DIMACS

Center for Discrete Mathematics &
Theoretical Computer Science

DIMACS EDUCATIONAL MODULE SERIES

MODULE 07-3
Using Population Models in the Teaching of Eigenvalues

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Module Description Information

- **Title:**

  Using Population Models in the Teaching of Eigenvalues

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- **Abstract:**

Leslie Matrix and Modified Leslie Matrix (Lefkovitch Matrix) are discussed in this module. These two matrices help us to discover that how the population structure changes with time. We take the approach of introducing the concepts through the real life examples i.e. we use biological data available for different populations. The examples and questions are constructed in such a way that after going through these, hopefully, the students will appreciate the importance of the eigenvalues and eigenvectors. This module can be used in a Linear Algebra class or any other appropriate level math course. A project is also added which one can use as a group project.

- **Informal Description:**

In this module we discuss how one can use matrix theory and eigenvalues to describe the way the population structure varies over time. We will use the real life examples (biological models) to explain and introduce concepts. In particular we will discuss two methods to study the population structure: Leslie Matrix and Modified Leslie Matrix (Lefkovitch Matrix). Leslie matrix is based on age-specific biological models while Lefkovitch matrix is based on stage-specific biological models. Exploratory exercises are presented throughout the module for the reader to work on whenever a new concept is introduced.

- **Target Audience:**

This module is aimed at the undergraduate students who are taking Linear Algebra, Differential Equations, Dynamical Systems or Mathematical Modeling course. Usually the students registered in these courses are at sophomore, junior or senior level.

- **Prerequisites:**

Basic knowledge of matrix theory like matrix operations, independent/dependent vectors, basis vectors, eigenvectors, eigenvalues and some probability theory.

- **Mathematical Field:**

Linear Algebra, Differential Equations, Dynamical Systems, Mathematical Modeling.

- **Application Areas:**

Dynamical systems, Biology, Ecology

- **Mathematics Subject Classification:**

MSC (2000): 37N25, 92B05, 78A70, 97D80

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- **Other DIMACS modules related to this module:**

None

Introduction

The purpose of this writing is to use actual biological data (population models) as a way to appreciate the importance of eigenvalues and eigenvectors. This module can be used in a Linear Algebra class or any other appropriate level math course. We will develop examples and questions for each topic which will show how eigenvalues and eigenvectors can be used to address questions regarding the long-term behavior of the population under study. It is assumed here that either the student will learn or already has the necessary prerequisite knowledge of the concepts needed to do these questions. A project is also added which one can use as a group project.

We envision that this module can be used in the following courses with some changes.

- **Linear Algebra:** This can serve as an application of the concepts of eigenvalues and eigenvectors. It is assumed that the concepts of linearly independent, basis, and matrix algebra are already covered. One can use the problems included as homework assignments or use the included project as group work. Students will need at least a week to do the group project.

- **Dynamical Systems/Math Modeling/Math Topics Course:** This module can be used as one of the topics covered in these types of courses. In this case, either the students will have necessary knowledge of the terminology used or the instructor will spend some time covering the basic knowledge needed. The time spent on basics and module will depend on the class level and student knowledge. For example, if students have already taken a Linear Algebra course, then one can just start with the module unless there is a need to refresh some of the terminology. Again, problems included can be used as homework assignments or group projects.

- **A Topic for Student Seminars:** Ideally this module can also be used in a Student Seminar course. This module can serve as a starting point (or reference) for the Leslie matrices topic and students can be asked to expand on it; for example, find some populations and data which follow Leslie type models and check the long-term behavior of populations, population distribution, growth rate, effects of culling, etc.

Our hope is that in the end this application will give students a greater appreciation for the mathematical ideas they are learning and also show them how sophisticated mathematical ideas are applied in other disciplines.

Leslie Matrices

Many species have a life-cycle with well-defined stages. For example, many insects go through the following four-stage cycle: egg, larvae, pupae and adult. A Leslie matrix uses age-specific or stage (class)-specific survival and fecundity rates for a population to describe the way the population structure varies over time.

To begin, let's suppose that the female members of a population are divided into two stages, each one year in length. Females in the first stage produce no offspring and have a 70% chance of surviving to the second stage. Females in the second stage produce an average of 3 female offspring per year, but are guaranteed to die after one year in stage 2. Let's also suppose that initially there are 100 females in the first stage and 100 females in the second stage. What will the distribution of the female population look like in year 1?

The number of stage 1 females in year 1 = (average number of offspring produced by stage 1 females x 100) + (average number of offspring produced by stage 2 females x 100) = (0 x 100) + (3 x 100) = 300.

Also, the number of stage 2 females in year 1 = number of stage 1 females reaching stage 2 + number of stage 2 females remaining in stage 2 = (probability of a stage 1 female reaching stage 2 x 100) + (probability of a stage 2 female remaining in stage 2 x 100) = (0.7 x 100) + (0 x 100) = 3. So, in year 1, there will be 300 females in stage 1 and 70 females in stage 2.

