Leslie Matrix Models

Sources:
2. Katja Fennel, Lectures in Marine Biology
The Leslie Model

**Age structured modeling provides:**
- Rates of growth
- Age distribution
- Stability

**History of application in:**
- Trout
- Rabbits
- Lice
- Beetles
- Pine trees
- Buttercups
- Killer Whales
- Humans

![US Census data](chart.png)

**Age Distribution, 2000**

- Female
- Male
Chinook Salmon Background

Population in Decline

As we learned in the last lecture, salmon have very strong age structure in breeding habits.

Peter Kareiva, Michelle Marvier, Michelle McClure
Vol. 290. no. 5493, pp. 977 - 979
DOI: 10.1126/science.290.5493.977

Use age structure model to study declines.
4 damns on lower Columbia basin contribute to decline.

*Or do they??*

This is an important question, the economics of dam removal are significant.
Implementing age structured model

Store population data in vector let each entry be age class
As before, this is only females.

3 x 1 matrix, or vector

\[
\begin{bmatrix}
  n_j \\
  n_{sa} \\
  n_a
\end{bmatrix}
\]

juveniles
sub-adults
adults

= \( n_t \)

age structured population at time \( t \)
The Leslie Matrix

Encode the **fecundity (or reproductive rate of 1 female)** and **survivorship (changes of lining to the next age stage)** in a matrix

Sub-Adult

Juv.

F

S

F

F

S

Juv. → Sub-Adult

Sub-Adult → Adult

Adult → Sub-Adult

Sub-Adult → Juv.

L =

the Leslie matrix

<table>
<thead>
<tr>
<th></th>
<th>F&lt;sub&gt;j&lt;/sub&gt;</th>
<th>F&lt;sub&gt;sa&lt;/sub&gt;</th>
<th>F&lt;sub&gt;a&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>S&lt;sub&gt;j&lt;/sub&gt;</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>S&lt;sub&gt;sa&lt;/sub&gt;</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

What would the values be for no births or deaths?
Finding the evolution of an age structured population

**Matrix - vector multiplication**

\[
\begin{align*}
n_{t+1} &= L n_t \\
n_{t+2} &= L n_{t+1} \\
n_{t+3} &= L n_{t+2} \\
&\ldots
\end{align*}
\]

\[
\begin{bmatrix}
F_j \\
F_{sa} \\
F_a
\end{bmatrix} =
\begin{bmatrix}
S_j & 0 & 0 \\
0 & S_{sa} & 0
\end{bmatrix}
\cdot
\begin{bmatrix}
\vdots \\
\vdots \\
\vdots
\end{bmatrix}
\]

% x = A * b
[M N] = size(A);
x = zeros(1,M);
for i = 1:M
  for j=1:N
    x(i) = x(i) + A(i,j) * b(j);
  end
end
Finding the evolution of an age structured population

Matrix - vector multiplication

\[ n_{t+1} = L \ n_t \]
\[ n_{t+2} = L \ n_{t+1} \]
\[ n_{t+3} = L \ n_{t+2} \]

\[ \begin{bmatrix} n_{j,t+1} \\ n_{sa,t+1} \\ n_{a,t+1} \end{bmatrix} = \begin{bmatrix} F_j & F_{sa} & F_a \\ S_j & 0 & 0 \\ 0 & S_{sa} & 0 \end{bmatrix} \begin{bmatrix} n_{j,t} \\ n_{sa,t} \\ n_{a,t} \end{bmatrix} \]

\% x = A * b

[M N] = size(A);
x = zeros(1,M);
for i = 1:M
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        x(i) = x(i) + A(i,j) * b(j);
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end
Finding the evolution of an age structured population

Matrix - vector multiplication

\[ n_{t+1} = L \ n_t \]
\[ n_{t+2} = L \ n_{t+1} \]
\[ n_{t+3} = L \ n_{t+2} \]

\[ \text{for } i = 1:M \]
\[ \text{for } j=1:N \]
\[ x(i) = x(i) + A(i,j) * b(j); \]
\[ \text{end} \]
\[ \text{end} \]

\% x = A * b

\[ [M \ N] = \text{size}(A); \]
\[ x = \text{zeros}(1,M); \]
\[ \text{for } i = 1:M \]
\[ \text{for } j=1:N \]
\[ x(i) = x(i) + A(i,j) * b(j); \]
\[ \text{end} \]
\[ \text{end} \]
Finding the evolution of an age structured population

**Matrix - vector multiplication**

\[ n_{t+1} = L \ n_t \]
\[ n_{t+2} = L \ n_{t+1} \]
\[ n_{t+3} = L \ n_{t+2} \]
\[ ...n_{t+3} = L \ n_{t+2} \]
\[ n_t = L \ n_{t-1} \]
Alternative Approach

