

Marine Population Dynamics

OCEA265, UC Santa Cruz

Alexa L. Fredston

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- Alan Hastings' book, "Population Biology: Concepts and Models"
- Hal Caswell's book, "Matrix Population Models"
- Nicholas J. Gotelli's book, "A Primer of Ecology"
- Marc Mangel's book, "The Theoretical Biologist's Toolkit"
- Marissa Baskett's ESP121 course notes (UC Davis)
- Dave Tilman's UCSB course ESM201, for which Alexa was a TA
- chatGPT, which generated a lot of the Quarto code for the math.

Welcome

Introduce yourselves:

- Your preferred name
- What you do at UCSC (your position, research, etc.)

Introduction to population modeling

What models are

Reflect individually: What do you think models are? What comes to mind with that word?

Classes of models:

- Static (e.g., linear regression) *vs.* dynamic (time is a variable; differential or difference equations describe system evolution over time)
- Discrete *vs.* continuous (is any biological data ever in continuous time?)

- Statistical / phenomenological *vs.* theoretical / mechanistic / process-based
- Stochastic (incorporates randomness) *vs.* deterministic (get the same outcome every time)

Structure and content of this class

Structure and content

- The course textbook is Population Biology: Concepts and Methods (Hastings, 2nd edition).
- We meet weekly to work through the math of biological models by hand. I suggest taking notes in a notebook or using a tablet and pencil. You can also generate notes like the ones I'm using with LaTeX (see overleaf.com) or Quarto (see posit.co). Classes will be a mix of lecture and in-class activities, with lots of breaks.
- Problem sets ask you to explore fitting the models we learned to data. You can do this in any software you like. This course is intentionally software-agnostic to allow you to practice skills in whatever language or interface you use in your own research.
- Review grading policy, the rest of the [syllabus](#), and introduce the [course repo on GitHub](#).

On math anxiety

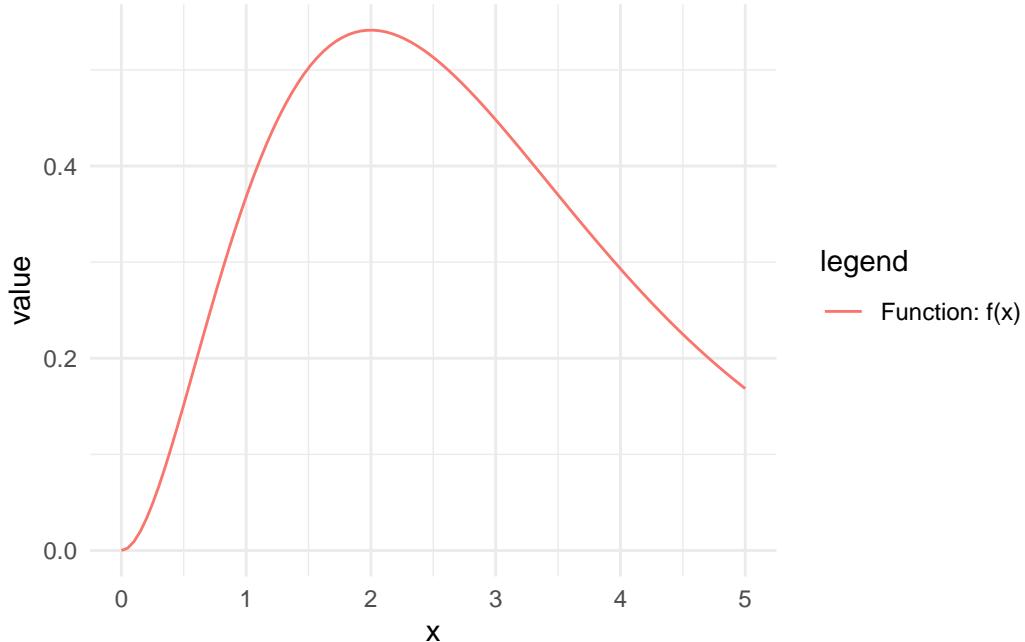
- “A feeling of tension, apprehension, or fear that interferes with math performance” (Ashcroft, 2002)
- Math can initiate physiological responses including increased heart rate and cortisol levels, and neural activations analogous to those from physical pain (Ramirez *et al.*, 2018)
- These responses are also associated with lower math performance, probably because the person is dividing their working memory between the math problem and anxiety-associated thoughts (e.g., about the consequences of failure) (Ramirez *et al.*, 2018)
- Math anxiety is extremely common in higher education and is not a binary classification; many students have some degree of math anxiety (Ramirez *et al.*, 2018)
- Socioenvironmental factors are a primary driver of math anxiety, including home experiences (parental involvement in schooling), exposure to negative framings (“math is confusing”, “I always hated math”), negative classroom experiences (often associated with teachers who also have math anxiety) or assessment outcomes, and students’ “self-concept” (Ramirez *et al.*, 2018)

