Calculating Biological Quantities

CSCI 2897

- Final — May 1, 2021 7:30 PM to 10:00 PM
- HW 5 — Thurs April 29, 11:59 PM.

Prof. Daniel Larremore

daniel.larremore@colorado.edu
@danlarremore

2021, Lecture 21

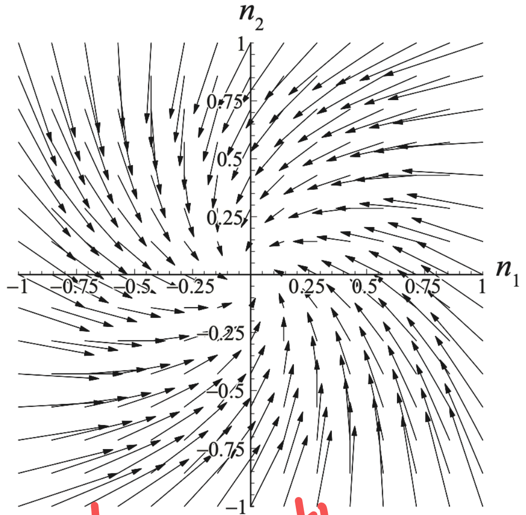
Last time on CSCI 2897

The eigenvalues of a **diagonal** or **triangular (upper or lower)** matrix are easy to get: they are just the values on the diagonal of the matrix!

Stability of equilibria (real eigenvalues):

- If all eigenvalues are negative, the system is stable.
- If one or more eigenvalues are positive, the system is unstable.

Re < 0
Im ≠ 0
spiraling inward

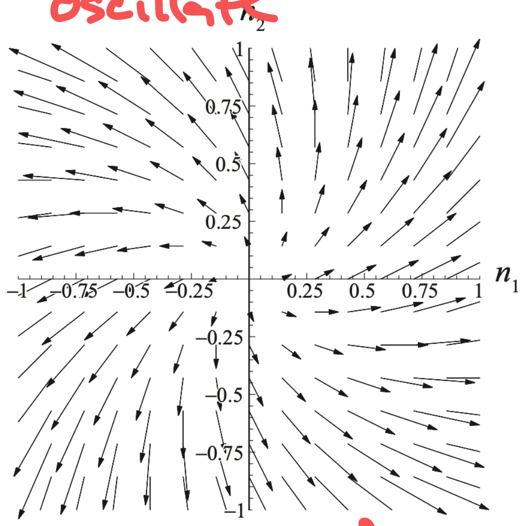


shrinking as they oscillate

Stability of equilibria (complex eigenvalues):

- If the real part of all eigenvalues is negative, the system is stable.
- The ~~complex~~ imaginary part of the eigenvalues tells us about rotation.

Re > 0
Im ≠ 0
Spiraling Out



growing while they oscillate.

The **complex conjugate** of a complex number $a + bi$ is $a - bi$.
If all the entries of a matrix are real, then the eigenvalues are real or come in conjugate pairs — no long complex eigenvalues.

Class structured populations

The study of population *age* structure or *size* structure is known as **demography**.

There are ~~four~~ three kinds of questions we can ask which commonly come up:

1. What is the **long-term growth rate** of a population?

2. What is the **long-term class structure** of a population?
(age, size)

3. Which **classes contribute most** to the long-term growth rate of a population.

Class structured populations: Juveniles & Adults

J A

Say we have a population with two classes: **juveniles & adults**.

Model:

- More A at t leads to more J at t+1, if b > 0. (birth rate)
- Juveniles become adults at rate p_j
- Adults become adults at rate p_a.

$$J(t+1) = bA(t)$$

$$A(t+1) = p_j J(t) + p_a A(t)$$

J A

All b, p_a, p_j are > 0.

Are these positive? Negative? >1? <1?

First, what is this model *doing*?

What clues has the modeler left for us?

- b is birth rate
- p_j is the prob that a juvenile survives to adulthood
- p_a is the prob that an adult survives to the next time step.

In discrete time $X(t+1) = \frac{1}{2} X(t)$ $X(t+1) = 2X(t)$

decay / decrease in pop. factor $\frac{1}{2} < 1$.

growth $2 > 1$

Class structured populations: Juveniles & Adults

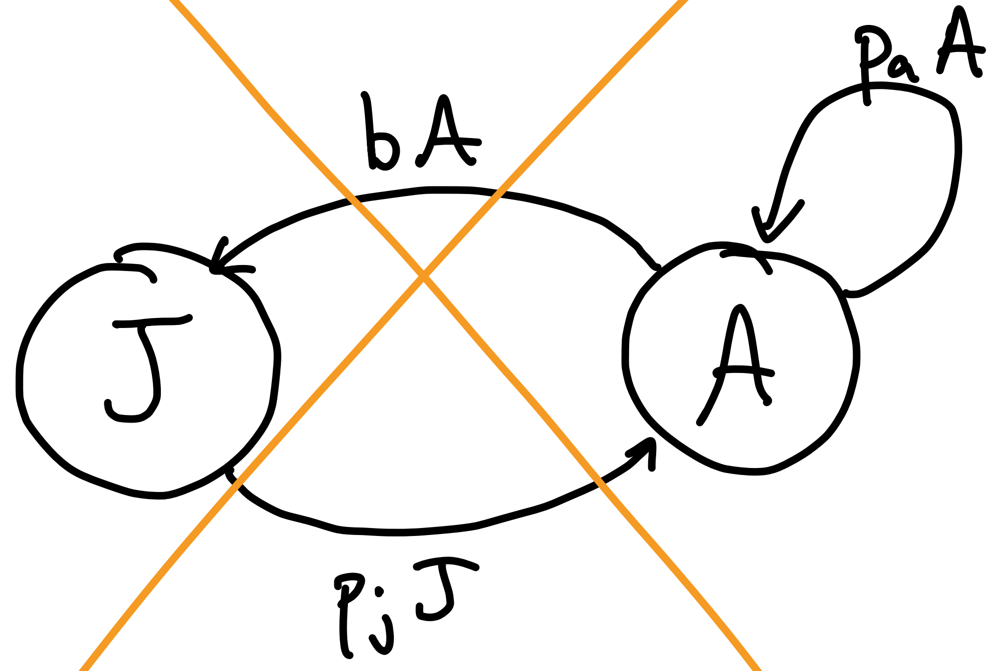
Rewrite this model in matrix form.

$J(t+1) = bA(t)$

$A(t+1) = p_j J(t) + p_a A(t)$

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

Flow Diagram



Recipe: equations to diagram.

1. one equation for each variable
   → one circled letter per variable.
2. Any non-zero flows between a variable and itself are on the diagonal of M.
3. flows between distinct variables are on the off-diagonal.

Class structured populations: Juveniles & Adults

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \boxed{\begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix}} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

$J(0) = 0.1$

$A(0) = 0.9$

$b = 10$ each adult produce 10 J per timestep.

$p_j = 0.1$ 10% of Juv. survive to adulthood.

$p_a = 0.2$ 20% of adults make it from one timestep to next.

In demography, the matrix of coefficients is referred to as the **transition matrix** or sometimes as the **projection matrix**.

Age-specific mortality rates and birth rates are known as **vital statistics**.

1. What is the long-term **long-term growth rate** of a population?
2. What is the **long-term class structure** of a population?
3. Which **classes contribute most** to the long-term growth rate of a population.

