricker (1958) to describe stocks in which recruitment declines as population size tends toward infinity.

The Beverton-Holt and Ricker models are both discrete-time population models which give the density of individuals at time $t + 1$ as a function of the number of individuals in the previous generation.

The functions are given as

$$f(N) = \frac{N}{1 + cN}, \quad (3.22)$$

for Beverton-Holt, where c is the carrying capacity and for Richer

$$f(N) = Ne^{-cN} \quad (3.23)$$

The two models described above are non-linear. This results in a complex model.

Illustrative example

Considering the salmon population, and letting $K = 100$, the density dependency parameter a becomes 0.0055781, by taking $\lambda = 1.5778$. This implies that $q(t) = 1.2008116$, taking $N(t) = 36$. Suppose the quantity is the same throughout, i.e the vital rates are all affected by the same amount of density, then

$$Q(t) = \begin{pmatrix} 1.2008116 & 0 & 0 \\ 0 & 1.2008116 & 0 \\ 0 & 0 & 1.2008116 \end{pmatrix}. \quad (3.24)$$

Therefore $\mathbf{A}Q^{-1}$ is

$$\begin{pmatrix} 0 & 3.33108 & 4.16385 \\ 0.44137 & 0 & 0 \\ 0 & 0.18321 & 0 \end{pmatrix}, \quad (3.25)$$

and the dominant eigenvalue and the corresponding eigenvectors are given by

$$\lambda = 1.31396 \quad (3.26)$$

$$\mathbf{v} = \{0.947016, 0.318110, 0.044355\}. \quad (3.27)$$

Subsequent to the incorporation of density dependence in the model we can plot the observed projection of the salmon population as in figure (3.2.1),

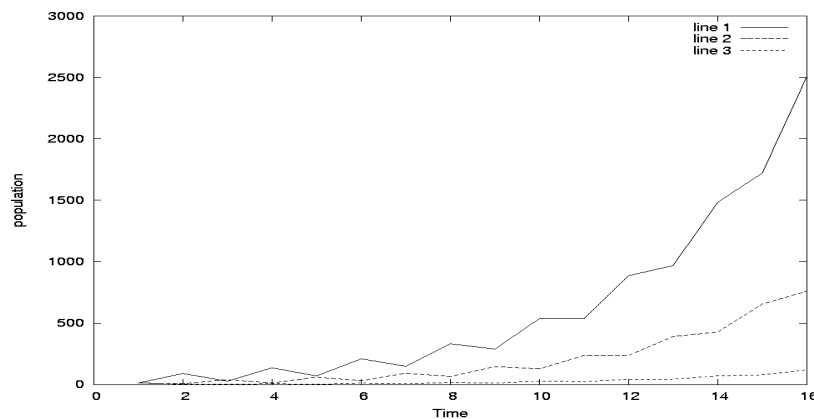


Figure 3.2: Density dependence population projection.

It can be seen that the effect on the projection of the population is an overall decrease, even though there is still growth within this particular projection, though not at the same rate as a non-density dependency model.

Looking at the incorporation of the Beverton-Holt and Ricker's model to the basic model by taking the value of c to be 2, then the matrix model for Beverton-Holt becomes

$$\begin{pmatrix} 0 & 0.054795 & 0.068493 \\ 0.53 & 0 & 0 \\ 0 & 0.22 & 0 \end{pmatrix}, \quad (3.28)$$

and the Richer projection matrix becomes

$$\begin{pmatrix} 0 & 2.1521e-31 & 2.6901e-31 \\ 0.53 & 0 & 0 \\ 0 & 0.22 & 0 \end{pmatrix}. \quad (3.29)$$

After the projection of the salmon population into the future, the resulting projection from Beverton-Holt is shown in the sketch below and the result from Richer produces nothing since the projection matrix is basically equals to zero.