Calculus refresher

(Drafted by chatGPT, edited by Alexa)

Differentiation

Let's say we have some function that looks like this:



We don't need to do anything to know what the value of $f(x)$ is at any x on this graph; we can already figure that out.

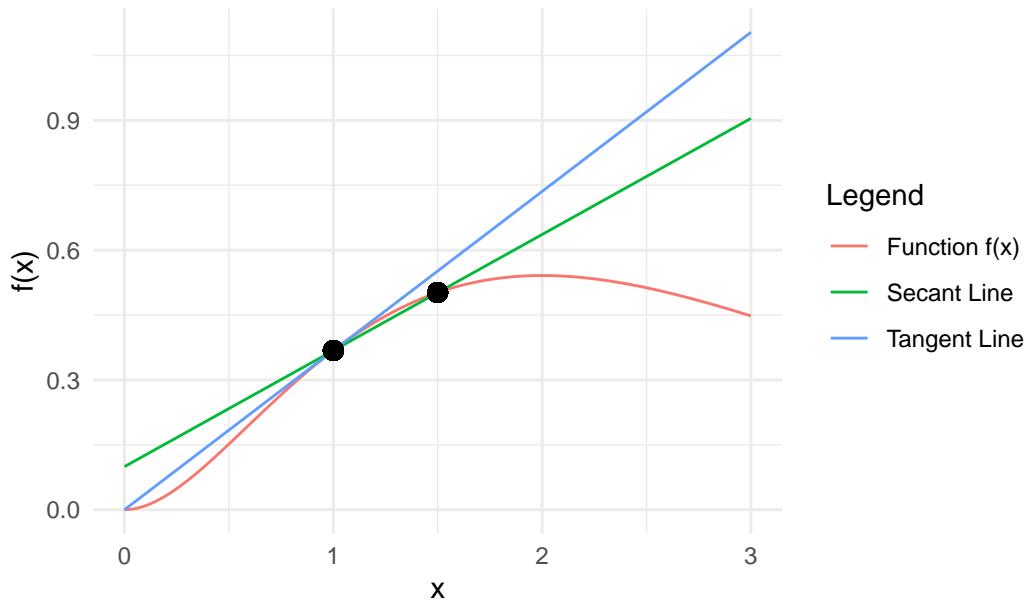
However, we don't currently know what the **rate of change** is in $f(x)$ at any x on this graph. To figure that out, we have to take the **derivative**, via "differentiation". Differentiation describes the rate of change of a function. If $f(x)$ represents a population size over time, its derivative measures the instantaneous rate of change.

We describe this mathematically using the concept of **limits**. These let us calculate the derivative at any x as the slope of a line from x to $x + \Delta x$. We define the derivative as the limit of this slope as Δx goes to 0.

$$\frac{d}{dx}f(x) = \lim_{\Delta x \rightarrow 0} \frac{f(x + \Delta x) - f(x)}{\Delta x}$$

Let's unpack limits a little more. Limits allow us to compute the derivative at any point x by considering the slope of a line connecting x to $x + \Delta x$. The derivative is then defined as the limit of this slope as Δx approaches zero. Let's explore this graphically with a secant line (a line that intersects a curve at two distinct points) and a tangent line (which touches a curve at just one point, and does not cross it).

Graphical Interpretation of Limits and Derivatives



This is a good time to remind you that this course has zero memorization! Don't worry if these terms are unfamiliar or don't stick.

Limits help us graphically understand differentiation, but they aren't always convenient for computation or calculation, because we calculate them one x at a time. Thankfully rules exist to derive a general formula to compute the slope of a function at any x in the function's domain. We're going to hold off on the derivatives refresher though, until it actually comes up in class; knowing the intuition behind what a derivative is will suffice for today.