Class structured populations: Juveniles & Adults

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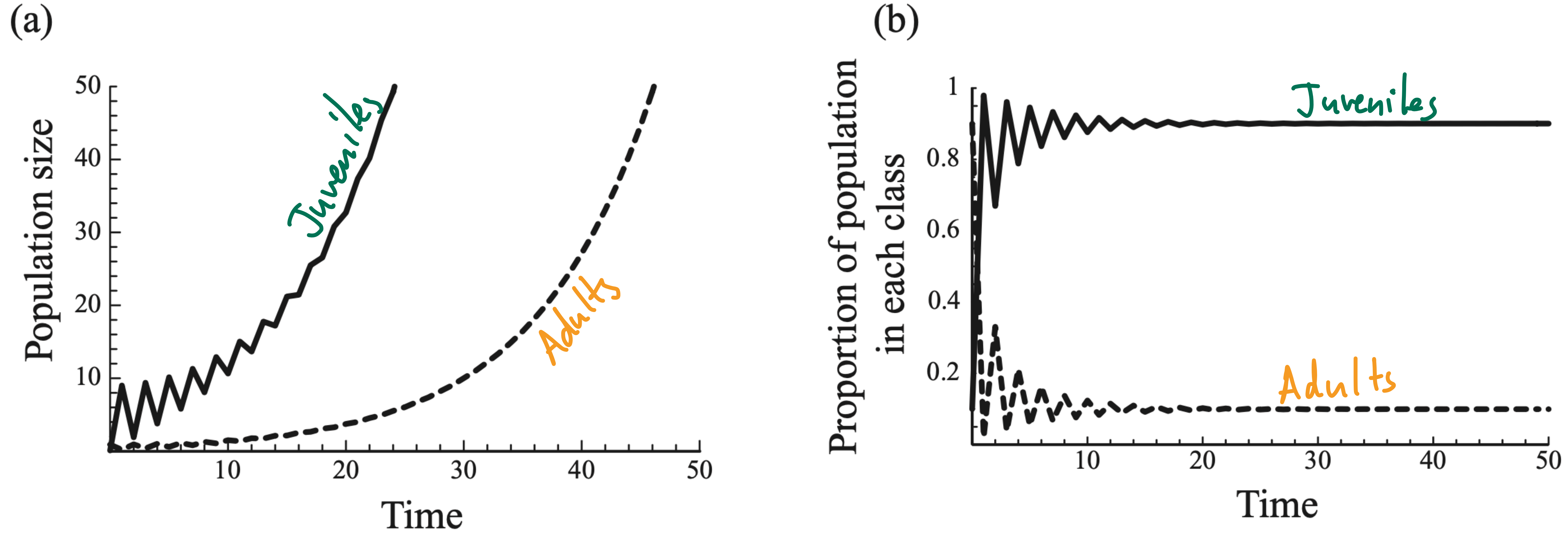

Class structured populations: Juveniles & Adults

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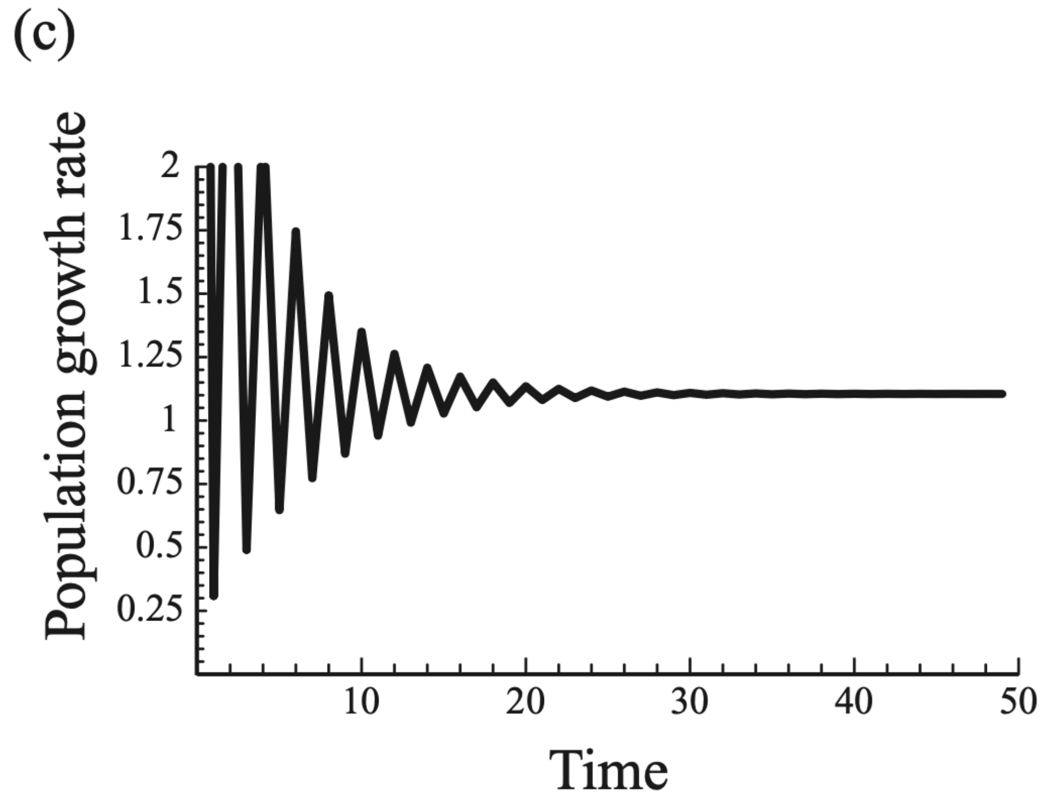
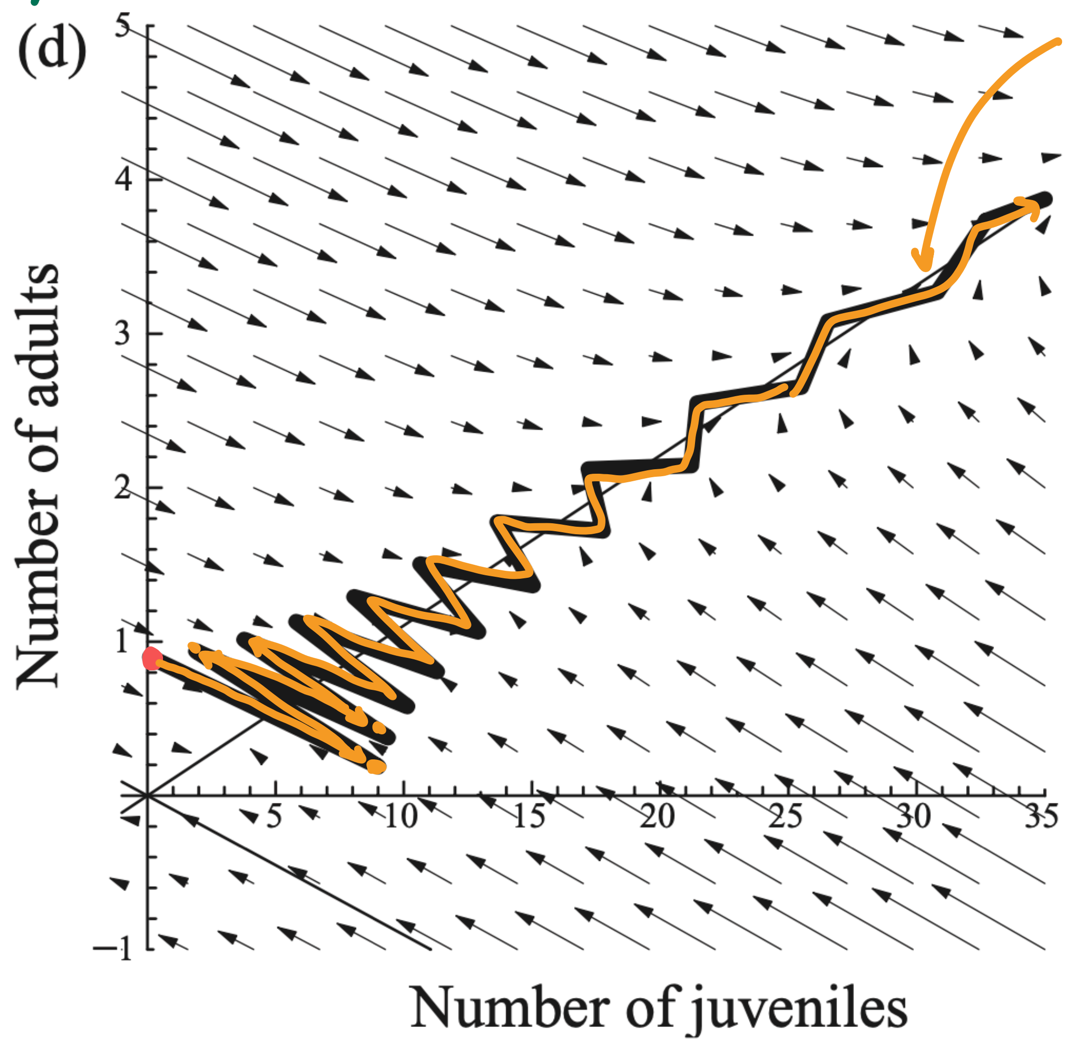