We can repeat this process to find the distribution of the female population in year 2. In other words, the number of stage 1 females in year 2 = (average number of offspring produced by stage 1 females x 300) + (average number of offspring produced by stage 2 females x 70) = (0 x 300) + (3 x 70) = 210. Also, the number of stage 2 females in year 2 = number of stage 1 females reaching stage 2 + number of stage 2 females remaining in stage 2 = (probability of a stage 1 female reaching stage 2 x 300) + (probability of a stage 2 female remaining in stage 2 x 70) = (.7 x 300) + (0 x 70) = 210. So, in year 2, there will be 210 females in stage 1 and 210 females in stage 2.

Can you find the distribution of the female population in year 3? You should get 630 females in stage 1 and 147 in stage 2.

What do we do if there are more than two stages for the female population? In general, suppose the female members of a population are divided into *n* stages or classes. Let F_i = the fecundity of a female in the i^{th} class, i.e., F_i = the average number of offspring per female in the i^{th} class. Also let P_i = the probability that a female in the i^{th} class will survive to become a member of the $(i+1)^{\text{st}}$ class. Let

$$\mathbf{x}^{(k)} = \begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ \vdots \\ x_n^{(k)} \end{pmatrix} = \begin{pmatrix} \textit{population of stage } 1 \textit{ females in year } k \\ \textit{population of stage } 2 \textit{ females in year } k \\ \vdots \\ \textit{population of stage } n \textit{ females in year } k \end{pmatrix}.$$

Then

$$
(1) \qquad \begin{aligned}
x_1^{(k+1)} &= F_1 x_1^{(k)} + F_2 x_2^{(k)} + \ldots + F_{n-1} x_{n-1}^{(k)} + F_n x_n^{(k)} \\
x_2^{(k+1)} &= P_1 x_1^{(k)} \\
x_3^{(k+1)} &= \qquad P_2 x_2^{(k)} \\
&\vdots \\
x_n^{(k+1)} &= \qquad\qquad\qquad P_{n-1} x_{n-1}^{(k)}
\end{aligned} .
$$

Then a **Leslie matrix** that describes the change in the population over time is given by

$$
L = \begin{pmatrix} F_1 & F_2 & \ldots & F_{n-1} & F_n \\ P_1 & 0 & \ldots & 0 & 0 \\ 0 & P_2 & \ldots & 0 & 0 \\ \vdots & \vdots & \ldots & \vdots & \vdots \\ 0 & 0 & \ldots & P_{n-1} & 0 \end{pmatrix}
$$

and we can represent the system of linear equations given in (1) by the matrix system

$$
\mathbf{x}^{(k+1)} = L\mathbf{x}^{(k)}.
$$

Also note that

$$
(2) \qquad \mathbf{x}^{(k+1)} = L^{k+1}\mathbf{x}^{(0)}.
$$

Of course not every species will follow this model so we will discuss some variations to this model later.

Let’s look at a simple example. In 1941, H. Bernadelli explored a beetle population that consists of three age-classes. One-half of the females survive from year 1 to year 2, one-third of the females survive from year 2 to year 3. The females reproduce in their third year, producing an average of six new females. After they reproduce, the females die.

Let’s construct the Leslie matrix for this beetle population. Following the construction of the Leslie matrix described on the previous page, we see that our Leslie matrix L is given by:

$$L = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}.$$

That seems easy enough. Now let's see how we can use matrix L and some linear algebra to describe how this population will change over time.

Question 1:
We're interested in the long-term behavior of the population. So let's see if we can answer the following questions.

a) Suppose that in a given year there are 60 beetles age 1 year, 60 beetles age 2 years and 60 beetles age 3 years. In other words, the population of beetles at time 0 is given by the vector $\mathbf{x}^{(0)} = \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix}$. What will the age distribution of the beetles look like in the following year? How about 5 years from now? How about 10 years from now?

The question we are most interested in answering is the following: What will happen to a population in the long run? Will it grow? Will it die out? Will it get younger? Older? The key to answering these questions is the eigenvalues and eigenvectors of L.

To see this, let's go back to our initial example, where the female members of a population are divided into two stages, each one year in length. Females in the first stage produce no offspring and have a 70% chance of surviving to the second stage. Females in the second stage produce an average of 3 female offspring per year, but are guaranteed to die after one year in stage 2. Let's also suppose that initially there are 100 females in the first stage and 100 females in the second stage.

The Leslie matrix L for this population is given by $L = \begin{pmatrix} 0 & 3 \\ .7 & 0 \end{pmatrix}$. We find the eigenvalues of L to be $\lambda_1 = \sqrt{2.1} \approx 1.45$ and $\lambda_2 = -\sqrt{2.1} \approx -1.45$. The corresponding eigenvectors are $\mathbf{e}_1 = (2.07,\ 1)$ and $\mathbf{e}_2 = (-2.07,\ 1)$. How will this help us determine the long-run population?