Integration

Integration finds the total accumulation of a quantity. The integral of $f(x)$ over an interval $[a, b]$ is:

$$\int_a^b f(x) dx$$

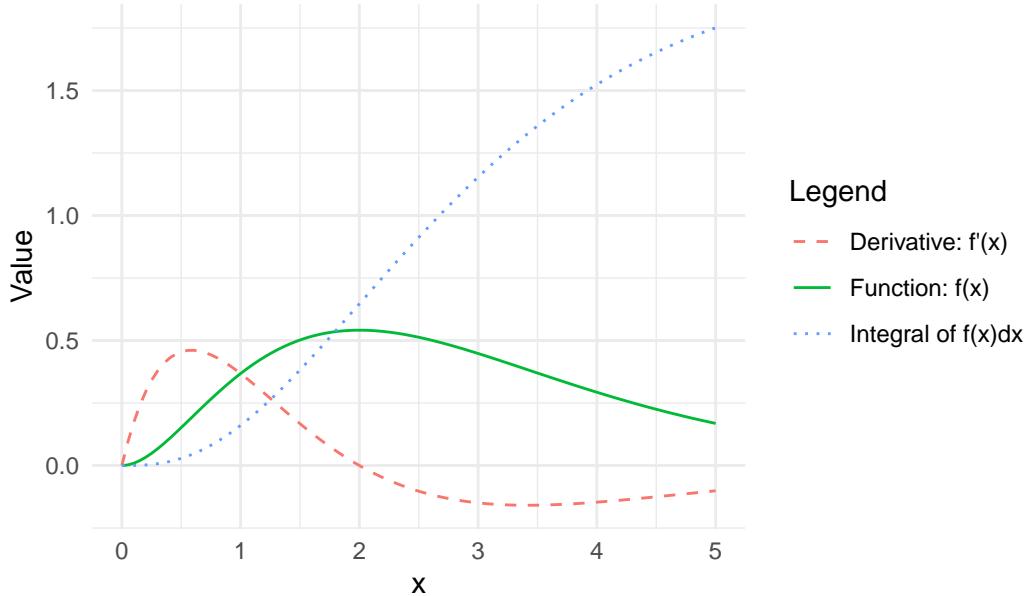
Common Integrals

- Power rule: $\int x^n dx = \frac{x^{n+1}}{n+1} + C$ (for $n \neq -1$)
- Exponential function: $\int e^x dx = e^x + C$
- Logarithmic function: $\int \frac{1}{x} dx = \ln|x| + C$

Graphical interpretation

To visualize differentiation and integration, consider the function $f(x) = x^2 e^{-x}$. The derivative represents the slope at each point, while the integral gives the accumulated area under the curve.

Graphical Interpretation of Differentiation and Integration



BREAK

Density-independent population growth

(Hastings pp1-16)

This is the simplest population model we can write down. It assumes that:

- The rate of births is proportional to the number of individuals present.
- The rate of deaths is proportional to the number of individuals present.

Discuss: What are the implications for this model at small population sizes? At large population sizes?

Here and forever, the population size is going to be denoted by N .

The discrete time case (geometric growth)

This model has separate time steps.

When would we want to use a model like this?

- Non-overlapping generations (e.g., seasonal insects)
- Synchronous and distinct reproductive events (e.g., salmon, annual plants)

For now, let's ignore organisms that live for more than one time step (i.e., no age structure), and just think about something whose entire life cycle happens between t and $t + 1$. Note that we often think of t as a year in discrete-time models, but it is actually in units of *a single generation*. This could be days, weeks, months, seasons, or many years.

All discrete-time models can be stated as:

$$N_{t+1} = F(N_t)$$

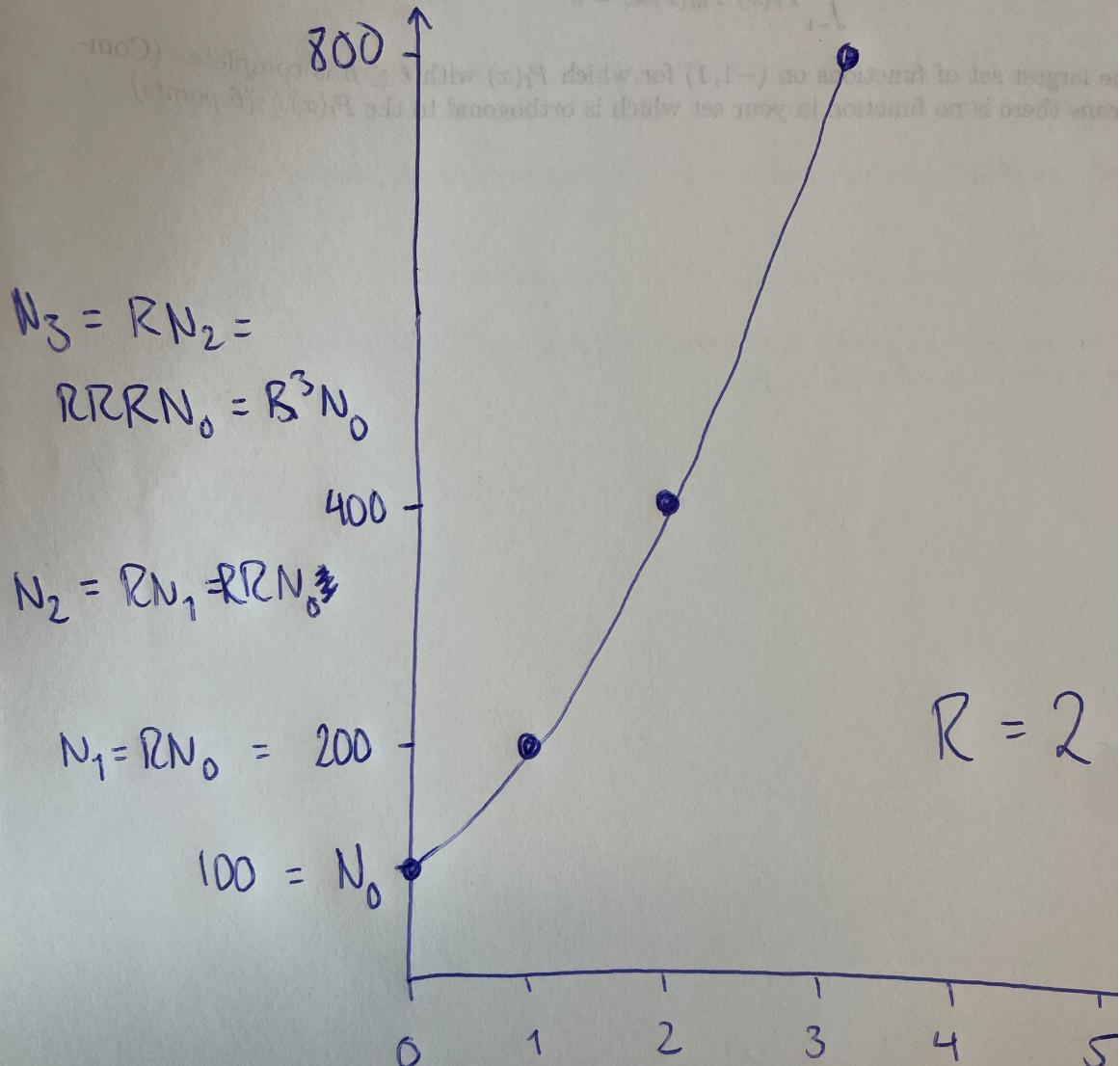
We'll spend a lot of this class talking about all the forms F can take!

The simplest form is a dimensionless coefficient:

$$N_{t+1} = RN_t$$

“Big R” represents the chance of survival *on average* per offspring. You can define $R = B - M$ where B is the average *per capita* birth rate and M is the average *per capita* death rate (mortality). Let's plot out the implications of this model for population dynamics, starting at $t = 0$ with an initial population size (defined as N_0) of 100 and set $R = 2$, with t on the x-axis and N on the y-axis. (This is a really common plot that we'll draw a zillion times in this course.)

(3)



$$N_1 = 2 \cdot 100 = 200$$

This implies a general way to calculate population size at any time step if we know the initial population size R_0 and the average chance of survival per offspring, R :

$$N_t = R^t N_0$$

Based on the example above, what does this imply for population change over time if R is relatively large?

What if $R = 1$?

Draw it out—the population stays constant; for any t , if $R = 1$, then $N_t = 1 \times N_0 = N_0$.

What happens if R is less than 1? **Ask the students to collectively plot** this graph (t vs. x) for $R = 0.5$ and $N_0 = 1000$. We call this “geometric decay” (the case above was “geometric growth”).

$N_t = R^t N_0$ is a **geometric population model**. Remember, this is a discrete-time model assuming that births and deaths are both proportional to N .