A



eigenvector?

growth rate = eigen value?

Phase Space

J

Class structured populations: Juveniles & Adults

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

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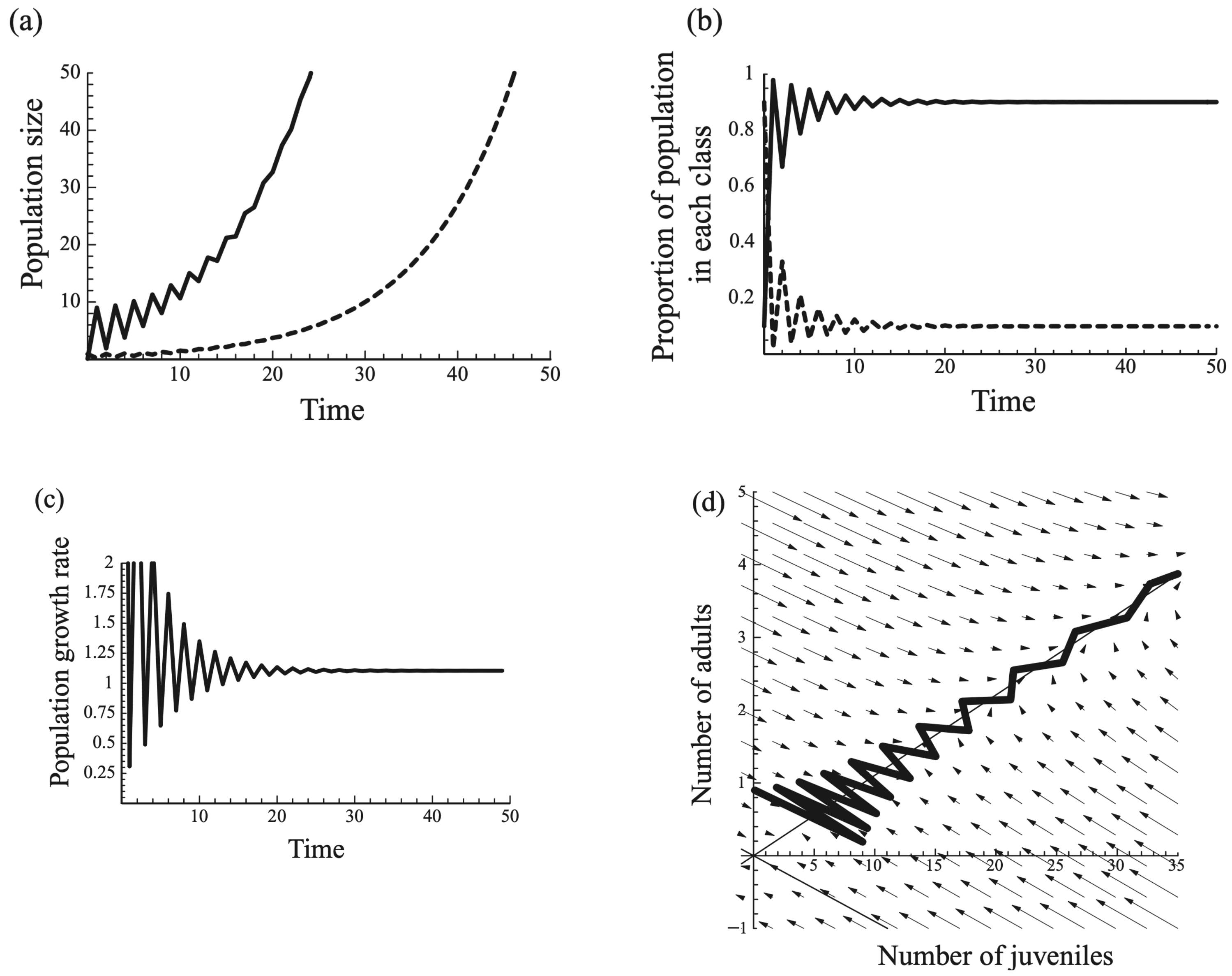


1. What is the **long-term growth rate** of a population?
2. What is the **long-term class structure** of a population?
3. Which **classes contribute most** to the long-term growth rate of a population.
4. Which **parameters have the greatest impact** on the long-term growth rate?

We have our answers!

But what if we had different parameters?

Or started from different conditions?

Class structured populations: Juveniles & Adults

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

transition matrix M

aka projection matrix.

$$\vec{n}(t+1) = M\vec{n}(t)$$

generic case.

The general solution for this kind of **linear discrete time** problem is given by:

$\vec{n}(t) = AD^tA^{-1}\ \vec{n}(0).$ Let's dissect this equation.

initial conditions

$$\vec{n}(t) = A\ D^t A^{-1} \vec{n}(0)$$

answer

Matrix whose columns are the eigenvectors of M.

3x3 example:

$$A = \begin{pmatrix} \begin{bmatrix} \vec{x}_1 \end{bmatrix} & \begin{bmatrix} \vec{x}_2 \end{bmatrix} & \begin{bmatrix} \vec{x}_3 \end{bmatrix} \end{pmatrix}$$

$M\vec{x}_1 = \lambda_1 \vec{x}_1$

3x3 Ex:

$$D = \begin{pmatrix} \lambda_1 & 0 & 0 \\ 0 & \lambda_2 & 0 \\ 0 & 0 & \lambda_3 \end{pmatrix}$$

Diagonal Matrix.

has on its diagonal entries the eigenvalues of M.

