

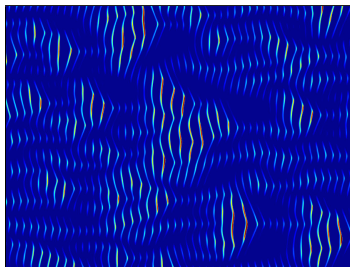
Ecological Dynamics

Structured population models

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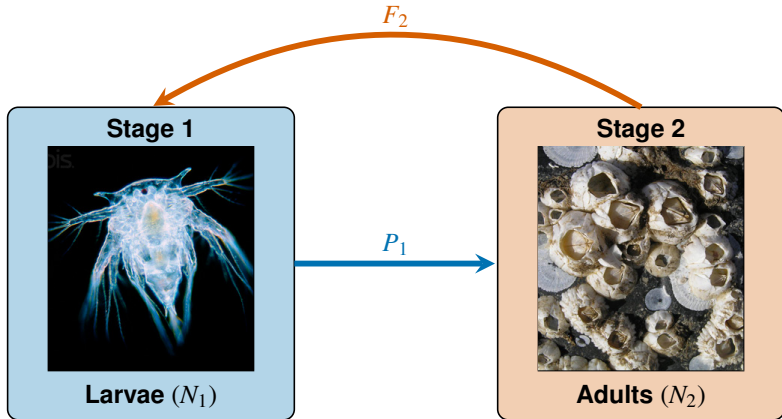
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From homogeneous to structured populations

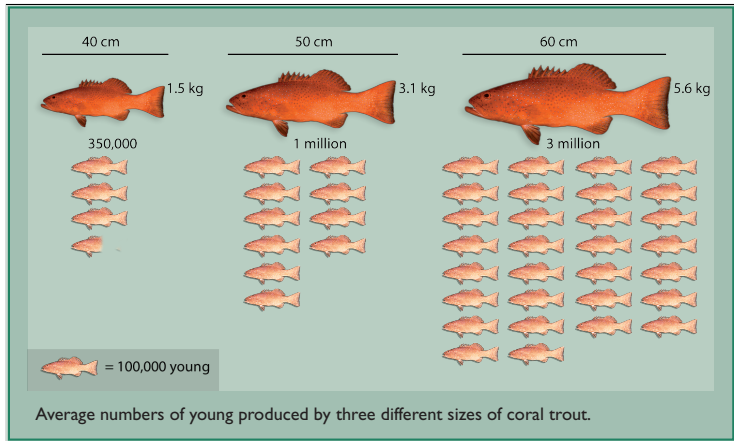
- The demographic models that we studied previously assumed no population structure: all individuals had the same mortality and reproductive rates
- While this assumption is fine for simple organisms such as microbes, it generally does not apply to longer-lived and more complex organisms such as vertebrates and mammals
- To study the demographic properties of such structured populations, one must turn to matrix models in order to keep track of the abundance of each stage or age of an organism
- These types of models are typically very data-hungry as they require measurements of **survivorship** and **fecundity** for each stage or age

Population growth for an organism with two stages



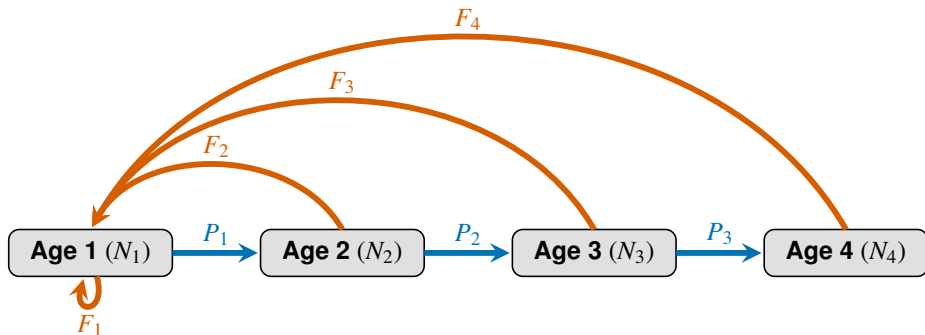
- Like marine invertebrates, barnacles have a complex life cycle: adults produce larvae at rate F_2 and P_1 of them survive to adulthood
- Here, the total population size $N = \sum_{i=1}^{i=2} N_i = N_1 + N_2$