This model implies that:

- If $R > 1$, populations will grow unbounded.
- If $R < 1$, populations will go extinct.

Under what circumstances are those reasonable assumptions and implications in nature?

The continuous time case (exponential growth)

Let's deal with one of those statements that is not always realistic: that generations are non-overlapping and reproduction is a discrete event. In many populations, generations are overlapping and reproduction is happening continuously.

Can you think of some examples?

- Most microbes, including plankton
- People

This necessitates a **continuous time model**. Because this isn't broken into time steps, rather than talking about the difference between N_t and N_{t+1} , we'll phrase this model in terms of dN/dt . This is defined as the **instantaneous rate of population change**.

The simplest model of continuous-time population change is:

$$\frac{dN}{dt} = rN$$

There's a new term here: r . "Little r" is also defined as the per-capita average birth rate b minus the per-capita average death rate m , but note that these are all lowercase letters: they're instantaneous rates. (Before they were also averaged over time within the generation t ; that's no longer true here.) Little r is also called the *intrinsic rate of increase* or *intrinsic growth rate*.

This is a really important concept in population biology so let's spend a little more time on the intuition behind r . If dN/dt is in units of population size / time, then dividing both sides of the equation above by N gives us $r = dN/Ndt$. Notice two things: r is a *per capita* rate (N is on the bottom of the equation), and the units of r itself are $1/\text{time}$. So, r is telling us about the per-capita average population change over a really, really, small—instantaneous!—time step.

It would be useful to have an explicit formula for $N(t)$, and $dN/dt = rN$ is simple enough that we can actually solve it for N . Let's integrate this. Assume the initial population size is ($N(0) = N_0$), and we want to find the population size at time (T), which we'll call ($N(T)$).

First, we'll *separate the variables*—put t on one side and N on the other.

$$\frac{dN}{dt} = rN$$

Divide both sides by N (assuming $N > 0$):

$$\frac{1}{N} \frac{dN}{dt} = r$$

Now multiply both sides by dt :

$$\frac{1}{N} dN = r dt$$

Now that we've separated the variables we can integrate both sides. Remember our very brief calculus refresher? What were the common integrals, again?

- Power rule: $\int x^n dx = \frac{x^{n+1}}{n+1} + C$ (for $n \neq -1$)
- Exponential function: $\int e^x dx = e^x + C$
- Logarithmic function: $\int \frac{1}{x} dx = \ln|x| + C$

So if we want to integrate both sides of this equation:

$$\int_{t=0}^{t=T} \frac{1}{N} dN = \int_{t=0}^{t=T} r dt$$

We can use the *logarithmic function* to integrate the left-hand side:

$$[\ln N(t)]_{t=0}^{t=T} = \ln N(T) - \ln N_0$$

On the right-hand side, we evaluate the integral of the constant r with respect to dt (which integrates to a constant, rt) at both values of t . This yields:

$$[rt]_{t=0}^{t=T} = rT - 0 = rT$$

(Why is the integral of any constant (like r) times dt just that same constant times t ? Again, let's think back to what led us to having $r dt$ in the derivative to begin with. We're asking, "What function has a derivative equal to a constant r ?" And the answer to that is, it's a straight line with slope r , so the equation for that line is rt . We'll unpack this more on your homework.)

Putting the two sides back together:

$$\ln N(T) - \ln N_0 = rT$$

Now we want to get $N(T)$ on its own. Recall that $\ln a - \ln b = \ln(a/b)$. In other words, the difference of two logarithms is the same as the logarithm of a quotient. So we can rewrite the above as,

$$\ln\left(\frac{N(T)}{N_0}\right) = rT$$

Now that we have only one logarithm we can exponentiate both sides:

$$\frac{N(T)}{N_0} = e^{rT}$$

or

$$N(T) = N_0 e^{rT}$$

This is the equation for exponential growth in continuous time. We don't actually need "big T" here, since it can be evaluated at any value of t , so it's usually written as $N(t) = N_0 e^{rt}$.