(Diagonal)^t ?

$$D^2 = \begin{pmatrix} \lambda_1^2 & 0 \\ 0 & \lambda_2^2 \end{pmatrix}$$

$$D = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}$$

$2\times2 \quad 2\times2 \quad \checkmark$

$$D^2 = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}\begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix} = \overset{2\times2}{\begin{pmatrix} \lambda_1^2 & 0 \\ 0 & \lambda_2^2 \end{pmatrix}}$$

Can show that for any diagonal matrix D, and any $\oplus$ integer power t,

$$D^t = \begin{pmatrix} D_{11}^t & & & & 0 \\ & D_{22}^t & & & \\ & & D_{33}^t & & \\ & & & \ddots & \\ 0 & & & & D_{nn}^t \end{pmatrix}$$

for a 2×2 dynamics.

$$\Rightarrow \quad D^t = \begin{pmatrix} \lambda_1^t & 0 \\ 0 & \lambda_2^t \end{pmatrix}$$

Class structured populations: Juveniles & Adults

$$\begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} = \underbrace{\left(\begin{bmatrix} \vec{x}_1 \end{bmatrix} \begin{bmatrix} \vec{x}_2 \end{bmatrix} \right)}_{A} \underbrace{\begin{pmatrix} \lambda_1^t & 0 \\ 0 & \lambda_2^t \end{pmatrix}}_{D^t} \underbrace{\left(\begin{bmatrix} \vec{x}_1 \end{bmatrix} \begin{bmatrix} \vec{x}_2 \end{bmatrix} \right)^{-1}}_{A^{-1}} \underbrace{\begin{pmatrix} n_1(0) \\ n_2(0) \end{pmatrix}}_{I.C.}$$

pull out λ_1^t

What happens here when t gets big?

$$D^t = \begin{pmatrix} \lambda_1^t & 0 \\ 0 & \lambda_2^t \end{pmatrix} = \lambda_1^t \begin{pmatrix} 1 & 0 \\ 0 & \frac{\lambda_2^t}{\lambda_1^t} \end{pmatrix} = \lambda_1^t \begin{pmatrix} 1 & 0 \\ 0 & \left(\frac{\lambda_2}{\lambda_1}\right)^t \end{pmatrix} \xrightarrow[t \to \infty]{} \lambda_1^t \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}$$

stays as a one.

"dominant"

"principal"

gets big.

If $\frac{\lambda_2}{\lambda_1} < 1$

this term goes to zero!

What happens if $\lambda_1 > \lambda_2$?

(and t gets large)

(1) Long term growth rate given by the largest eigenvalue

(2) Long term growth direction is $\vec{x}_1$.

Class structured populations: Juveniles & Adults

$$\begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} = \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right) \begin{pmatrix} \lambda_1^t & 0 \\ 0 & \lambda_2^t \end{pmatrix} \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right)^{-1} \begin{pmatrix} n_1(0) \\ n_2(0) \end{pmatrix}$$

What happens here when t gets big?

$$\begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} = \lambda_1^t \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right) \begin{pmatrix} 1 & 0 \\ 0 & \left[\frac{\lambda_2}{\lambda_1} \right]^t \end{pmatrix} \left(\left[\vec{x}_1 \right] \left[\vec{x}_2 \right] \right)^{-1} \begin{pmatrix} n_1(0) \\ n_2(0) \end{pmatrix}$$

1. What is the **long-term growth rate** of a population? ✅ λ_1
2. What is the **long-term class structure** of a population? ✅ $\vec{x}_1$

normalize $\vec{x}_1$ to sum to one, then x_i tells me what frac of pop'n is age group i.

Class structured populations: right whales

Class structured populations: right whales

- Up to 60 feet (18m) long — 300k lbs (135k kg).
- Distinguished by rough patches on head, which are parasitized by whale lice, making them white.
- Migratory seasonally, for feeding and calving.
- Gentle, docile, surface feeding, with lots of blubber — thus, killed by whalers for their oil. The blubber makes them float upon death.
- Now threatened by entanglements and fishing.
- ~400 alive in the N. Pacific. ~1150 W. Pacific.

Population growth rates are **absolutely critical for conservation**.

