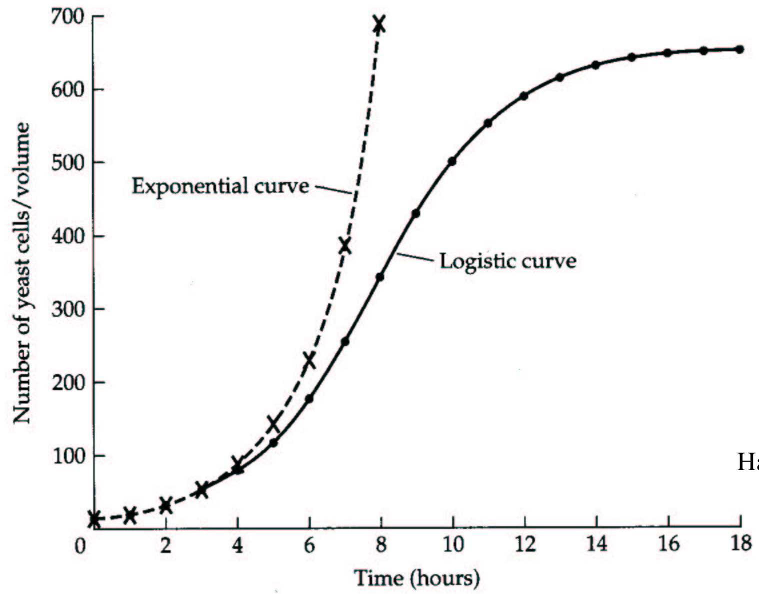
Age-Structured Populations

A. Population growth in unstructured populations - some simple examples



Hartl & Clark 1997

Figure 1.7 Increase in the number of cells of the yeast *Saccharomyces cerevisiae* in a defined quantity of culture medium (dots). The smooth curves are made from mathematical models of exponential growth or logistic growth. (Data from Pearl 1927.)

1. exponential growth

discrete time model: $N_t = N_{t-1} + rN_{t-1}$

$$= (1+r)N_{t-1}$$

$$= (1+r)^t N_0$$

continuous time model: $N(t) = N(0)e^{r_0 t}$ $\qquad r_0 = \ln(1+r)$

2. logistic growth

discrete time: $N_t = N_{t-1} + rN_{t-1}\left(\frac{K-N_{t-1}}{K}\right)$

continuous time: $\frac{dN(t)}{dt} = r_0 N(t)\left(\frac{K-N(t)}{K}\right)$

$$N(t) = \frac{K}{1+Ce^{-r_0 t}} \qquad C = \frac{K-N(0)}{N(0)}$$

3. <u>link between demography and population genetics</u>

Two haploid genotypes, A and B, with population growth rates of a and b; let the number of individuals of type A at time t be A_t and of B be B_t, then

$$A_t = (1 + a)^t A_0$$
$$B_t = (1 + b)^t B_0$$

The frequency of type A is $p_t = \frac{A_t}{A_t + B_t}$, the frequency of type B is $q_t = \frac{B_t}{A_t + B_t}$,

$$\frac{p_t}{q_t} = \frac{A_t}{B_t} = \left(\frac{1+a}{1+b}\right)^t \frac{A_0}{B_0} = \left(\frac{1+a}{1+b}\right)^t \frac{p_0}{q_0} = w^t \frac{p_0}{q_0}$$

where $w = \left(\frac{1+a}{1+b}\right)$ gives the relative fitness of genotype A to genotype B

this can also be written as: $$\ln\left(\frac{p_t}{q_t}\right) = \ln\left(\frac{p_0}{q_0}\right) + t \ln w$$

continuous time version: $$\frac{p_t}{q_t} = e^{mt} \frac{p_0}{q_0}$$ where $m = \ln w$