BREAK

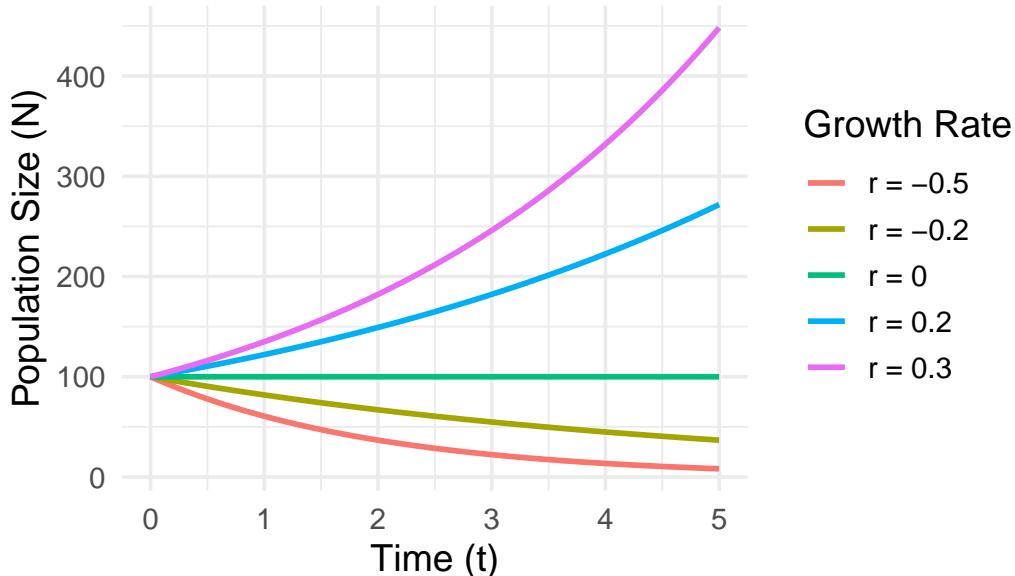
Relationship between continuous and discrete time (r and R)

Since it's a little harder to do exponents in your head, we won't manually calculate the population size in an exponential growth model for different values of r the way we did for the discrete time case, with the exception of $r = 0$. What does that evaluate to?

$$N(t) = N_0 e^0 = N_0$$

Here is the exponential growth curve for some other values of r .

Exponential Growth and Decline for Different r



Let's think back to how this model connects to the discrete-time case. To recap, we started thinking about rates of population change in discrete time:

$$N_{t+1} = RN_t$$

And in continuous time:

$$\frac{dN}{dt} = rN$$

In both cases, we wanted to get a general equation for N . We were able to get this algebraically for the discrete time case:

$$N_{t+1} = N_0 R^t$$

And we integrated the continuous-time case to get:

$$N(t) = N_0 e^{rt}$$

What do these equations—and N and r —have to do with each other *mathematically*? We saw graphically that they result in the same curve shapes, which we called “geometric” in the discrete case and “exponential” in the continuous case.

Question: For what values of R and r respectively do the discrete- and continuous-time models lead to stable population sizes over time?

We can think of e^r and R as being analogous to one another. If we compare the discrete and continuous time equations, we see that they can essentially be substituted for one another. But remember that r is **not the same** as R . To convert instantaneous to time-averaged per capita population change, we need to integrate, which is what e^r does.

In reality, which set of math you use (continuous vs discrete time) depends partly on the system you’re studying and partly on mathematical convenience.