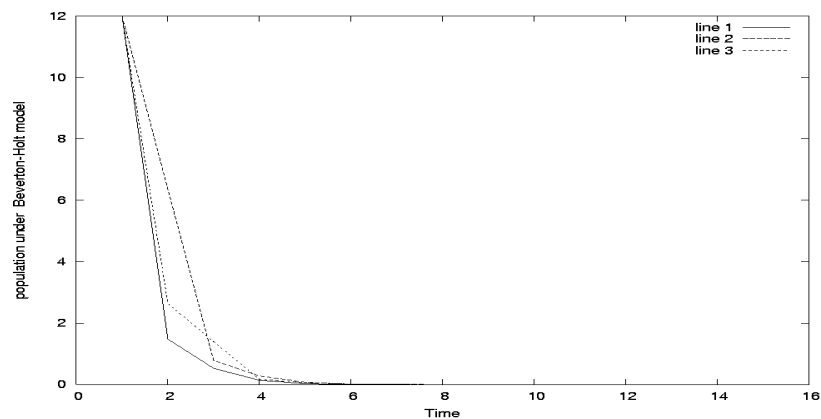


Figure 3.3: Beverton-Holt model with $c = 2$.

The total population of the salmon species after the Beverton-Holt model projection in the sketch below.

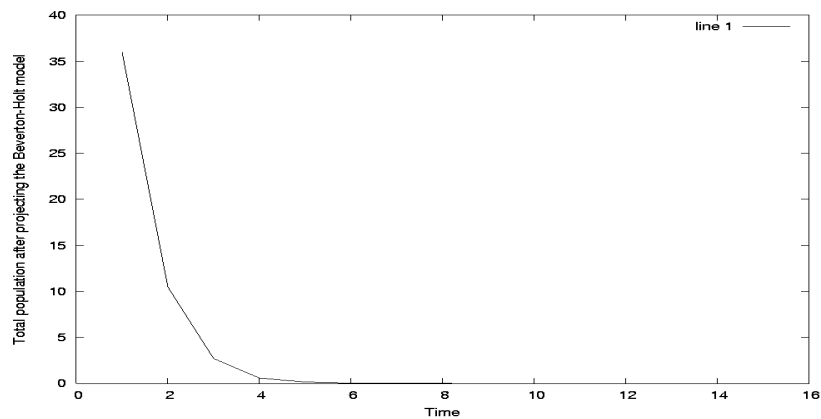
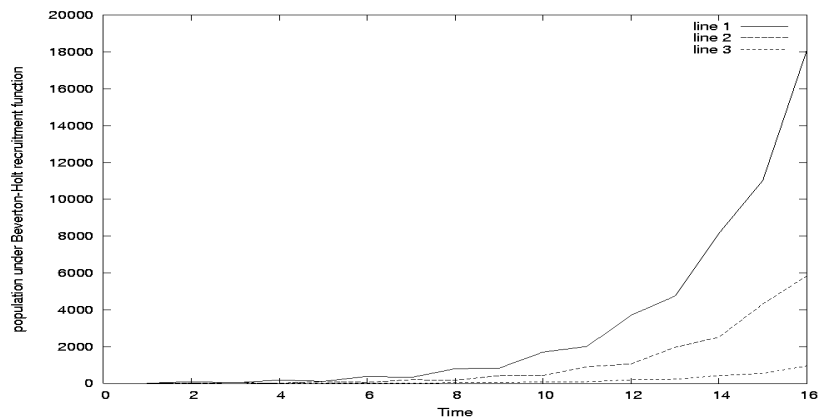
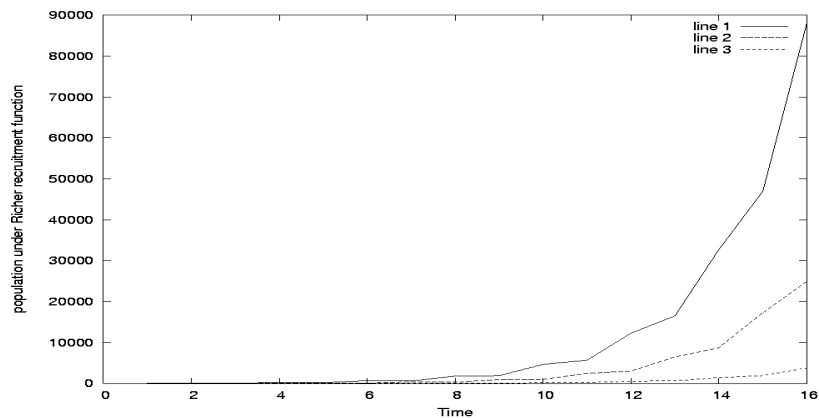


Figure 3.4: The total population after the Beverton-Holt model projection.