Class structured populations: right whales

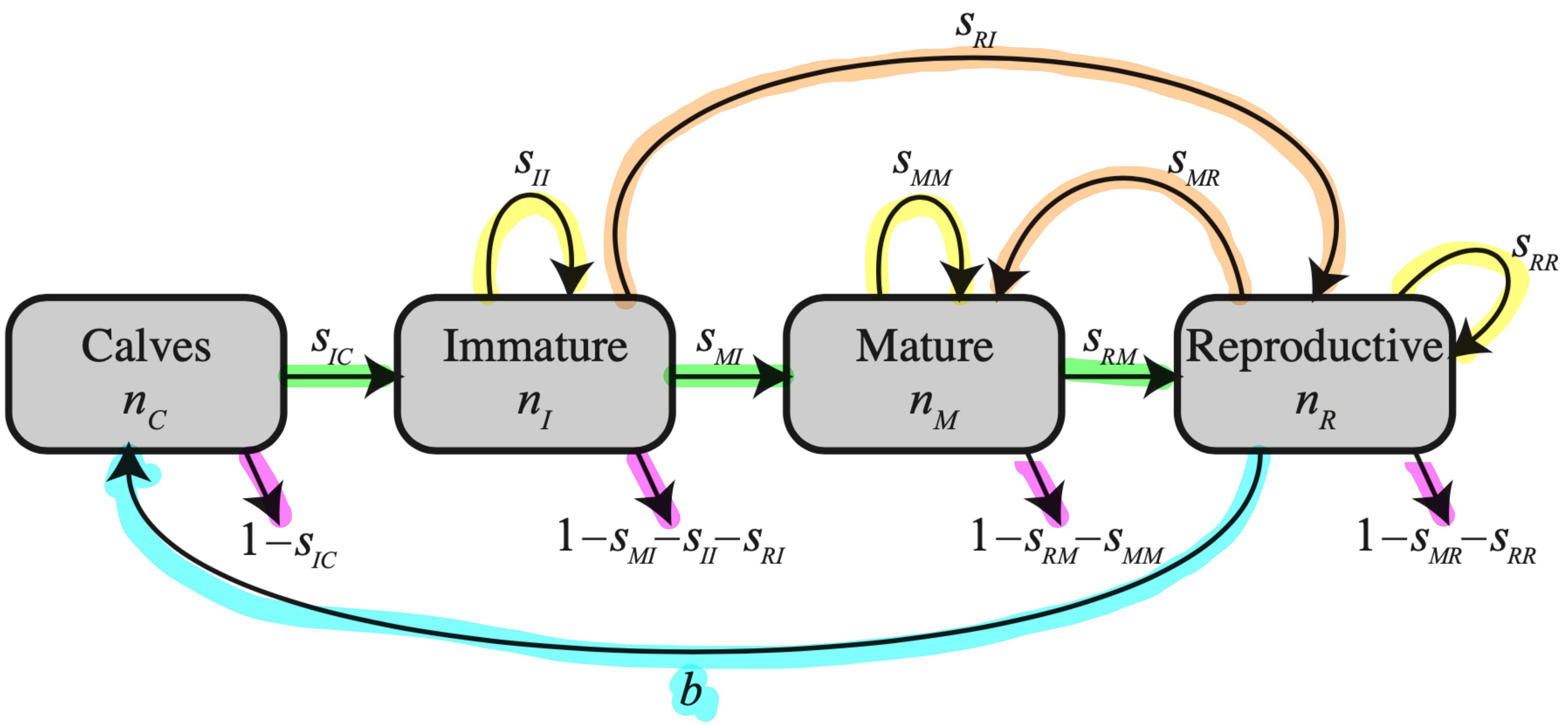
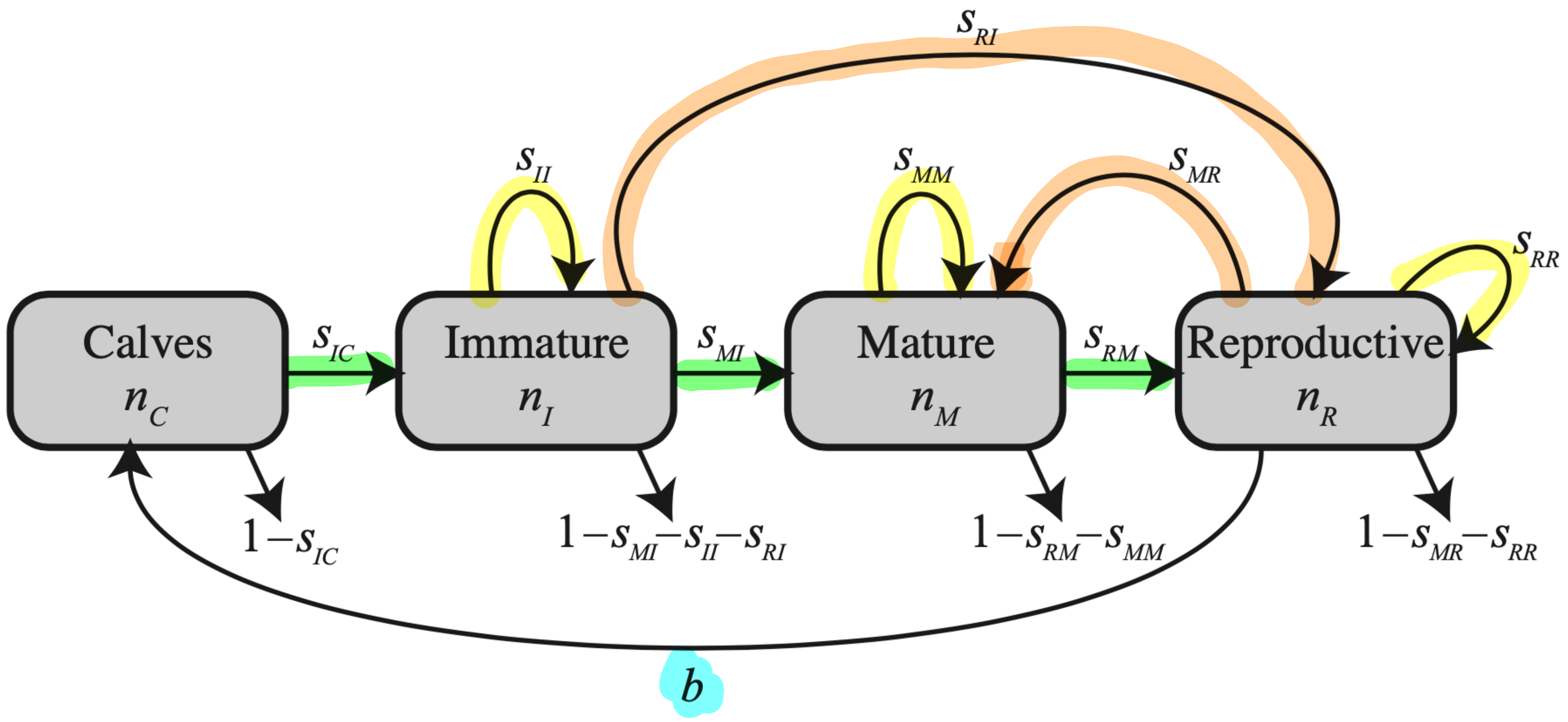


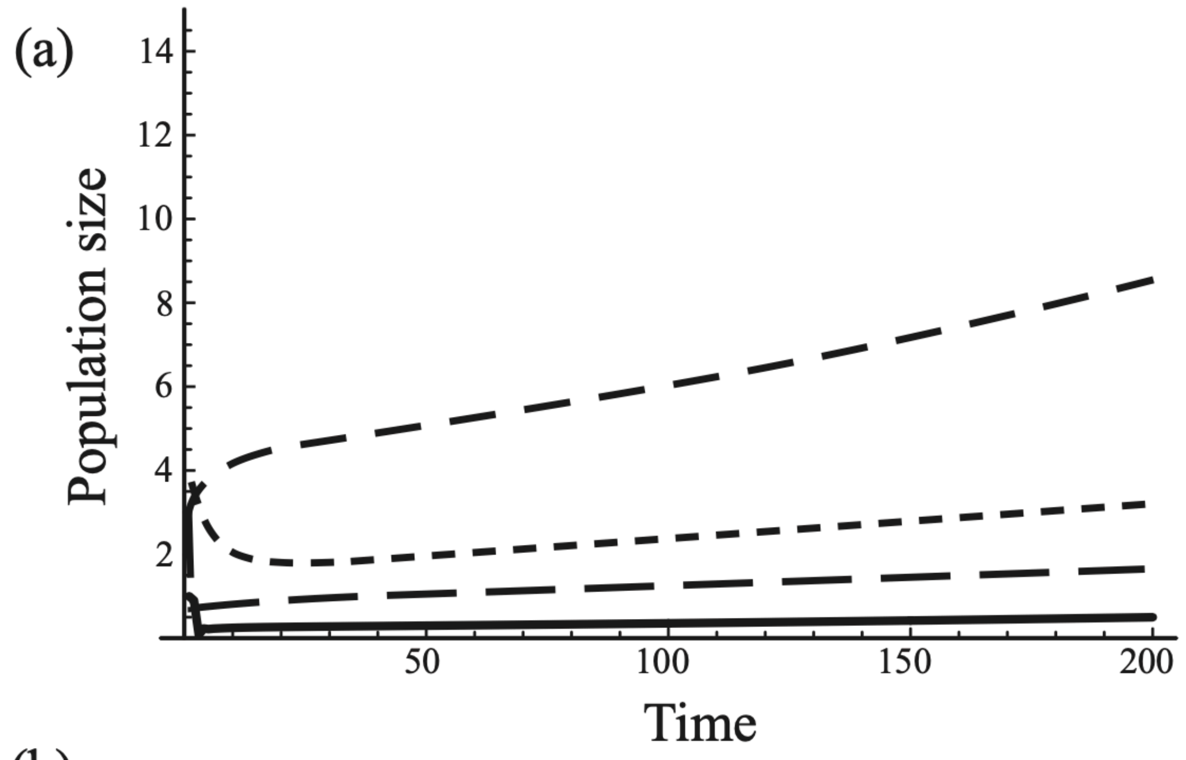
Figure 10.1: A flow diagram for the discrete-time model of right whales. The parameters, s_{ij} give the probabilities of an individual moving from j to i, and b is the fecundity of a reproducing female.