Powers of the matrix

\[ n_{t+1} = L \ n_t \]
\[ n_{t+2} = L \ n_{t+1} \]
\[ n_{t+2} = L(L \ n_t) \]
\[ n_{t+2} = L^2 \ n_t \]
\[ n_{t+3} = L^3 \ n_t \]
\[ n_{t+4} = L^4 \ n_t \]
\[ \ldots \]

Matrix multiplication

\[ c_{ij} = \sum_k a_{ik}b_{kj} \]

% C = A * B
[M N] = size(A);
C = zeros(N,N);
for i = 1:N
    for j = 1:N
        for k = 1:N
            C(i,j) = C(i,j) + A(i,k) * B(k,j);
        end
    end
end
Alternative Approach

Powers of the matrix

\[ n_{t+1} = L \cdot n_t \]
\[ n_{t+2} = L \cdot n_{t+1} \]
\[ n_{t+2} = L(L \cdot n_t) \]
\[ n_{t+3} = L^2 \cdot n_t \]
\[ n_{t+k} = L^k \cdot n_t \]

Matrix multiplication

\[ c_{ij} = \sum_k a_{ik} b_{kj} \]

Take the easy route.
Stability

Assuming constant growth across age groups:

\[ n_k = \lambda n_{k+1} \]

Where

- \( \lambda < 1 \) population is in decline
- \( \lambda = 1 \) population is constant
- \( \lambda > 1 \) population is growing

\( \lambda \) is called the dominant 'eigen-value' of the matrix \( L \). Formally, they are defined as:

\[ \lambda n_k = L n_k \]

The vector returns itself (eigen = own, the matrices own vectors).
Simplified Activity

To try out these ideas, try the following simplified salmon biology setup.

\[
\begin{align*}
n_0 &= \\
L &= 
\end{align*}
\]

![Table]

Plot the time evolution of all three population segments. To show the trends, use a logarithmic y axis. What happens if the fecundity for adults drops to 1000? What is \( \lambda \) in each case?
Try it out!

Use the Leslie matrix model to compute salmon stocks.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td></td>
<td>$\mu s_1 b_3 m_3 / 2$</td>
<td>$\mu s_1 b_4 m_4 / 2$</td>
<td>$\mu s_1 b_5 m_5 / 2$</td>
</tr>
<tr>
<td>2</td>
<td>$s_2$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>$s_3$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td>$(1 - b_3) s_4$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td>$(1 - b_4) s_5$</td>
<td></td>
</tr>
</tbody>
</table>

**Table 1.** Structure of demographic matrices for female SRSS chinook salmon. $s_x$ is the probability of survival from age $(x - 1)$ to age $x$, $b_x$ is age-specific propensity to breed, $\mu$ is survival during upstream migration, and $m_x$ is the number of eggs per female spawner of age $x$. The parameters $s_2$ and $\mu$ were further defined as follows: $s_2 = [zs_z + (1 - z)s_d]s_e$, where $z$ is the proportion of fish transported, $s_d$ is survival during in-river migration, $s_z$ is survival during transport, and $s_e$ is survival in the estuary and during entry into the ocean. $\mu = (1 - h_{ms})s_{ms}(1 - h_{sb})s_{sb}$, where $h_{ms}$ is harvest rate in the main stem of the Columbia River, $s_{ms}$ is survival of unharvested spawners from Bonneville Dam to their spawning basin, $h_{sb}$ is harvest rate in the subbasin, and $s_{sb}$ is survival of unharvested adults in the subbasin before spawning.
Table 2. Parameter values used in the baseline matrix developed for Poverty Flat index stock of SRSS chinook salmon. The corresponding population growth rate $\lambda$ is 0.760 (9).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Reference no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s_1$</td>
<td>0.022</td>
<td>(13)</td>
</tr>
<tr>
<td>$s_2$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$z$</td>
<td>0.729</td>
<td>(14)</td>
</tr>
<tr>
<td>$s_z$</td>
<td>0.98</td>
<td>(14)</td>
</tr>
<tr>
<td>$s_d$</td>
<td>0.202</td>
<td>(14)</td>
</tr>
<tr>
<td>$s_e$</td>
<td>0.017</td>
<td>(15)</td>
</tr>
<tr>
<td>$s_3, s_4, s_5$</td>
<td>0.8, 0.8, 0.8</td>
<td>(16)</td>
</tr>
<tr>
<td>$b_3, b_4, b_5$</td>
<td>0.013, 0.159, 1.0</td>
<td>(17)</td>
</tr>
<tr>
<td>$\mu$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h_{ms}$</td>
<td>0.020</td>
<td>(8)</td>
</tr>
<tr>
<td>$s_{ms}$</td>
<td>0.794</td>
<td>(14)</td>
</tr>
<tr>
<td>$h_{sb}$</td>
<td>0</td>
<td>(8)</td>
</tr>
<tr>
<td>$s_{sb}$</td>
<td>0.9</td>
<td>(8)</td>
</tr>
<tr>
<td>$m_3, m_4, m_5$</td>
<td>3257, 4095, 5149</td>
<td>(18)</td>
</tr>
</tbody>
</table>