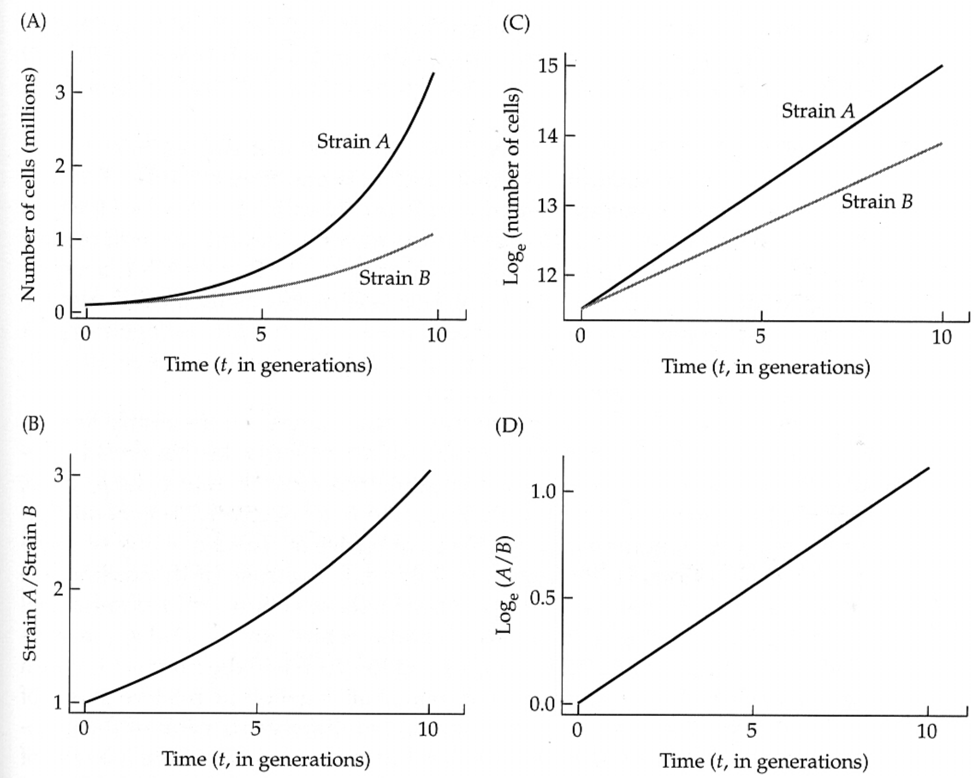


FIGURE 5.1 (A) Population growth of two hypothetical bacterial strains, A and B, in which the growth rates are 41% per generation for A and 26% per generation for B. The initial cell numbers are 10^5 for A and 10^5 for B. (B) Ratio of cell numbers of $A : B$. Because the A population grows faster than the B population, the proportion of A in the total population increases. (C) and (D) are the growth trajectories and their ratio on a log scale.

Hartl & Clark 2007

change in allele frequency

	haploid genotype	
Generation $t-1$	A	B
freq. before selection	p_{t-1}	q_{t-1}
relative fitness	w	1
freq. after selection	$p_{t-1}w$	q_{t-1}
Generation t	$p_t = \frac{p_{t-1}w}{p_{t-1}w + q_{t-1}}$	$q_t = \frac{q_{t-1}}{p_{t-1}w + q_{t-1}}$

$$\Delta p = p_t - p_{t-1} = \frac{p_{t-1}w}{p_{t-1}w+q_{t-1}} - p_{t-1} = \frac{pq(w-1)}{pw+q}$$

continuous time version: $\frac{dp}{dt} = pqm$

In-class Activities: Lecture #1 - Part A

Exercise 1

Derive the continuous time equation for change in allele frequency, $\frac{dp}{dt} = pqm$.

Exercise 2

For *E. coli*, two strains are competed on the same growth medium for 35 time units. The frequencies of the two strains are given below for the initial population and for the population at the end of the experiment.