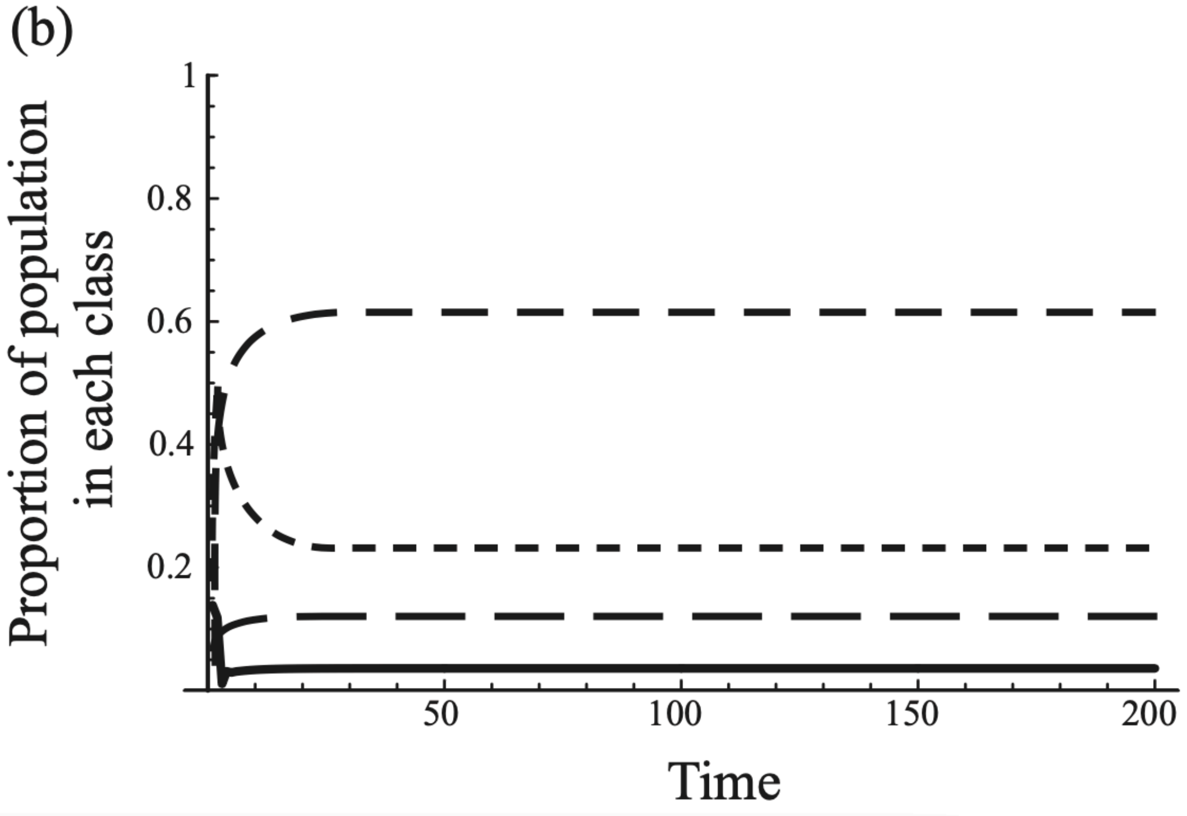
Class structured populations: right whales



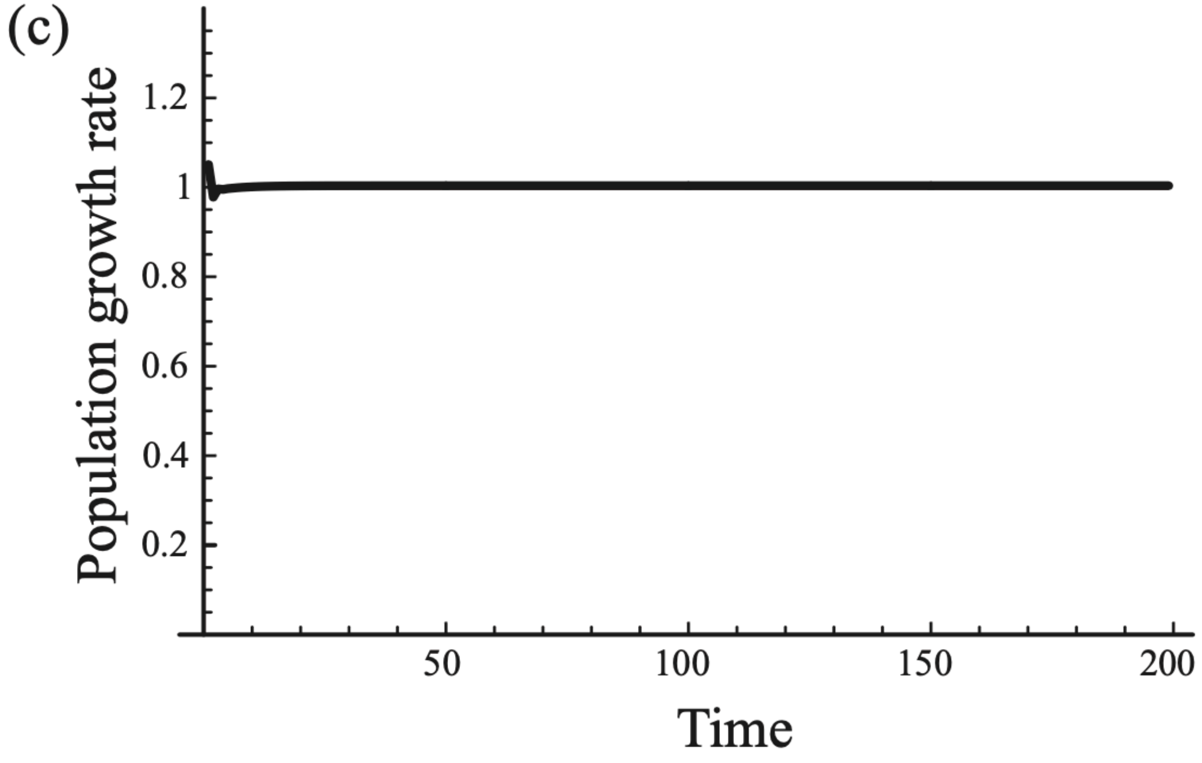
$$\begin{pmatrix} n_C(t+1) \\ n_I(t+1) \\ n_M(t+1) \\ n_R(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & b \\ s_{IC} & s_{II} & 0 & 0 \\ 0 & s_{MI} & s_{MM} & s_{MR} \\ 0 & s_{RI} & s_{RM} & s_{RR} \end{pmatrix} \begin{pmatrix} n_C(t) \\ n_I(t) \\ n_M(t) \\ n_R(t) \end{pmatrix}.$$