The BOFF concept: Big, Old, Fecund, Females



Bigger, older female fish tend to be much more fecund than their younger counterparts and thus of greater conservation value; this is called the **BOFF** concept.

Population growth for BOFF organisms



- The diagram above represents an organism that lives to age class 4 with age-dependent fecundity and/or mortality
- By convention age class i represents individuals ages $i - 1$ to i
- Here, the total population size $N = \sum_{i=1}^{i=4} N_i = N_1 + N_2 + N_3 + N_4$

Data: the life-blood of matrix models

x	$S(x)$	$b(x)$	$l(x)$	$g(x)$	$l(x)b(x)$	$l(x)b(x)x$	$N(x) / \sum_{i=0}^{i=k} N(i)$
0	1000	5	1.0	0.6	5	0	0.982
1	600	2000	0.6	0.166	1200	1200	0.0181
2	100	10000	0.1	0.5	1000	2000	0.00009
3	50	300000	0.05	0.0	15000	45000	0.000001
4	0	400000	0.0	NA	0	0	0.0

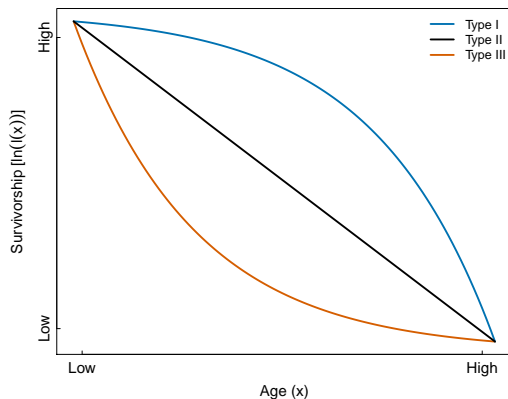
- x : Age bins
- $S(x)$: cohort survival; i.e., number of females in a single cohort surviving at each age
- $b(x)$: fecundity schedule; i.e., average number of offspring per female at each age
- All other quantities are derived from these columns

Data: the life-blood of matrix models

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- $l(x)$: proportion of original cohort surviving at each age
- $g(x) = \frac{l(x+1)}{l(x)}$: survivorship schedule; probability that an individual of age x survives to age $x + 1$
- The rest of the columns are needed to compute summary statistics and the stable population structure $N(x) / \sum_{i=0}^{i=k} N(i)$

Survivorship schedules in nature



- **Type I**: survivorship is high early and low later in life (e.g., mammals)
- **Type II**: survivorship is constant over lifetime (e.g., some birds)
- **Type III**: survivorship is low early and high later in life (e.g., insects)

Important summary statistics in matrix models

The first important statistic is called the **net reproductive rate** R_0 , which corresponds to the average number of female offspring produced per female over her lifetime: $R_0 = \sum_{x=0}^{x=k} l(x)b(x)$. For our example, $R_0 = 17205$.

A second important statistic is the **generation time** G , which corresponds to the average age of the parents of all offspring produced by a single cohort (Caughley, 1977): $G = \frac{\sum_{x=0}^{x=k} l(x)b(x)x}{\sum_{x=0}^{x=k} l(x)b(x)}$. For our example, $G \approx 2.802$

With these statistics, we can estimate (Mertz, 1970) the **intrinsic rate of increase** $r = \frac{\ln(R_0)}{G}$. For our example, $r = \frac{\ln(17205)}{2.802} \approx 3.48$.