	$t = 0$	$t = 35$
strain 1	0.45	0.22
strain 2	0.55	0.88

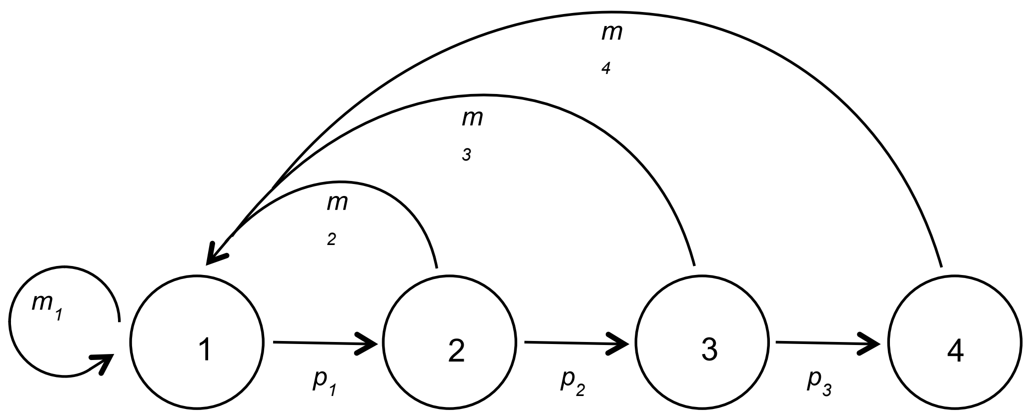
Estimate the fitness of strain 1 relative to the fitness of strain 2 on this growth medium.

B. Age-structured populations: the Leslie matrix

Consider a population where we wish to follow different types of individuals; for example, individuals of different ages. We will use an example from Otto & Day (2007) that follows females of the three-spine stickleback (a freshwater fish).

Since the sticklebacks have seasonal reproduction, we measure age in years, and track the number of females that are 1, 2, 3, and 4 years old, censusing the population at the beginning of the season, prior to reproduction.

We can visualize the life history using a life cycle graph:



discrete time recursion equations for each age class:

$$n_1(t+1) = n_1(t)m_1 + n_2(t)m_2 + n_3(t)m_3 + n_4(t)m_4$$

$$n_2(t+1) = n_1(t)p_1$$

$$n_3(t+1) = n_2(t)p_2$$

$$n_4(t+1) = n_3(t)p_3$$

Leslie matrix model:

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{pmatrix} = \begin{pmatrix} m_1 & m_2 & m_3 & m_4 \\ p_1 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 \\ 0 & 0 & p_3 & 0 \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}$$

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

projection of stickleback model:

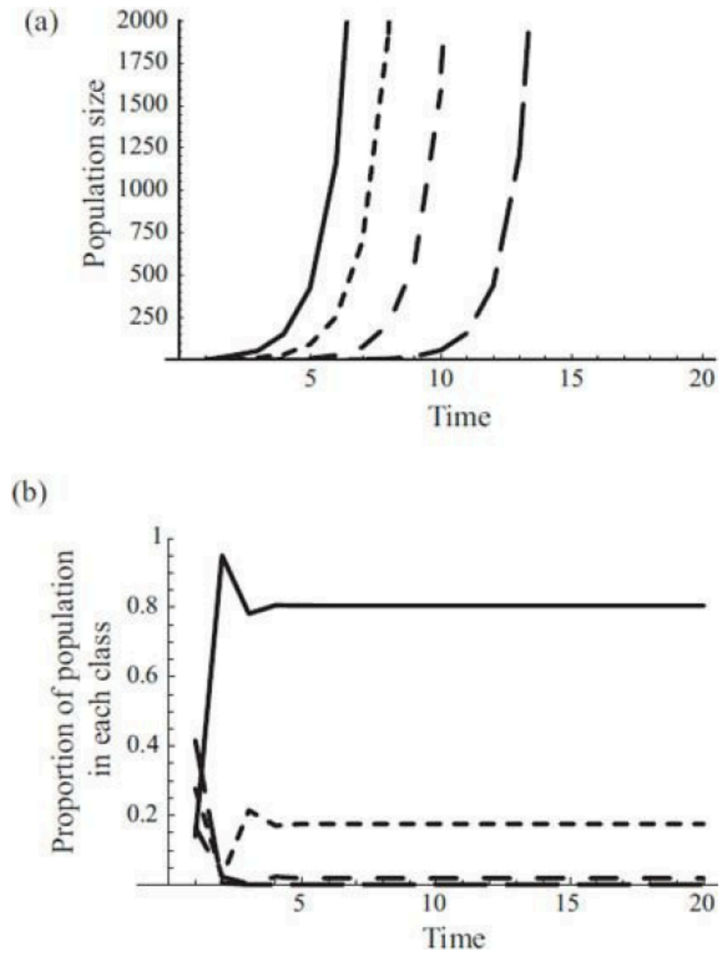


Figure 10.6: Growth of each age class of sticklebacks. Model (10.16) is iterated for a stickleback population. The 1-year old class is depicted by the solid line, and 2-, 3-, and 4-year old classes are depicted by lines with increasingly long dashes. (a) Population size of each age class. (b) Proportion of the population in each age class (the 4-year-old class is too rare to appear in the figure). Parameter values: $m_1 = 2$, $m_2 = 3$, $m_3 = 4$, $m_4 = 4$, $p_1 = 0.6$, $p_2 = 0.3$, and $p_3 = 0.1$.

Otto & Day 2007

analysis of age-structured models and the Euler-Lotka equation

characteristic polynomial of Leslie matrix (Euler-Lotka equation):

$$1 = \sum_{i=1}^{n} \frac{l_i m_i}{\lambda^i}$$

n = # age classes

$l_i = p_1 p_2 \dots p_{i-1}$ = probability that an individual survives to age class i

$l_1 = 1$

the n eigenvalue of the Leslie matrix (λ) are the n roots of this equation

Note: the continuous form of this equation is:

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

where newborns start at time $x = 0$ and the intrinsic rate of increase is $r = \ln \lambda$.

Derivation of Euler-Lotka equation:

For $$\mathbf{A} = \begin{pmatrix} m_1 & m_2 & \cdots & m_n \\ p_1 & 0 & \cdots & 0 \\ 0 & \ddots & \ddots & \vdots \\ 0 & \cdots & p_{n-1} & 0 \end{pmatrix}$$

any eigenvalue λ of the matrix **A** must satisfy: $\text{Det}(\mathbf{A} - \mathbf{I}\lambda) = 0$

Using the definition of the determinant for an n x n square matrix, we can use the kth row of the matrix to find:

$$|\mathbf{A}| = (-1)^{k+1} \sum_{j=1}^{n} (-1)^{j+1} a_{kj} |\mathbf{A_{kj}}|$$

example for a 3 x 3 matrix, starting with the 1st row:

$$\begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} = a_{11} \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} - a_{12} \begin{vmatrix} a_{21} & a_{23} \\ a_{31} & a_{33} \end{vmatrix} + a_{13} \begin{vmatrix} a_{21} & a_{22} \\ a_{31} & a_{32} \end{vmatrix}$$

the determinant of a 2 x 2 matrix is defined as: $\text{Det} \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{vmatrix} a & b \\ c & d \end{vmatrix} = ad - bc$

applying this to the 3 x 3 matrix above gives:

$$a_{11} \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} - a_{12} \begin{vmatrix} a_{21} & a_{23} \\ a_{31} & a_{33} \end{vmatrix} + a_{13} \begin{vmatrix} a_{21} & a_{22} \\ a_{31} & a_{32} \end{vmatrix} = a_{11}(a_{22}a_{33} - a_{23}a_{32}) - \ ...$$

then, for a Leslie matrix:

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

$$(-1)^0 (m_1 - \lambda)(-\lambda)^{n-1} + (-1)^1 m_2 p_1 (-\lambda)^{n-2} + (-1)^2 m_3 p_1 p_2 (-\lambda)^{n-3} + \cdots \\ + (-1)^{n-1} m_n p_1 p_2 \ldots p_{n-1} (-\lambda)^0 = 0$$

Letting $l_i = p_1 p_2 \dots p_{i-1}$ and $l_1 = 1$ gives:

$$(-\lambda)^n + m_1(-\lambda)^{n-1} + (-1)^1 m_2 l_2 (-\lambda)^{n-2} + (-1)^2 m_3 l_3 (-\lambda)^{n-3} + \cdots + (-1)^{n-1} m_n l_n = 0$$

Factoring out $(-\lambda)^n$:

$$1 - m_1\lambda^{-1} - m_2 l_2 \lambda^{-2} - m_3 l_3 \lambda^{-3} - \cdots - m_n l_n \lambda^{-n} = 0$$

$$1 = \sum_{i=1}^{n} \frac{l_i m_i}{\lambda^i}$$

<u>Long-term growth rate:</u>

The *<u>long-term growth rate</u>* of a population is given by the leading eigenvalue of the transition matrix (the largest root of the characteristic polynomial). If $\lambda_1 > 1$, the population is increasing, if $\lambda_1 < 1$, the population is decreasing, and if $\lambda_1 = 1$, the population size is constant.

Euler-Lotka equation for the stickleback example:

$$1 = m_1\lambda^{-1} + m_2 p_1 \lambda^{-2} + m_3 p_1 p_2 \lambda^{-3} + m_4 p_1 p_2 p_3 \lambda^{-4}$$

Letting $m_1 = 2, m_2 = 3, m_3 = 4, m_4 = 4, p_1 = 0.6, p_2 = 0.3$, and $p_3 = 0.1$,

$$1 = 2\lambda^{-1} + 1.8\lambda^{-2} + 0.72\lambda^{-3} + 0.072\lambda^{-4}$$

We can solve this (I used the program *Mathematica*) to find the four eigenvalues:

$$\lambda_1 = 2.75$$
$$\lambda_2 = -0.3 + 0.3i$$
$$\lambda_3 = -3 - 0.3i$$
$$\lambda_4 = -0.14$$

The *<u>long-term growth rate</u>* for this example is then $\lambda_1 = 2.75$.

Stable-age distribution and age-specific reproductive values:

The elements of the dominant right eigenvector give the proportions of the population in each age class *x* at the *stable-age distribution*:

$$u_x = \frac{l_x \lambda_1^{-(x-1)}}{\sum_{i=1}^{n} l_i \lambda_1^{-(i-1)}}$$

The elements of the dominant left eigenvector give the *long-term reproductive value* of individuals in class *x* relative to the youngest age class (class 1):

$$\frac{v_x}{v_1} = \frac{\lambda_1^{x-1}}{l_x} \sum_{i=x}^{n} \frac{l_i m_i}{\lambda_1^i}$$

and we let $v_1 = 1$.

Note:
The continuous version of this equation gives *Fisher's reproductive value*:

$$\frac{v(x)}{v(0)} = \frac{e^{rx}}{l(x)} \int_x^\infty e^{-ry} l(y) m(y) dy$$

where again newborns start at time $x = 0$ and the intrinsic rate of increase is $r = \ln \lambda_1$.

In-class Activities: Lecture #1 - Part B

Exercise 1
Find the stable-age distribution for the stickleback example, using the calculated leading eigenvalue $\lambda_1 = 2.75$ and the parameter values given above.

Do these values agree with the simulation results obtained by iterating the projection matrix shown above in Figure 10.6(b)?

Exercise 2
Which age group contributes most to the growth of the population?

Can you explain why this is so in terms of the biology of the fish as given by the example?