First, we will express our initial population vector $\mathbf{x}^{(0)} = (100,\ 100)$ as a linear combination of the eigenvectors $\mathbf{e}_1$ and $\mathbf{e}_2$. This gives: $\mathbf{x}^{(0)} = 74.15\mathbf{e}_1 + 25.85\mathbf{e}_2$. Then

$$
\begin{aligned}
\mathbf{x}^{(1)} = L\mathbf{x}^{(0)} &= L(74.15\mathbf{e}_1 + 25.85\mathbf{e}_2) \\
&= 74.15(L\mathbf{e}_1) + 25.85(L\mathbf{e}_2) \\
&= 74.15(1.45\mathbf{e}_1) + 25.85(-1.45\mathbf{e}_2) \\
&= (222.56, 107.52) + (77.58, -37.48) \\
&= (300.14, 70.04)
\end{aligned}
$$

as we saw above.

From (2) above we see that

$$
\begin{aligned}
\mathbf{x}^{(n)} = L^n\mathbf{x}^{(0)} &= L^n(74.15\mathbf{e}_1 + 25.85\mathbf{e}_2) \\
&= 74.15(L^n\mathbf{e}_1) + 25.85(L^n\mathbf{e}_2) \\
&= 74.15\left((1.45)^n\mathbf{e}_1\right) + 25.85\left((-1.45)^n\mathbf{e}_2\right) \\
&= (1.45)^n\left(74.15\mathbf{e}_1 + 25.85\cdot(-1)^n\mathbf{e}_2\right) \\
&= (1.45)^n\left(2.07(74.15 + 25.85\cdot(-1)^{n+1}),\ 74.15 + 25.85\cdot(-1)^n\right)
\end{aligned}
$$

and now we can see that as n gets larger, both stages of our population will continue to grow due to $(1.45)^n\cdot$

Now let's return to our beetle population example. Recall that the Leslie matrix for our beetle population is given by

$$
L = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}.
$$

Question 2:
What will happen to the population of beetles in the long run? Will it die out? Will it grow? Will the population get younger? Older? Let's see if we can determine what will happen.

a) Beginning with $\mathbf{x}^{(0)} = \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix}$, calculate $\mathbf{x}^{(1)}, \mathbf{x}^{(2)},$ and $\mathbf{x}^{(3)}$. What will happen if I calculate $\mathbf{x}^{(4)}, \mathbf{x}^{(5)},$ and $\mathbf{x}^{(6)}$? Can you now describe the long-term behavior of the beetle population?

b) Find the eigenvalues $\lambda_1, \lambda_2, \lambda_3$ for the matrix L. Also find the norm of each eigenvalue. What do you see? Does this help explain the behavior you observed in the previous problem?

Modified Leslie Matrix:

Lefkovitch Matrix Models (Stage-Structured Models)

We will present here yet another application of matrices in modeling life-cycles of biological systems. Unlike Leslie matrix models, which are based on age-specific survival and fecundity rates, Lefkovitch matrix models are based on stage-specific survival rates. For example, it is very difficult to get an accurate count of individuals who are classified as "extremely old." Classifying individuals by stage rather than age has been used, for example, in plant ecology where size was more often a better predictor of demographic fate than age ([2]). Lefkovitch models are more useful for several reasons:

- It's often difficult or impossible to classify animals and plants accurately with respect to their age. For instance, in the fish population scientists determine the age of fish by counting growth rings. These growth rings are found on vertebrae, ear bones and some types of scales. One pair of such rings represents one year of growth. However, before scientists can accurately age the animal, they must verify when the rings are deposited.

- In some organisms, especially perennial plants, survivorship and fecundity are more related to size than to age.

- In some organisms, especially herbaceous perennial plants, individuals may actually revisit stages they already left, e.g., they may get smaller from one season to the next.

- Focusing on life-cycle stages helps to focus attention on identifying the critical transitions that may provide opportunities for management.

Applications: Both animal and plant population life-cycles can be modeled using stage structured models. Examples include: trees, sea turtles, desert tortoise, geese, corals, copepods and fish.

There are two methods of constructing Lefkovitch models: life-cycle graphs and matrices that are associated with the life-cycle graphs. For completeness we present both methods.