When reducing the value of c to 0.003 the observed trajectories of the salmon population for both recruiting model can be seen in the sketch below,

Figure 3.5: Beverton-Holt model for $c = 0.003$.Figure 3.6: Richer's model for $c = 0.003$

The Beverton-Holt model has similar effect on the population as when we incorporated the value of the quantity q , but Richer's model support the increase in the population, thus the value of c in the model does not cause the vital rates to decrease.

3.2.2 Stochastic in the model

The stochastic process is always determined if and only if there is a random variation over time, and this in the Leslie model forces \mathbf{A} to be \mathbf{A}_t (\mathbf{A} is now a function of time). Variation can be due to the physical or biological factors in the ecosystem, and this result in having two types of stochasticity:

- Environmental stochastic and
- Demographic stochastic (determined by applying fixed vital rates to a finite number of individuals).

There is one important step involved in making a basic stochastic projection model.

- Incorporation of *variance* to shift from deterministic to stochastic and the matrix model will be given by

$$\mathbf{n}(t+1) = \mathbf{A}_t \mathbf{n}(t), \quad (3.30)$$

where \mathbf{A}_t is a column-stochastic transition matrix.

- If \mathbf{A}_t is constant then the environment is said to be *homogeneous* otherwise it is *inhomogeneous* [1, 8].

We shall consider only the environmental stochasticity in our model. Denoting $n_i(t)$ as the population vector in the i th age class at time t and the total population size is given by $N(t) = \sum n_i(t)$.

Constructing a stochastic projection model

We still consider the female population at a discrete interval, and let $n_i(t)$ to be a random variable [9] with its expected value given by $e_i(t)$ and the variance $C_{i,i}(t)$. Therefore, the covariance is given as $cov(n_i(t), n_j(t)) = \mathbb{E}[(n_i(t) - \overline{(n_i(t))}) * (n_j(t) - \overline{(n_j(t))})]$ and denoted by $C_{i,j}(t)$. If $n_i(t)$ and $n_j(t)$ are independent, then

$$cov(n_i(t), n_j(t)) = \mathbb{E}[(n_i(t) - \overline{(n_i(t))})] \mathbb{E}[(n_j(t) - \overline{(n_j(t))})] \quad (3.31)$$

$$= 0, \text{ or} \quad (3.32)$$

$n_i(t)$ and $n_j(t)$ are correlated [1] if $cov(n_i(t), n_j(t))$ is not equal to zero. Also if we let the number of population in the first class age to be a random variable.

Now, considering the fact that the number of females of age i at time t , each has a fixed P_i and F_i and mutually independent, therefore $n_i(t+1)$ is a binomial variable, $B(n_i(t), P_i)$. Similarly, $n_1(t+1)$ is a binomial variable $B(n_1(t), F_i)$. The Leslie model is now constructed using the expectation of the variables $n_i(t)$, thus

$$\begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ \cdot \\ \cdot \\ \cdot \\ e_w \end{pmatrix} (t+1) = \begin{pmatrix} F_1 & F_2 & F_3 & \dots & F_{w-1} & F_w \\ P_1 & & & & & \\ 0 & P_2 & & & & \\ \cdot & & P_3 & & & \\ \cdot & & & & & \\ \cdot & & & \ddots & & \\ 0 & \cdot & \cdot & \dots & P_{w-1} & 0 \end{pmatrix} \cdot \begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ \cdot \\ \cdot \\ \cdot \\ e_w \end{pmatrix} (t). \quad (3.33)$$