Class structured populations: right whales

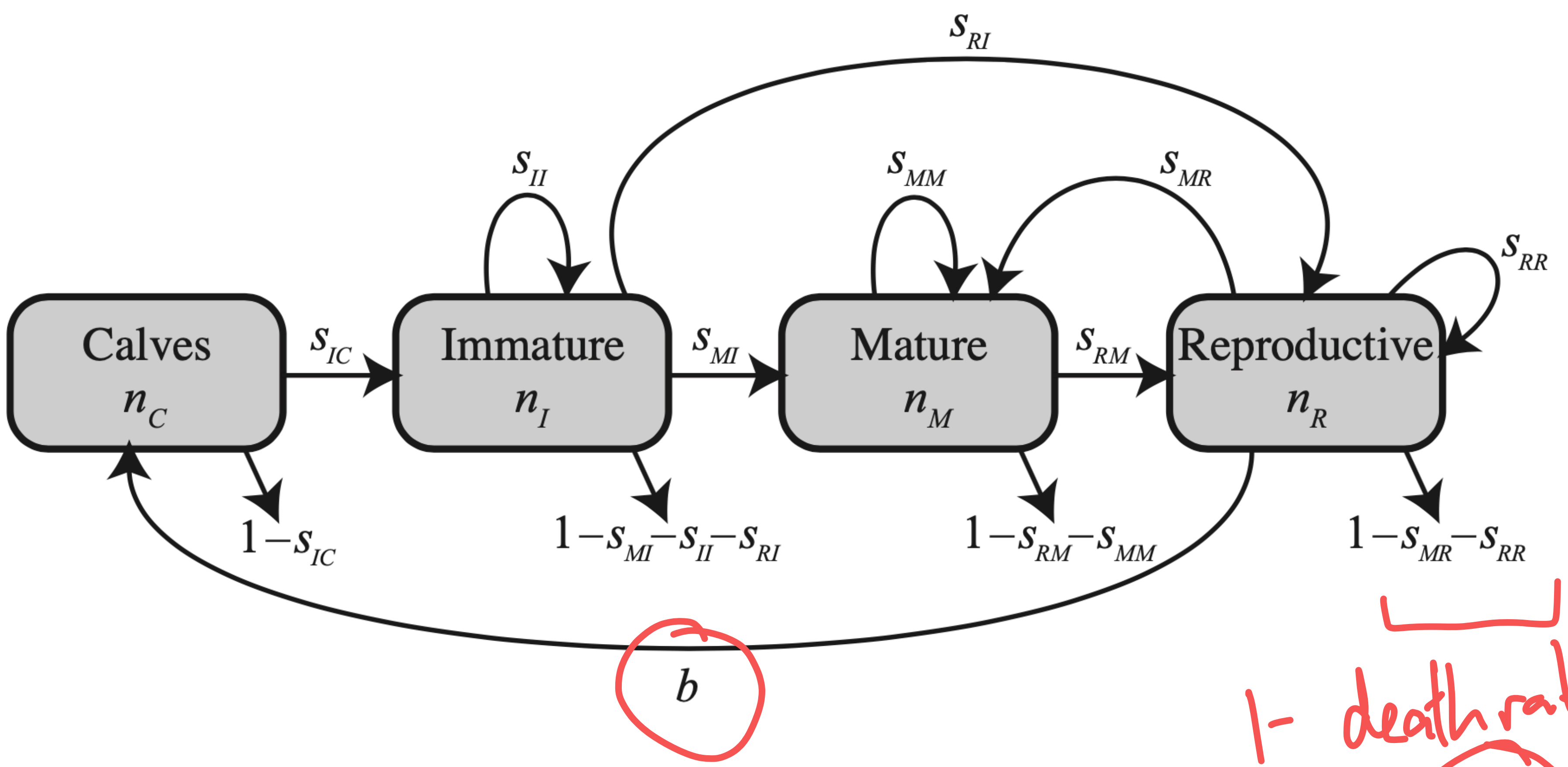




1. What is the **long-term growth rate** of a population?
2. What is the **long-term class structure** of a population?



Class structured populations: right whales



$$\begin{pmatrix} n_C(t+1) \\ n_I(t+1) \\ n_M(t+1) \\ n_R(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & b \\ s_{IC} & s_{II} & 0 & 0 \\ 0 & s_{MI} & s_{MM} & s_{MR} \\ 0 & s_{RI} & s_{RM} & s_{RR} \end{pmatrix} \begin{pmatrix} n_C(t) \\ n_I(t) \\ n_M(t) \\ n_R(t) \end{pmatrix}.$$

1- deathrate of reproductive females.

μ

if $\lambda_1 > \lambda_2, \lambda_3, \lambda_4$

$$\boxed{\begin{pmatrix} n_C(t) \\ n_I(t) \\ n_M(t) \\ n_R(t) \end{pmatrix} = \mathbf{A}\,\mathbf{D}^t\mathbf{A}^{-1} \begin{pmatrix} n_C(0) \\ n_I(0) \\ n_M(0) \\ n_R(0) \end{pmatrix},}$$

1. What is the **long-term growth rate** of a population? λ_1.
2. What is the **long-term class structure** of a population? $\vec{x}_1$.

General rules for class-structured populations

L T G R

1. What is the **long-term growth rate** of a population?

If there exists one eigenvalue larger than others, λ_1

then LTGR is λ_1

L T C S

2. What is the **long-term class structure** of a population?

In scenario above, LTCS would be $\vec{x}_1$

where $M\vec{x}_1 = \lambda_1 \vec{x}_1$ i.e. $\vec{x}_1, \lambda_1$ are an "eigenpair"

3. Which **classes contribute most** to the long-term growth rate of a population.

stay tuned!

Perron Frobenius

Population **transition matrices** have interesting properties:

1. All entries are ≥ 0.
2. The matrix is square.

When these conditions are met, the **Perron-Frobenius Theorem** tells us that:

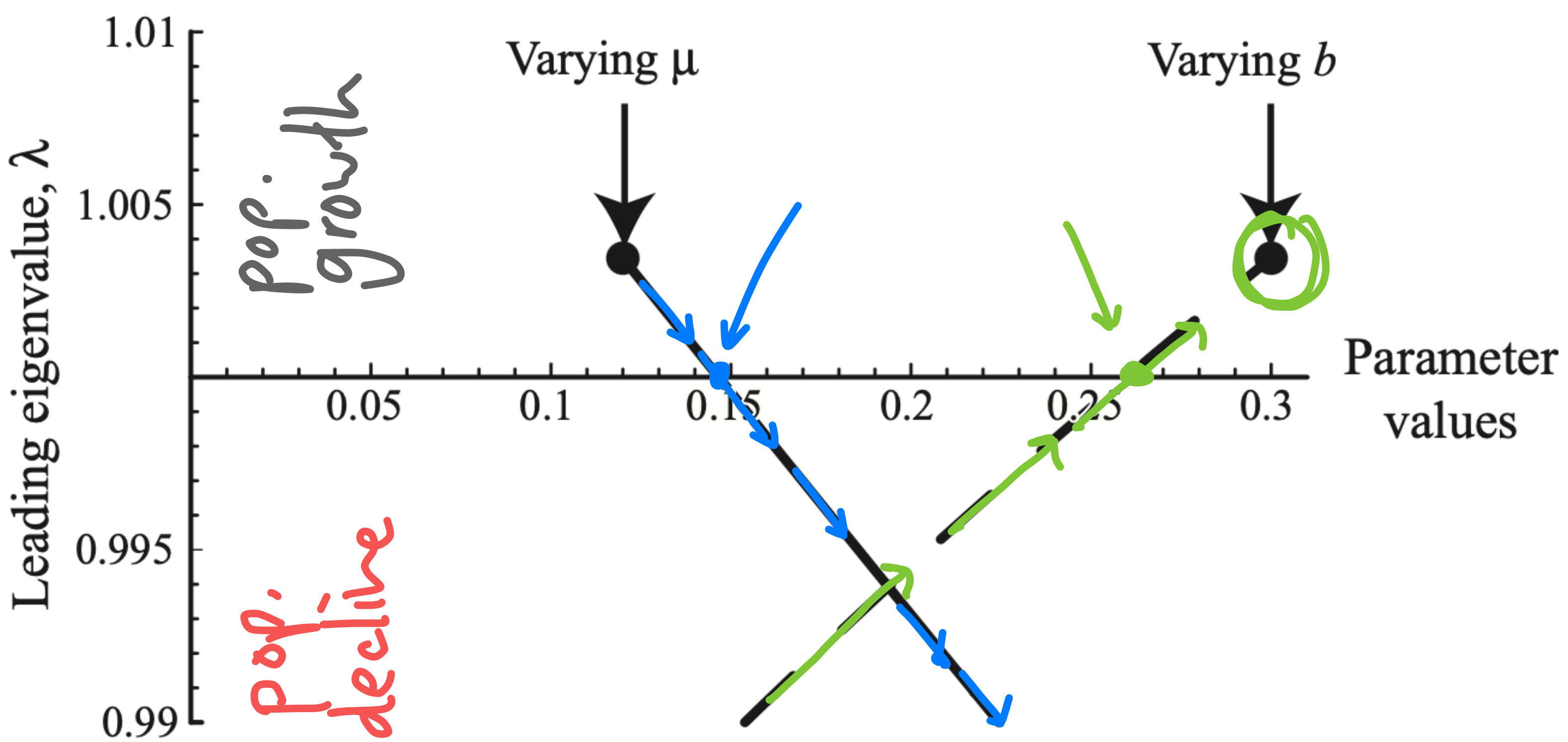
1. The eigenvalue with largest magnitude λ_1 will *never be negative*. → no nonsensical negative growth rates.
2. This eigenvalue will also *always be real*. → no nonsensical complex growth rate.
3. The eigenvector $\overrightarrow{x}_1$ associated with this eigenvalue will *also* be non-negative and real.