Euler's equation: an exact method for computing r I

The approximation above generally falls within 10% of the exact value of r . To get an exact estimate, we must track the total number of births $B(t)$ at time t :

$$B(t) = \sum_{x=0}^{x=k} (\text{births from parents of age } x)$$

As the age intervals become infinitesimally small, this equation becomes:

$$B(t) = \int_0^k (\text{births from parents of age } x) dx$$

Euler's equation: an exact method for computing r II

The number of births from parents of age x is the product of the number of individuals born at time $t - x$, offspring production $b(x)$ and survivorship $l(x)$, so our equation becomes:

$$B(t) = \int_0^k B(t-x) l(x) b(x) dx$$

Since the population increases exponentially, for an initial population size of C , we have $B(t) = Ce^{rt}$. Substituting this back into our original equation, we get:

$$Ce^{rt} = \int_0^k Ce^{r(t-x)} l(x) b(x) dx$$

Dividing both sides by Ce^{rt} yields the Euler equation:

$$1 = \int_0^k e^{-rx} l(x) b(x) dx$$

Using Euler's equation to estimate proportional abundance

Euler's equation can be used to estimate the **stable population structure**, which corresponds to the proportional size $c(x)$ of each age or stage x as $t \rightarrow \infty$. Specifically, $c(x) = \frac{e^{-rx}l(x)}{\sum_{x=0}^k e^{-rx}l(x)}$.

This means that even if the population increases exponentially, we can still determine the relative abundance of each age or stage.

Simulating the model

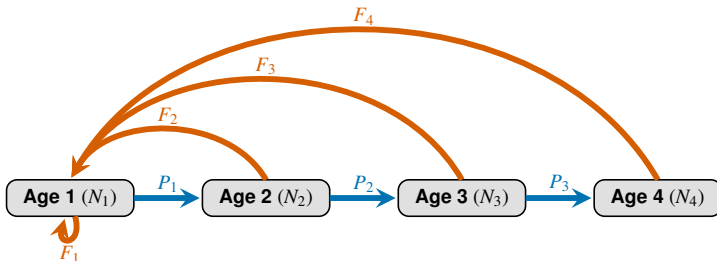
We will assume a **birth-pulse model** whereby individuals give birth to all of their offspring as soon as they enter a new age class and a **post-breeding census** whereby individuals are counted just after they breed.

To compute the dynamics of each age class (i.e., $N(x)$), we must quantify the **survival probability** P_i for each age class i , with $P_i = \frac{l(i)}{l(i-1)}$. This means that the survival probability for age class i is equal to the survivorship $l(i)$ of age i divided by the survivorship $l(i-1)$ of age $i-1$.

For our particular example, this is enough to compute the size N_i of all but the first age class i at each time step, with $N_{i+1}(t+1) = P_i N_i(t)$ and $i \neq 1$.

To compute the size of the first age class, we must first compute the **fertilities** F_i for each age class i , with $F_i = b(i) P_i$. The size of the first age class is then $N_{1+t} = \sum_{i=1}^k F_i N_i(t)$.

Simulating the model



For our example, this means that we have:

$$N_1(t+1) = F_1N_1(t) + F_2N_2(t) + F_3N_3(t) + F_4N_4(t)$$

$$N_2(t+1) = P_1N_1(t)$$

$$N_3(t+1) = P_2N_2(t)$$

$$N_4(t+1) = P_3N_3(t)$$

Using matrix notation

Leslie (1945) developed a shortcut to simulate and analyze the dynamics of a k stage or age structured population using matrix notation:

$$\begin{bmatrix} N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \\ N_4(t+1) \\ N_5(t+1) \\ \vdots \\ N_k(t+1) \end{bmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 & \dots & F_k \\ P_1 & 0 & 0 & 0 & \dots & 0 \\ 0 & P_2 & 0 & 0 & \dots & 0 \\ 0 & 0 & P_3 & 0 & \dots & 0 \\ 0 & 0 & 0 & P_4 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \dots & P_{k-1} & 0 \end{bmatrix} \times \begin{bmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ N_4(t) \\ N_5(t) \\ \vdots \\ N_k(t) \end{bmatrix}$$
$$\mathbf{N}(t+1) = \mathbf{A} \times \mathbf{N}(t)$$

\mathbf{A} is a square k by k matrix called the **Leslie matrix**. Matrices and vectors are typically typeset in **bold face**.