Using the definition of the expectation, variance and covariance. If we let $1 - P_i = Q_i$ and $1 - F_i$

$= G_i$, then the variance and covariance are given by the following equations [9] ,

$$C_{i+1,i+1}(t+1) = P_i^2 C_{i,i}(t) + P_i Q_i e_i(t) \text{ for } i \geq 0, \quad (3.34)$$

$$C_{i+1,j+1}(t+1) = P_i P_j C_{i,j}(t) \quad i, j \geq 0, i \neq j, \quad (3.35)$$

$$\text{cov}(n_1^i(t+1), n_i(t+1)) = F_i P_i C_{i,i}(t) \quad i \geq 0, \quad (3.36)$$

$$\text{cov}(n_1^i(t+1), n_j(t+1)) = F_i P_j C_{i,j}(t) \quad i \neq j, \quad (3.37)$$

$$\text{cov}(n_1^i(t+1), n_1^j(t+1)) = F_i F_j C_{i,j}(t) \quad i \neq j, \quad (3.38)$$

$$\text{var}(n_1^i(t+1)) = F_i^2 C_{i,i}(t) + F_i G_i e_i(t) \quad i \geq 0. \quad (3.39)$$

It can be concluded that

$$C_{1,1}(t+1) = \sum_{i=0}^w (F_i^2 C_{i,i}(t) + F_i G_i e_i(t)) + \sum_{i \neq j} F_i F_j C_{i,j}(t); \quad \text{and} \quad (3.40)$$

$$C_{1,j+1}(t+1) = \sum_{\text{all } i} F_i P_j C_{i,j}(t). \quad (3.41)$$

The recurrence relation for the mean, variance, and covariance is defined well by Eq. (3.33), (3.34), (3.35), (3.41), and (3.40), which are linear recurrence. Thus, the recurrence relation can be written in a matrix form as

$$\begin{pmatrix} \mathbf{e} \\ \mathbf{C} \end{pmatrix} (t+1) = \begin{pmatrix} \mathbf{A} & \mathbf{0} \\ \mathbf{D} & \mathbf{A} \times \mathbf{A} \end{pmatrix} \cdot \begin{pmatrix} \mathbf{e} \\ \mathbf{C} \end{pmatrix} (t), \quad (3.42)$$

where \mathbf{A} is the Leslie matrix, $\mathbf{e}(t)$ is the vector of expectations, $\mathbf{C}(t)$ has its elements as the variance and the covariance.

Illustrative example

Constructing a simple stochastic projection, one needs to specify the stochastic process. Suppose we let the the stochastic process to be $g(t)$, and assume a good year to have $g(t)$ equals to 1.5, and in a bad year $g(t)$ equals to 0.43. Then allow the good and bad year to occur randomly [1] by flipping a fair coin, and independently with probability 0.6. Therefore, \mathbf{A} can be written as

$$\mathbf{A}_t = \begin{pmatrix} 0 & 4g(t) & 5g(t) \\ 0.53 & 0 & 0 \\ 0 & 0.22 & 0 \end{pmatrix}. \quad (3.43)$$

The result from the stochastic projection is shown in the diagram below. It is clear from the graph that the salmon population is increasing even though fluctuations can be seen after three iteration.

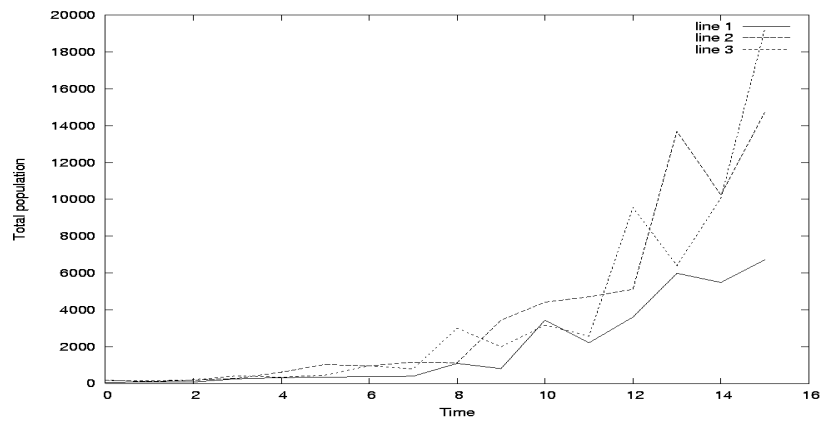


Figure 3.7: Three realization of the stochastic population model.