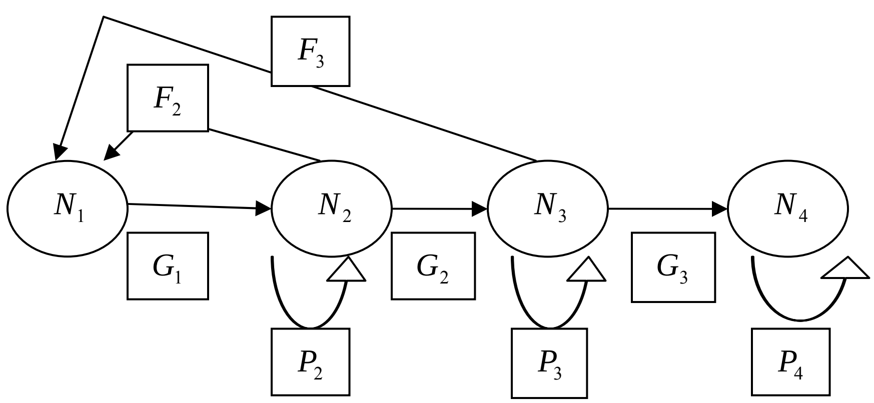
The Life-Cycle Graph: One of the easiest ways to understand Lefkovitch Models is by constructing a life-cycle graph. A life-cycle graph is a graphical description of a life-cycle of a biological species. To construct a life-cycle graph one can proceed as follows:

- Select a set of stages that are used to describe the life-cycle.

- Choose a projection interval. Depending on the species and stages, the projection interval can be in years, months, weeks or even days. Denote time intervals by $(t, t+1)$.
- Assign a node for each stage. Denote the nodes by N_i where i denotes the $i-th$ stage.
- Put an arc from N_j to N_i if an individual in stage j at time t can contribute individuals (by development or reproduction) to stage i at time $t+1$. If an individual in stage j at time t can contribute to stage j at time $t+1$ (by remaining in the same stage from one time to the next), put an arc from N_j to itself. Such an arc is called a self-loop.
- Label each arc by a coefficient $a_{i,j}$. The coefficient $a_{i,j}$ on the arc from N_j to N_i gives the number of individuals in stage i at time $t+1$ per individual in stage j at time t. The coefficients $a_{i,j}$ may be transition probabilities or reproductive outputs. Thus,

  $n_i(t+1) = \sum_{j=1}^{s} a_{i,j} n_j(t)$, where $n_j(t)$ is the population in stage j at time t.

Example: A life-cycle graph for the killer whale *Orcinus orca* (Source: [2]). Consider the killer whale *Orcinus orca* with four stages: yearlings, juveniles (past their first year but not mature), mature females, and postreproductive females. Let the projection interval be one year. Denote by P_i the probability of surviving and staying in stage i, by G_i the probability of surviving and growing from stage i to stage $i+1$, and by F_i the fertility of stage i. The nodes represent stages: N_1 = yearlings, N_2 = juveniles, N_3 = mature females and N_4 = postreproductive females. Below is the life cycle graph under these assumptions.



In the above life-cycle graph it is worth mentioning that individuals cannot remain in stage one from one time to the next. This is because the projection interval (one year) and the time period for the juveniles are the same. Hence, it is assumed that $P_1 = 0$ and no self-loop has been used for node N_1. Another important fact is that there is a postreproductive stage which does not contribute to any other stage. Positive fertility for juvenile females is also assumed since some juveniles may mature during the time interval t to $t+1$ and produce prior to time $t+1$.

Model Construction: Life-cycle graphs easily show the interaction and/or transition among the stages. From the life-cycle graph we can construct a matrix model that will be used to analyze the long-term behavior of the biological species. Matrix models are used to answer questions related to stability of the system using concepts such as eigenvalue and eigenvectors from linear algebra. We believe that the use of matrix models constructed from biological data will give strong motivation for students to learn abstract concepts in linear algebra. In addition, it shows concrete application of linear algebra concepts in areas such as biology.

The basic matrix equation for the number of individuals from one stage to another can be calculated by $\vec{n}(t) = A\ \vec{n}(t-1)$, where $\vec{n}(t)$ stands for the number of individuals at stage t and A is the coefficient matrix which can be constructed from the probabilities of transition among the various stages. It is important to mention that $\vec{n}(t)$ is a vector whose components are the different stages that individuals of the biological species undergo in their life-cycle. The structure of the Lefkovitch matrix is similar to that of the Leslie matrix. However, since Lefkovitch matrices are based on stages rather than age, it is possible to have non-zero transition probabilities in the main diagonals. For example for a four-stage model the Lefkovitch matrix has the form

$$A = \begin{pmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

Stable Stage Distribution: Once again we have that $\vec{n}(t) = A^t\ \vec{n}(0),$ where $\vec{n}(0)$ is the initial population size and t is time. Further one can show that $\vec{n}(t) = \lambda\, \vec{n}(t-1)$ in stable stage. Here λ denotes the largest eigenvalue of A. The largest eigenvalue λ gives the asymptotic rate of population increase. Further it can be shown that for stable stage $\vec{n}(t-1) \propto x_1$, where x_1 is the eigenvector corresponding to the largest eigenvalue. When the population has reached its asymptotic growth rate, the stage-structure of the population is proportional to x_1. The eigenvector corresponding to the largest eigenvalue gives the stable-stage structure. In other words, the components of the eigenvector corresponding to the dominant eigenvalue will give the proportions of the species in each stage in the long run.