A brief introduction to linear algebra

Mathematical operations on matrices follow slightly different rules than those we are accustomed to for single values or **scalars**. For instance, matrix **A** and **B** can be added or subtracted if and only if they have the same number of rows and columns:

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \\ a_{31} & a_{32} \end{bmatrix} + \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \\ b_{31} & b_{32} \end{bmatrix} = \begin{bmatrix} a_{11} + b_{11} & a_{12} + b_{12} \\ a_{21} + b_{21} & a_{22} + b_{22} \\ a_{31} + b_{31} & a_{32} + b_{32} \end{bmatrix}$$

A + **B** = **A + B**

A brief introduction to linear algebra

Additionally, matrix multiplication is not commutative. This means that $\mathbf{A} \times \mathbf{B} \neq \mathbf{B} \times \mathbf{A}$. In fact, matrix multiplication is only defined for $\mathbf{A} \times \mathbf{B} = \mathbf{C}$ if \mathbf{A} is an n -row \times m -column matrix and \mathbf{B} is an m -row by k -column matrix. In such a case, \mathbf{C} will be an n -row by k -column matrix:

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \\ a_{31} & a_{32} \end{bmatrix} \times \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix} = \begin{bmatrix} a_{11}b_{11} + a_{12}b_{21} & a_{11}b_{12} + a_{12}b_{22} \\ a_{21}b_{11} + a_{22}b_{21} & a_{21}b_{12} + a_{22}b_{22} \\ a_{31}b_{11} + a_{32}b_{21} & a_{31}b_{12} + a_{32}b_{22} \end{bmatrix}$$

$\mathbf{A} \quad \times \quad \mathbf{B} \quad = \quad \mathbf{A} \times \mathbf{B}$

Here, \mathbf{A} is a 3-row \times 2-column matrix, \mathbf{B} is a 2-row \times 2-column matrix and \mathbf{C} is a 3-row by 2-column matrix.

Using linear algebra to solve structured population models I

Recall that we were able to express the population model as:

$$\mathbf{N}(t+1) = \mathbf{A} \times \mathbf{N}(t)$$

To solve this model, we write:

$$\mathbf{A}\mathbf{N} = \lambda\mathbf{N}$$

We now solve for λ . Unfortunately, we cannot simply divide both sides by \mathbf{N} . Instead, we subtract \mathbf{N} from both sides:

$$\mathbf{A}\mathbf{N} - \lambda\mathbf{A}\mathbf{N} = 0$$

Using linear algebra to solve structured population models II

Next, we introduce the identity matrix, which is a square $k \times k$ matrix with ones along the diagonal and zeros everywhere else:

$$\mathbf{A}\mathbf{N} - \lambda\mathbf{I}\mathbf{N} = 0$$

We now factor by \mathbf{N} :

$$(\mathbf{A} - \lambda\mathbf{I})\mathbf{N} = 0$$

The solution exists if the determinant of the matrix $\mathbf{A} - \lambda\mathbf{I}$ is zero. To prepare to compute the determinant for a 2×2 Leslie matrix \mathbf{A} , we first compute $\mathbf{A} - \lambda\mathbf{I}$:

$$\mathbf{A} - \lambda\mathbf{I} = \begin{bmatrix} F_1 & F_2 \\ P_1 & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix} = \begin{bmatrix} F_1 - \lambda & F_2 \\ P_1 & -\lambda \end{bmatrix}$$