When projecting a stochastic matrix, it is sometimes impossible to predict the dynamics of the population due to fluctuations and no sign of convergence is visible. In order to see the variations clearly, one can iterate the stochastic model for a longer time, say $t = 100$ since I iterated till $t = 16$.

4. Vertical and Horizontal life table

4.1 Demographic Analysis

There are two different types of collecting data in the life table, the vertical and horizontal life table. The vertical life table consists of species that does not live for long and the horizontal life table is for a long lived species [10]. In the illustrative example, we will treat the salmon population data as the vertical life table and the 1985 U.S. Vital Statistics data as the horizontal life table.

Most of the time the information obtained from *demography* allows measurements of the rate of population growth, projection of future population size, and the analysis of life history tactics.

4.1.1 Life Table

Life table analysis is based on a system of tabulating age-specific survivorship and reproduction/age-specific fecundity [1, 4]. The two most basic parameters of a population are an individual's chances of surviving and breeding and both of these factors depend on age in most cases.

Survival

Survival is described by three functions of age which are not independent:

- Survivorship function or the $l(x)$ curve

which is given by the probability of survival from birth to age x or simply $\frac{N_x}{N_0}$. There are two methods that can be used to determine $l(x)$ which are **Cohort method** (i.e observe a set of individual through time) and the **Static method** (i.e assume a stable age distribution).

- The distribution of age at death function or the $s(x)$ curve

which is given by the probability density function for the age at which individual die and the values are used to compare the risk of death for different age classes or simply $\frac{N_{x+1}}{N_x}$ (equals to $\frac{l(x+1)}{l(x)}$)

- The mortality rate or hazard function or the $\mu(x)$ curve

which is given by $\frac{s(x)}{l(x)}$.

Reproduction

Reproduction is described by the maternity function or the fecundity curve. In practice the maternity function, $m(x)$ is measured as *female offspring per female of age x* thus,

- $m(x)$ equals to Expected offspring per individual aged x per unit time or simply $\frac{1}{2}$ number of offspring born to parent of age x
- The total lifetime reproduction in the absence of mortality is given by the **Gross reproductive rate** equals to $\sum m(x)$ and this is useful in considering potential population growth if all ecology limits were removed for a population.
- The average number of offspring produced by an individual in its lifetime is given by **Net reproductive rate**, R_0 equals to $\sum l(x)m(x)$ and the **replacement rate**, R_0 is given by $l(x)m(x)$.

Now, when

- R_0 is less than 1 i.e individuals are not replacing themselves, the population is shrinking.
- R_0 is greater than 1 i.e individuals are more than replacing themselves, the population is growing.
- R_0 equals to 1 i.e individuals are exactly replacing themselves, the population is stable.

Since R_0 measures the reproduction on the basis of individual lifetime or the basis of birth minus death per unit time, preferably years. Then one can talk of the measure of population growth which is called the **intrinsic rate of increase**, r given by

$$r \approx \frac{\ln R_0}{T}, \quad (4.1)$$

where T is the **generation time** given by

$$T = \frac{\sum xl(x)m(x)}{\sum l(x)m(x)}, \quad (4.2)$$

x is the age class and r is birth per unit time minus death per unit time (i.e $r = b - d$) and T is simply a weighted average, thus T will be long if most offspring are produced when mothers are old and short when most offspring are produced when others are young.