Question 3:
The following example is about the life cycle of the killer whales *Orcinus orca* (Source: [6]).

$$B = \begin{pmatrix} 0 & 0.0043 & 0.1132 & 0 \\ 0.9775 & 0.9111 & 0 & 0 \\ 0 & 0.0736 & 0.9534 & 0 \\ 0 & 0 & 0.0452 & 0.9804 \end{pmatrix}$$

Answer the following questions for the projection matrix of the *Orcinus orca*: use of a computer algebra system such as Maple is recommended.

a) Find all eigenvalues of *B*. Which eigenvalue is the dominant eigenvalue?

b) Find an eigenvector corresponding to the dominant eigenvalue.

c) Using the initial vector $x_0 = [15, 50, 80, 60]$, estimate the distribution of the stages of the whale population after 20 years.

d) What can you say about the stable-stage distribution of the whale population in the long run? Compare your answer with problem (c) and comment on your findings!

Project A:

The Honu or Hawaiian Green Sea Turtle has life stages of varying lengths. A matrix model for the Honu population must allow for some turtles to survive and remain in their present stage while others will survive and move into the next stage. In this project you will use basic principles of probability to develop a Lefkovitch (stage-structured) matrix model for the Honu population and use it to investigate the long-term behavior of the Honu population.

Data set:

The five life-stages of the Hawaiian Green Sea Turtle are: eggs (hatchlings), juveniles, sub-adults, novice breeders, and mature breeders. The ages, annual survivorship, and number of eggs laid per year for each stage are provided in the following table:

Stage Description	Ages	Annual Survivorship	Eggs Laid for Each Stage
Eggs (hatchlings)	<1	0.23	0
Juveniles	1-16	0.68	0
Sub-Adults	17-24	0.75	0
Novice Breeders	25	0.89	280
Mature Breeders	26-50	0.92	70

For our five-stage model, the Lefkovitch matrix has the form

$$A=\begin{pmatrix} p_1 & e_2 & e_3 & e_4 & e_5 \\ q_1 & p_2 & 0 & 0 & 0 \\ 0 & q_2 & p_3 & 0 & 0 \\ 0 & 0 & q_3 & p_4 & 0 \\ 0 & 0 & 0 & q_4 & p_5 \end{pmatrix},$$

where e_i represents the number of eggs laid per year by turtles in the i^{th} stage, p_i represents the proportion remaining in stage i and q_i represents the proportion that will survive and move into stage $(i+1)$.

The following six questions will assist you in constructing a Lefkovitch matrix for the Honu population. Let s_i denote the annual survivor rate for the i^{th} stage and d_i denote the duration (in years) of the i^{th} stage. For example, for the "sub-adults" stage: $i = 3, s_3 = 0.75, d_3 = 8$.

1. Determine the probability that a sea turtle beginning the "juvenile" stage (i.e., age 1) survives to age 3. Determine the probability that it survives to age 7. What is the probability that the one-year old sea turtle will survive to age 17 and move into the "sub-adults" stage?

2. Suppose 100 sea turtles enter the "juvenile" stage. Find the number of these sea turtles that will survive this stage and move on to "sub-adults" stage. Now, suppose 100 sea turtles enter stage *i*. Find an expression for the numbers of these sea turtles that will survive stage *i* and move into stage *i* + 1.

3. Suppose that 100 turtles enter the "juvenile" stage from the "egg" stage each year. Explain why $100\left(1+s_i+s_i^2+\cdots+s_i^{15}\right)$ represents the total number of turtles in the entire "juvenile" stage. What will be the expression for the total number of turtles in the entire stage *i* if 100 sea turtles enter stage *i* from stage (*i* -1) each year?

4. Use the previous two answers to find an expression for q_i, the proportion of turtles that will survive stage "*i*" and move into stage $(i+1)$.

5. Recall p_i represents the proportion of turtles remaining in stage *i*. Use the fact that $p_i + q_i = s_i$ to show:

$$p_i = \left[\frac{1-(s_i)^{d_i-1}}{1-(s_i)^{d_i}}\right]\cdot s_i, i = 1\ldots5$$

   Hint: You may want to use the following equation to rewrite q_i:

$$\left(1+s_i+s_i^2+\cdots+s_i^{d_i-1}\right)(1-s_i)=1-s_i^{d_i}$$

6. Determine the values of p_i, q_i and e_i for *i* = 1…5 and use these values to construct the Lefkovitch matrix *A* for the five-stage model for the Honu population.

In the following seven problems we will investigate the long-term behavior of the Honu population using the Lefkovitch matrix and techniques from linear algebra involving eigenvalues and eigenvectors.

7. Given that the population at each stage in 2006 is:

$$P_0 = \begin{pmatrix} 346000 \\ 240000 \\ 110000 \\ 2000 \\ 3500 \end{pmatrix}.$$

   Find the estimated sea turtle population by stages in 2010 and 2020. What is your long-term prediction for the Honu populations?