Using linear algebra to solve structured population models III

Now we can compute the determinant which is also called the characteristic polynomial:

$$\det(\mathbf{A} - \lambda \mathbf{I}) = (F_1 - \lambda)(-\lambda) - (P_1 F_2) = \lambda^2 - \lambda F_1 - P_1 F_2$$

We can solve for λ via the quadratic formula with $a = 1$, $b = -F_1$, $c = P_1 F_2$:

$$\lambda = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} = \frac{F_1 \pm \sqrt{F_1^2 - 4P_1 F_2}}{2}$$

λ are called the **eigenvalues**. The dominant eigenvalue (largest positive λ_1) determines the growth rate of the population, with $\lambda_1 > 1$ indicating exponential growth and $\lambda_1 < 1$ indicating exponential decay as $t \rightarrow \infty$. Indeed, the intrinsic rate of increase is directly related to λ_1 :

$$r = \log(\lambda_1)$$

Using linear algebra to find the stable population structure I

The dominant eigenvalue is associated with an **eigenvector** that gives the stable population structure (i.e., the asymptotic proportional abundance of each age or stage). For example let's find the eigenvalues and eigenvectors of the following Leslie matrix **A**:

$$\mathbf{A} - \lambda \mathbf{I} = \begin{bmatrix} 2 & 3 \\ 1 & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix} = \begin{bmatrix} 2 - \lambda & 3 \\ 1 & -\lambda \end{bmatrix}$$

The characteristic polynomial of the equation is found by taking the determinant:

$$\det(\mathbf{A} - \lambda \mathbf{I}) = (2 - \lambda)(-\lambda) - (1 \cdot 3) = \lambda^2 - 2\lambda - 3$$

Using linear algebra to find the stable population structure II

Using the quadratic formula with $a = 1$, $b = -2$, $c = -3$:

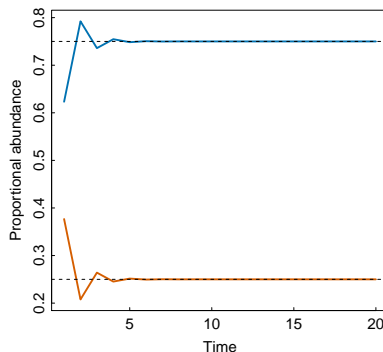
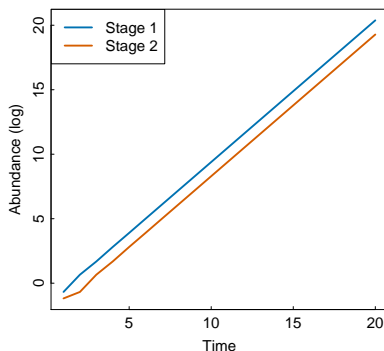
$$\lambda = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} = \frac{2 \pm 4}{2} = \{-1; 3\}$$

The dominant eigenvalue is $\lambda_1 = 3$. The corresponding eigenvector can be found by plugging the eigenvalue into the original matrix:

$$\mathbf{A}\mathbf{N} = \begin{bmatrix} 2 & 3 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix} = \lambda \mathbf{N} = \begin{bmatrix} 3N_1 \\ 3N_2 \end{bmatrix}$$

Solving this linear system of equations yields $N_2 = \frac{N_1}{3}$. This means that 3/4 of the population will be in stage N_1 and 1/4 of the population will be in stage N_2 .

Simulate to confirm analytical results



```
eigen(A)$values
```

```
## [1] 3 -1
```

```
eigen(A)$vectors[, 1]/sum(eigen(A)$vectors[, 1])
```

```
## [1] 0.75 0.25
```

Dealing with more complex scenarios computationally

The degree of the characteristic polynomial used to solve λ increases with the number of ages or stages, which means it rapidly becomes analytically intractable.

To solve these more realistic but complex scenarios, we use computational algorithms to find the eigenvectors and eigenvalues numerically.

This was just an introduction to structured population models. If you are interested in pursuing this further, I recommend the definitive book on the subject by Caswell (2001).

References I

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