When,

- R_0 equals to 0, and $r = 0$, then we have a stable population
- R_0 is less than 0, and r is less than 0, then the population is shrinking or decreasing.
- R_0 is greater than 0, and r is greater than 0, then the population is growing

Now, the equation for r only gives accurate results when $R_0 \approx 1$ ($r \approx 0$). Therefore, the exact solution comes from Euler's equation,

$$1 = \sum e^{-rx} l(x)m(x). \quad (4.3)$$

To get the accurate results the equation above is solved by iteration using approximation solution to get a close estimate of r and the relative error will determine whether does the comparison of the intrinsic rate matter in practical applications.

Illustrative example

Without any lose of generality, we take only about half of the data to compare the demographic analysis that can be carried out to the projection model results. The results obtained are shown in the life table below,

x	$N(x)$	$l(x)$	$m(x)$	$l(x)m(x)$	$xl(x)m(x)$
0	36	1	0	0	0
1	117	3.25	0	0	0
2	97	2.69	7.547	20.3	40.6
3	269	7.47	22.72	169.7	509.1552
4	274	7.6	0	0	0
5	627	17.4	0	0	0
-	-	-	$\sum m(x)=30.27$	$\sum l(x)m(x)=190$	$\sum xl(x)m(x)=549.7$

The generation time is, $T = 2.89$, the intrinsic rate gives, $r = 1.8156$ and the rate of reproduction is, $R_0 = 190$. Since R_0, r greater than 0 this shows that the population is growing or the individuals are more than replacing themselves resulting in over population and one might think of harvesting as an option to keep the ecosystem in an equilibrium state.

Now, to find the actual growth rate for the salmon by finding the value of r that makes the sum 1 using the Euler equation.

x	e^{-rx}	$e^{-rx}l(x)m(x)$
0	1	0
1	0.16274	0
2	0.026484	0.53763
3	0.0043101	0.73142
4	0.00070142	0
5	0.00011415	0
-	-	$\sum e^{-rx}l(x)m(x) = 1.2692$

The approximated value of $\sum e^{-rx}l(x)m(x)$ after few iterations is shown in the graph below, in order to find the actual growth rate for the salmon population. The true intrinsic rate of increase is $r = 1.9$, compared with original estimate of $r = 1.8156$. This is a difference of 8.44 percent, which is big enough to matter in practical applications.

Below is data obtained from [11]: Female survivorship and fertility data are modified from 1985 U.S. Vital Statistics. Fertility is based on the average number of daughters born in the five year intervals.

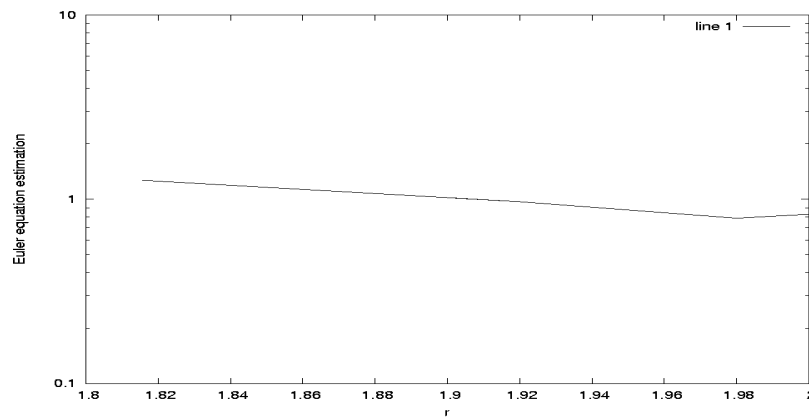


Figure 4.1: approximated value of r .