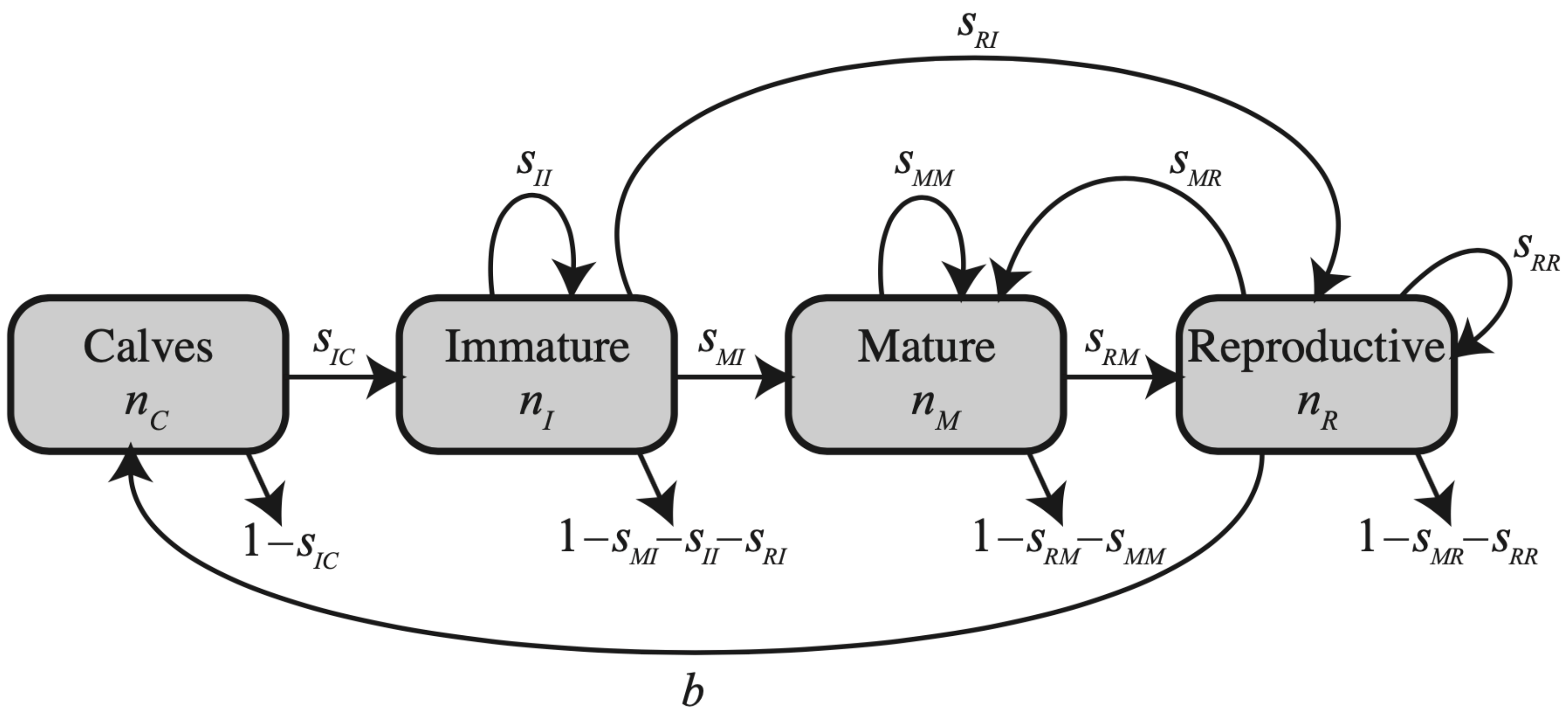
population demographics, long term, will make sense.

This means that we can ask how λ_1 is affected by the model's parameters!

How do parameters affect the leading eigenvalue?

Figure 10.4: The influence of the unknown parameters on the growth rate of the right whale population. The right whale population grows over the long term as long as the leading eigenvalue is greater than one (above the horizontal axis). The solid and dashed lines show how the leading eigenvalue depends on the unknown parameters, μ and b, respectively, holding all other parameters at their values in Figure 10.3. The dots show the leading eigenvalue when $\mu = 0.12$ and $b = 0.3$ as in Figure 10.3.





fecundity b

death rate $\mu = 1 - s_{MR}$

General rules for class-structured populations

$M\vec{x}_1 = \lambda_1 \vec{x}_1$

right eigenvalue

1. What is the **long-term growth rate** of a population?
2. What is the **long-term class structure** of a population? $\vec{x}_1$
3. Which **classes contribute most** to the long-term growth rate of a population.

Alternative phrasing: you are a conservation biologist and you can introduce 1 new right whale. What age whale would be best to introduce, in terms of future population size?

The values of adding population in each bin are called **reproductive values**.

$\vec{y}_1^T M = \lambda_1 y_1^T$

left eigenvalue.

Matrices as machines

$M\vec{x}_1 \longrightarrow$ future.

$y_1^T M \longrightarrow$ past-ish.

Clauset CBIO Bio. Nets.

Network: $\vec{x}_1$ eigenvector centrality. (out-degrees)

$\vec{y}_1$ eigenvector centrality (in-degree)

General rules for class-structured populations

1. What is the **long-term growth rate** of a population?

The **long-term growth rate** of a population is given by the **leading eigenvalue**.

2. What is the **long-term class structure** of a population?

The **stable class distribution** describes the long-term proportion of individuals in each class; these proportions are given by the leading **right eigenvector**.

3. Which **classes contribute most** to the long-term growth rate of a population.

The **reproductive value** of each class is proportional to the **left eigenvector** associated with the leading eigenvalue.

Otto & Day.

- HW5
- EC