8. Use a computer or calculator to compute the eigenvalues $\lambda_1 \ldots \lambda_5$ and the corresponding eigenvectors $\vec{w}_1 \ldots \vec{w}_5$ for the matrix *A*.

9. Write the population vector in 2006 as a linear combination of the eigenvectors, i.e.,

$$P_0 = a_1 \vec{w}_1 + \ldots + a_5 \vec{w}_5$$

   for some constants $a_1 \ldots a_5$.

10. Use the previous problem and your knowledge about eigenvalues and eigenvectors to write an expression for $A^n P_0$.

11. What is the long-term outlook for the Honu population? Does this agree with your response in problem 7?

12. Select the eigenvector, call it $\vec{u}$, corresponding to the eigenvalue with largest magnitude. Compute

$$\vec{u}_\infty = \frac{1}{k}\vec{u},$$

   where *k* is the sum of the components of $\vec{u}$. The vector $\vec{u}_\infty$ approximates the long-term proportions of the populations in each stage.

13. Using the population sizes for each stage in the year 2020 computed in problem 7, find the proportion of the total 2020 population in each stage and compare it to the corresponding component of $\vec{u}_\infty$. Are they close?

Question 4: Life history for the Pacific ocean Chinook salmon (Source:[4])
In the fall adult female salmon return to their stream to produce fertilized eggs, a process we describe as spawning. After they produce the fertilized eggs, the female salmon die. The fertilized eggs then hatch into small fish and live in the stream for several months. After

surviving in the stream for several months, they will swim back to the ocean. The percentage of eggs still alive the next fall and present in the ocean is 4%. These are called "*Age 1 fish*". Of the *Age 1 fish*, 20% will go back spawning and produce 2000 eggs. The remaining 80% will stay in the ocean. Of those remaining in the ocean, 50% will survive until the next fall season. Label these "*Age 2 fish*". Of the *Age 2 fish* 25% will go back spawning and produce 4000 eggs, while the remaining 75% remain in the ocean. Finally, 40% of these *Age 2 fish* in the ocean will survive until the next fall. These are labeled "*Age 3 fish*". All of the *Age 3 fish* will then go back spawning and produce 6000 eggs per individual. Introduce three nodes, N_0, N_1, N_2, where N_0= for stage *Eggs*, N_1= for stage *Age 1 fish in the ocean after spawning,* and N_2 = for stage *Age 2 fish in the ocean after spawning*. Note that there are no *Age 3 fish* left in the ocean after spawning.

a) Draw a life-cycle graph for these three nodes.

b) Find the Lefkovitch matrix corresponding to this life cycle graph.

c) Find the stable stage distribution of the salmon population.

Question 5: Life history for female grey seals (Source: [4]).
On average adult female seals, age five and older, give birth to 0.52 female seals during October. The newly born female seals live to age 1 with probability 0.72. The annual survival rate for all subsequent years is 0.95.

a) Construct the Lefkovitch matrix for a population of female seals: Age 1 females, Age 2 females, Age 3 females, Age 4 females and Age 5 and above females.

b) Determine the growth rate of the female seal population and the corresponding proportions by age.

<u>References:</u>

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Solutions to the Problems

Question 1:

a) The age distribution of the beetles in year one is given by

$$L\mathbf{x}^{(0)} = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix} \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix} = \begin{pmatrix} 360 \\ 30 \\ 20 \end{pmatrix}$$

The age distribution of the beetles five years from now is given by

$$L^5\mathbf{x}^{(0)} = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}^5 \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix} = \begin{pmatrix} 120 \\ 180 \\ 10 \end{pmatrix}$$

The age distribution of the beetles ten years from now is given by

$$L^{10}\mathbf{x}^{(0)} = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}^{10} \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix} = \begin{pmatrix} 360 \\ 30 \\ 20 \end{pmatrix}$$

Question 2:

a) $$\mathbf{x}^{(1)} = L\mathbf{x}^{(0)} = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix} \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix} = \begin{pmatrix} 360 \\ 30 \\ 20 \end{pmatrix}$$

$$\mathbf{x}^{(2)} = L^2\mathbf{x}^{(0)} = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}^2 \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix} = \begin{pmatrix} 120 \\ 180 \\ 10 \end{pmatrix}$$

$$\mathbf{x}^{(3)} = L^3\mathbf{x}^{(0)} = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}^3 \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix} = \begin{pmatrix} 60 \\ 60 \\ 60 \end{pmatrix}$$

We see the population cycling through $\mathbf{x}^{(1)}, \mathbf{x}^{(2)},$ and $\mathbf{x}^{(3)}$. So $\mathbf{x}^{(4)} = \mathbf{x}^{(1)}, \mathbf{x}^{(5)} = \mathbf{x}^{(2)},$ and $\mathbf{x}^{(6)} = \mathbf{x}^{(3)}$. The population will cycle through these three vectors forever.

b) The eigenvalues of L are $\lambda_1 = 1, \lambda_2 = \dfrac{-1+i\sqrt{3}}{2}$, and $\lambda_3 = \dfrac{-1-i\sqrt{3}}{2}$ (the cube roots of 1). Each eigenvalue has norm 1. Since the 3rd power of each eigenvalue is 1, we observe the cyclic nature of the population.