C. Sensitivity analysis and life-history theory

We can consider the *sensitivity* of the eigenvalues (and thus the growth rate of the population) to changes in the matrix elements a_{ij}. This type of analysis has been important in *life-history theory*, which seeks to explain how natural selection shapes the way individuals invest their resources in fecundity and survival at different ages. The underlying assumption is that limited resources result in trade-offs between different aspects of the life history.

The sensitivity of the eigenvalue λ to a change in the matrix element a_{ij} is given by:

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{\bar{v}_i u_j}{\langle \mathbf{u}, \mathbf{v} \rangle}$$

where $\langle \mathbf{u}, \mathbf{v} \rangle = u_1 v_1 + u v_2 + \cdots + u_n v_n$ is the scalar product of the right and left eigenvectors, and $\bar{v}_i$ is the complex conjugate of v_i.

Note: In the analysis of the leading eigenvalue, λ_1, since all of the entries of the left eigenvector are real, we can simply write v_i instead.

For the Leslie matrix, since there are only two kinds of non-zero entries (for the fecundities and the survival probabilites, sensitivity analysis is greatly simplified.

age-specific fecundities

$$\frac{\partial \lambda_1}{\partial m_i} = \frac{v_1 u_i}{\langle \mathbf{u}, \mathbf{v} \rangle} = \frac{l_i \lambda_1^{-(i-1)}}{T}$$

where

$$T = \sum_{x=1}^{n} \sum_{j=x}^{n} l_j m_j \lambda_1^{-j} = \sum_{x=1}^{n} x l_x m_x \lambda_1^{-x}$$

The quantity *T* gives a measure of *generation time* - it gives the mean age of the parents of a set of age 1 individuals in a population at the stable age-distribution (see Charlesworth 1980, section 1.3.2).

Also, for the Leslie matrix, $\langle \mathbf{u}, \mathbf{v} \rangle$ gives the frequency of each age class at the stable age distribution (u_i) times its reproductive value (v_i), which is the *long-term average reproductive value* of the population.

We can consider how the sensitivies change with age by considering

$$\frac{\partial\lambda_1/\partial m_i}{\partial\lambda_1/\partial m_{i+1}} = \frac{u_i}{u_{i+1}} = \frac{\lambda_1}{p_i}$$

<u>age-specific survival probabilities</u>

$$\frac{\partial\lambda_1}{\partial p_i} = \frac{v_{i+1}u_i}{\langle \mathbf{u}, \mathbf{v} \rangle} = \frac{\sum_{j=i+1}^{n} l_j m_j \lambda_1^{-(j-1)}}{p_i T}$$

To consider how the sensitivies change with age:

$$\frac{\partial\lambda_1/\partial p_i}{\partial\lambda_1/\partial p_{i+1}} = \frac{v_{i+1}u_i}{v_{i+2}u_{i+1}} = \frac{\lambda_1}{p_i}\left(\frac{m_{i+1} + p_{i+1}v_{i+2}}{\lambda_1 v_{i+2}}\right) = \frac{p_{i+1}}{p_i} + \frac{m_{i+1}}{p_i v_{i+2}}$$

Note:

$$\frac{\partial\lambda_1/\partial p_i}{\partial\lambda_1/\partial p_{i+1}} \geq 1 \text{ if } p_{i+1} \geq p_i \text{ or } m_{i+1} \geq p_i v_{i+2}$$

<u>In-class Activities: Lecture #1 - Part C</u>

<u>Exercise 1</u>

Calculate the effects of changing the life history parameters on population growth in the stickleback example.
Which age-specific fecundity has the greatest effect on population growth?
Which age-specific survival probability has the greatest effect on population growth?

<u>Exercise 2</u>

Assuming a positive growth rate ($\lambda_1 > 1$), how does the sensitivity of population growth to fertility change with increasing age?

How is this changed if the population is decreasing in size?