Age	x	$l(x)$	$m(x)$	$l(x)m(x)$	$xl(x)m(x)$
0-1	0	1.00	0	0	0
1-5	1	0.991	0	0	0
5-10	2	0.989	0	0	0
10-15	3	0.988	0	0	0
15-20	4	0.987	0.025	0.02467	0.098700
20-25	5	0.985	0.240	0.23640	1.1820
25-30	6	0.982	0.500	0.49100	2.9460
30-35	7	0.979	0.140	0.13664	0.95648
35-40	8	0.975	0.095	0.092625	0.74100
40-45	9	0.970	0.020	0.019400	0.17460
45-50	10	0.961	0	0	0
50-55	11	0.948	0	0	0
55-60	12	0.926	0	0	0
60-65	13	0.893	0	0	0
65-70	14	0.844	0	0	0
70-75	15	0.776	0	0	0
75-80	16	0.681	0	0	0
80-85	17	0.553	0	0	0
85-90	18	0.388	0	0	0
90-95	19	0.120	0	0	0
95-100	20	0.005	0	0	0
100+	21	0.000	0	0	0
-	-	-	$\sum m(x) = 1.0200$	$\sum l(x)m(x) = 1.0007$	$\sum xl(x)m(x) = 6.0988$

The net reproduction rate is 1.0007, the generation time is 6.0945 and the intrinsic rate is 0.00011482. Now, since R_0 and r are greater than 0, this implies that the US population is growing.

5. Discussion and Conclusion

The primary purpose of this essay was to demonstrate how the Leslie matrix can be constructed, providing a thorough understanding of the mathematics behind the parameters in the matrix. One of the major findings we made was that the matrix depends only on the fertility and survival rates, referred to as the *vital rates*. A few necessary estimations were made in order to predict the future behaviour of the population. We normally tend to deal with two kinds of populations, birth-flow and birth-pulse populations. While it is theoretically possible to construct a more elaborate matrix to include all the possible transitions, it was to our advantage to instead consider a simpler case. In chapter two, we select a simple hypothetical salmon population in order to demonstrate how to project population using the basic Leslie matrix model, and to describe the population dynamics by looking at the eigenvalues and corresponding eigenvectors.

From this illustrative example, most of the Leslie model's properties surfaced:

- All age classes were identified, each with their own vital rates.
- Each individual in a particular age class had the same chances of surviving to the next consecutive age class.
- After the projection of the population into the future, the population either grows or decreases in an exponential manner.
- All considered age classes grow or shrink at exactly the same rate.

We observed the changes in the dominating eigenvalue by using sensitivity and elasticity analysis. The advantage of this approach is that once all the measurements of the vital rates are completed, it is not necessary to manipulate the rates experimentally; rather, one carry out the manipulation mathematically, and subsequently determine what effect it has on the population. One disadvantage of this approach is that some of the survival rate variables are intrinsically restricted in their range to values between 0 and 1, while the fertility rate variables may be very large.

When projecting the basic Leslie matrix model, the dynamics of a projected population either results in a population growing, decreasing or being stable in the general case. But species do not inhibit the ecosystem by themselves. Two factors that limit the population size and growth significantly were discussed. The incorporation of density-dependence into the Leslie model, or indeed any population model, was discussed. One density-dependence variable that was discussed in details was the q quantity that Leslie investigated in 1959. When he considered the quantity, he allowed for its effect on the growth of the population in the presence of other population members. We then introduced the Beverton-Holt and Richer models into the basic model. The basic model shows variation when variance is incorporated into the matrix to make the shift from a deterministic to a stochastic model, since there are many stochastic processes that affect population size.

In order to construct a life table that is as useful as possible to demographers, we used the data from the salmon example in order to see whether there is a relation between the Leslie model and the life table. The analysis of both the Leslie model and the life table describes the same dynamics for the salmon population. To illustrate how a life table works, we constructed one using data [11] from the US Vital Statistics of 1985 as an example.

Matrix model have been widely used in biological research because of their simplicity. A recent review [1] showed that they constitute a powerful tool for analysing population dynamics, the influence of the present population state on its capacity for growth, and the sensitivity of the dynamics to quantitative changes in the vital rates. When using the matrix model, it is possible to combine the computational ease of the matrix with the flexibility of continuous time models.

In summary, we achieved an understanding of the construction and contents of the matrix. We demonstrated that all age classes eventually grow at the same rate, that the asymptotic rate of growth is the leading or most positive eigenvalue, and the eigenvector corresponding to the largest eigenvalue gives the stable age structure.