Question 3:

a) The eigenvalues of B: (rounded to four significant digits). All four eigenvalues λ_i are distinct and real: $\lambda_1 = 0.0048$, $\lambda_2 = 0.8342$, $\lambda_3 = 1.0254$ and $\lambda_4 = 0.9804$. The dominant eigenvalue is $\lambda_4 = 1.0254$.

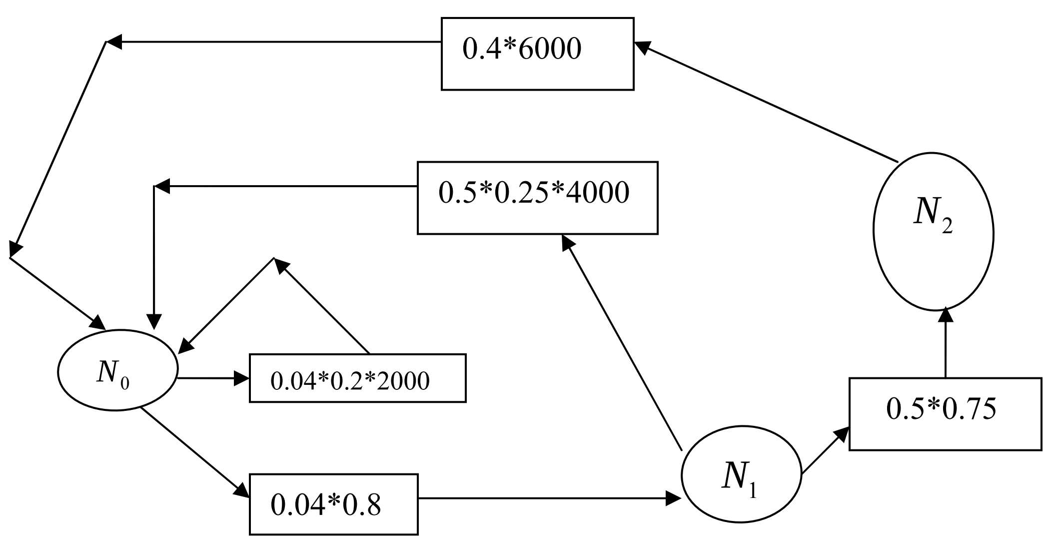
b) The eigenvector corresponding to the dominant eigenvalue is $\mathbf{w} = \begin{pmatrix} 0.0664 \\ 0.5672 \\ 0.5795 \\ 0.5815 \end{pmatrix}$ or any scalar multiple of this vector.

c) The population size in each stage is given by $\mathbf{w} = \begin{pmatrix} 13.5 \\ 114.84 \\ 117.91 \\ 112.07 \end{pmatrix}$

d) The stable stage distribution is given by $\mathbf{u}_\infty = \begin{pmatrix} 0.037 \\ 0.316 \\ 0.323 \\ 0.324 \end{pmatrix}$. This is done by normalizing the dominant eigenvector so that its components add up to 1. Note that the percentage of the population size in each stage from c) is a good approximation of the stable stage distribution.

Question 4:

a) Life cycle graph for adult female salmon:



b) The Lefkovitch matrix is: $\begin{pmatrix} 16 & 500 & 2400 \\ 0.032 & 0 & 0 \\ 0 & 0.375 & 0 \end{pmatrix}$

c) The dominant eigenvalue is $\lambda_1 = 17.038269332216206$ with a corresponding eigenvector $w = \begin{pmatrix} 0.99999 \\ 0.00188 \\ 0.00004 \end{pmatrix}$ or any scalar multiple of this vector. The stable stage distribution is given by $u_\infty = \begin{pmatrix} 0.99808 \\ 0.00188 \\ 0.00004 \end{pmatrix}$

Question 5:

a) The Lefkovitch matrix is $\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0.52 \\ 0.72 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.95 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.95 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.95 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.95 & 0.95 \end{pmatrix}$ with a dominant eigenvalue $\lambda_1 = 1.1217$. The corresponding eigenvector is $\mathbf{w} = \begin{pmatrix} 0.3856 \\ 0.2475 \\ 0.2096 \\ 0.1775 \\ 0.1504 \\ 0.8318 \end{pmatrix}$ or any scalar multiple of this vector.

b) The stable stage distribution is given by $\mathbf{u}_\infty = \begin{pmatrix} 0.19 \\ 0.12 \\ 0.10 \\ 0.09 \\ 0.08 \\ 0.42 \end{pmatrix}$.

Project A:

1. $(.68)^2, (.68)^6, (.68)^{16}$.

2. $100 \cdot (0.68)^{16}, 100 \cdot (s_i)^{d_i}$.

3. $100 \cdot (0.68)$ is the number of sea turtles that survived and reached age 2. $100 \cdot (0.68)^2$ is the number that survived and reached age 3. So $100 \cdot (1 + 0.68 + (0.68)^2 + \cdots + (0.68)^{16})$ is the total number of turtles in "Juvenile" stage for the duration of this stage and $100\left(1 + s_i + s_i^2 + \cdots + s_i^{d_i - 1}\right)$ for any stage *i*.

4. $q_i = \dfrac{100(s_i)^{d_i}}{100(1 + s_i + s_i^2 + \cdots + s_i^{d_i - 1})} = \dfrac{(s_i)^{d_i}}{1 + s_i + s_i^2 + \cdots + s_i^{d_i - 1}}$. Note that q_i does not depend on the numbers that enter the stage each year if it remains the same for that stage.

5.
$$\begin{aligned} p_i &= s_i - q_i \\ &= s_i - \frac{s_i^{d_i}}{1 + s_i + \cdots + s_i^{d_i - 1}} \\ &= \frac{s_i + s_i^2 + \cdots + s_i^{d_i - 1}}{1 + s_i + \cdots + s_i^{d_i - 1}} \cdot \frac{1 - s_i}{1 - s_i} \\ &= \frac{s_i\left(1 - s_i^{d_i - 1}\right)}{1 - s_i^{d_i}} \end{aligned}$$

6.
$$A = \begin{pmatrix} 0 & 0 & 0 & 280 & 70 \\ 0.23 & 0.679 & 0 & 0 & 0 \\ 0 & 0.001 & 0.711 & 0 & 0 \\ 0 & 0 & 0.039 & 0 & 0 \\ 0 & 0 & 0 & 0.89 & 0.909 \end{pmatrix}$$

7.

$$P_{2010} = A^4 P_0 = \begin{pmatrix} 1332271 \\ 734236 \\ 29162 \\ 1567 \\ 11301 \end{pmatrix} \quad \text{and} \quad P_{2020} = A^{14} P_0 = \begin{pmatrix} 596701 \\ 552238 \\ 3226 \\ 144 \\ 7287 \end{pmatrix}$$

You may suspect that the Honu population will eventually die out.

8.

$$\lambda = \begin{pmatrix} \lambda_1 \\ \lambda_2 \\ \lambda_3 \\ \lambda_4 \\ \lambda_5 \end{pmatrix} = \begin{pmatrix} -.0584 \\ .0686 \\ .6694 \\ .6969 \\ .9225 \end{pmatrix} \quad \vec{w}_1 = \begin{pmatrix} .9546 \\ -.2978 \\ .0004 \\ -.0003 \\ .0002 \end{pmatrix} \quad \vec{w}_2 = \begin{pmatrix} -.9358 \\ .3526 \\ -.0005 \\ -.0003 \\ .0003 \end{pmatrix} \quad \vec{w}_3 = \begin{pmatrix} .0418 \\ -.9988 \\ .0240 \\ .0014 \\ -.0052 \end{pmatrix} \quad \vec{w}_4 = \begin{pmatrix} .0772 \\ .9944 \\ -.0703 \\ -.0039 \\ .0165 \end{pmatrix} \quad \vec{w}_5 = \begin{pmatrix} .7270 \\ .6866 \\ .0032 \\ .0001 \\ .0090 \end{pmatrix}$$

Note that any scalar multiples of $\vec{w}_1 \ldots \vec{w}_5$ will also be eigenvectors.

9. $P_0 = 4.0444\times10^{11}\,\vec{w}_1 + 3.9355\times10^{11}\,\vec{w}_2 - 3.2919\times10^{11}\,\vec{w}_3 - 1.1150\times10^{11}\,\vec{w}_4 + 6.2481\times10^{9}\,\vec{w}_5$

10.

$$\begin{aligned} A^n P_0 = {} & 4.0444\times10^{11}(-0.0584)^n\,\vec{w}_1 + 3.9355\times10^{11}(0.0686)^n\,\vec{w}_2 - 3.2919\times10^{11}(0.6694)^n\,\vec{w}_3 \\ & -1.1150\times10^{11}(0.6969)^n\,\vec{w}_4 + 6.2481\times10^{9}(0.9225)^n\,\vec{w}_5 \end{aligned}$$

11. The Honu population will eventually become extinct since each of the eigenvalues has a magnitude less than 1. This agrees with our prediction in problem 7.

12.

$$\vec{u}_\infty = \begin{pmatrix} .50985 \\ .48152 \\ .00224 \\ .00007 \\ .00630 \end{pmatrix}$$

13. The proportion of the total 2020 population in each stage is:

$$\begin{pmatrix} .5146 \\ .4762 \\ .0027 \\ .0001 \\ .0063 \end{pmatrix}$$

This is fairly close to $\vec{u}_\infty$.