Since the Leslie model has been shown to be a good model in describing the dynamics of population, the model is now used in epidemiology field [12] to find a general value of R_0 .

- Considering a sexually transmitted disease in a completely heterosexual population, with both females and males. When a multiple discrete types of infected individuals is experienced, the Leslie model is constructed similar to the basic model, except here
 - P_i is the expected number of male infected who were in contact with a female in a completely susceptible population,
 - F_i is the rate of expected number of infected set, and
 - $n_i(t)$ gives the number of female at time 0, and a number of males at time 0.

The only thing that have changed in this epidemiology model is the definitions of the vital rates. This implementation shows that the Leslie model is not only of important use to ecologists.

Acknowledgement

I wish to thank Professor David Sherwell and Doctor Londiwe Vilakazi Masinga for their insightful reviews on this essay. May GOD bless you. I would like to thank Professor Neil Turok and the director of AIMS, Professor Fritz Hahne for the encouragement they gave through out the 18 months I spend here at AIMS.

I would like to thank all the tutors for their aid to make my studies as bearable as possible, Anahita, Paul, Jean-Marie, Christian, Laure, Eman, Henry and Sam. My most gratitude goes out to Igsaan and Emmanuel for keeping all the students safe at all times, not forgetting the administration staff, Mirjam, Theresa and Lynne.

Last but not least, many thanks goes to the UBUNTU fellas, Jan and Andy, you are the best.

I wish to thank all my fellow students for being there when help was needed, the discussions we had, living in harmony and learning a lot about one another, I will always cherish those moments. To the 2005/6 AIMS students and Dr Mike Pickles, you guys are the best. Cho my brother, may GOD furnish you with blessings. Alfred and Sara (Nashua) there is none like you. Miangaly Gaelle Andriamaro, all I can say is "Ariva Big Belly"! Dorian, thank you very much for your help.

Most of all, I would like to thank my family for the love they showed me since from the beginning of my studies. The support I got from Johann Potgieter is also gratefully acknowledged.

May GOD bless you all.

Ke rata go ka lebisa lekwalo le go batswadi ba me, Itumeleng and Matshediso, bokgaityadi ba ka ba ba rategang, Lesego, Kadimo le Masedi, mologoaka, Tuelo.

Bibliography

- [1] H. Caswell. *Matrix Population Models: Construction, analysis, and interpretation*. 2nd Edition, 2001.
- [2] M. Kot. *Elements of Mathematical Ecology*. Cambridge University Press, 2001.
- [3] M. B. Usher. *Developments in the leslie model in mathematical models in ecology*, 1971. Blackwell Scientific Publications.
- [4] P. H. Leslie. Some further notes on the use of matrices in population mathematics. *Biometrika*, 35:213–245, 1948.
- [5] T. J. Quinn and R. B. Deriso. *Quantitative Fish Dynamics*. Oxford University Press, 1999.
- [6] E. C. Pielou. *An introduction to mathematical ecology*, 1969.
- [7] E. Ranta, P. Lundberg, and V. Kaitala. *Ecology of Populations*. Cambridge University Press, 2006.
- [8] S. Engen, R. Lande, B. Sather, and H. Weimerskirch. Extinction in relation to demographic and environmental stochasticity in age-structured models. Available from <http://www.elsevier.com/locate/mbs>, 2005.
- [9] J. H. Pollard. *Mathematical models for the growth of human populations*. Cambridge University press, Cambridge, 1973.
- [10] A. Hastings. *Population Biology : Concepts and models*. Springerlink, 1997.
- [11] G. L Peters and R. P Larkin. *Population Geography*. Kendall/Hunt, 1989.
- [12] O. Diekmann and P.J Heesterbeek. *Mathematical epidemiology of infectious diseases: Mathematical and Computational Biology*. 2000.
- [13] N. J. Gotelli. *A Primer of Ecology*. 3rd edition. Sinauer Associates, Inc, Sunderland, Massachusetts, 2001.