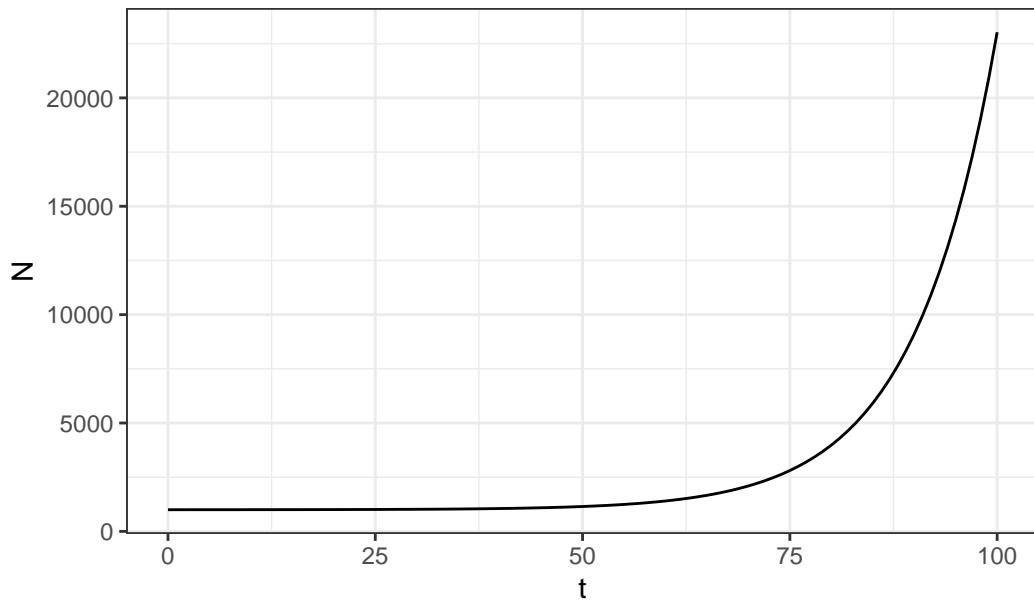
BREAK

Per capita population change in continuous-time exponential growth

We’ve been talking about several quantities: Population size N and its change (dN/dt), and per capita population growth rate (R or r). I want to build your intuition for the relationships between these quantities in the continuous-time exponential model.

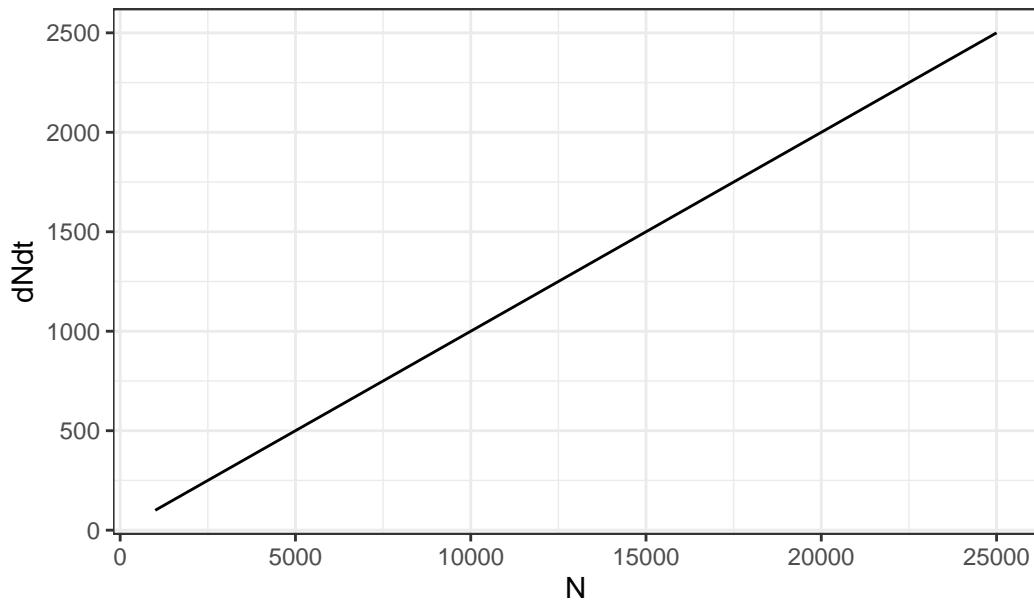
Here’s a graph of N vs t :

Exponential growth in continuous time, $r = 0.1$



Now, let's plot the derivative of this curve:

Population rate of change vs. population size, $r = 0.1$



Talk through the intuition behind this graph—that the population-level rate of change is proportional to the population size. (This is true in both continuous and discrete time.) This was obvious mathematically because we knew $dN/dt = rN$, which is the equation for a line of

slope r , but it isn't always obvious graphically. If we divide both sides of that equation by N , we would get a flat line, $r = dN/Ndt$.

Density-dependent population growth

Hastings pp81-95

Logistic model

Exponential (or geometric) growth are rare in nature. **Discuss: Why?**

The growth of natural populations cannot continue forever. Eventually population growth rates must slow down. **Discuss:** Can we think of examples of this in nature? At what population sizes was the population growth rate (dN/dt) fast *vs.* slow? Sketch N *vs.* t on the board.

Over and over we see a pattern of fast growth when things are rare (i.e., populations are small) and slowing growth as populations get bigger—think of diseases and invasive species.

Reflect individually: Many hypotheses have been proposed for what regulates the growth of populations.

- Changing weather and climate
- Resources, such as food supply
- Interactions with other species: predation, parasitism, competition
- Populations regulate themselves through behavior (territoriality, cannibalism)

The simplest case is one of intrinsic factors (e.g., running out of resources), so we'll start with that one. Earlier we discussed the simplest possible (continuous-time) population model,

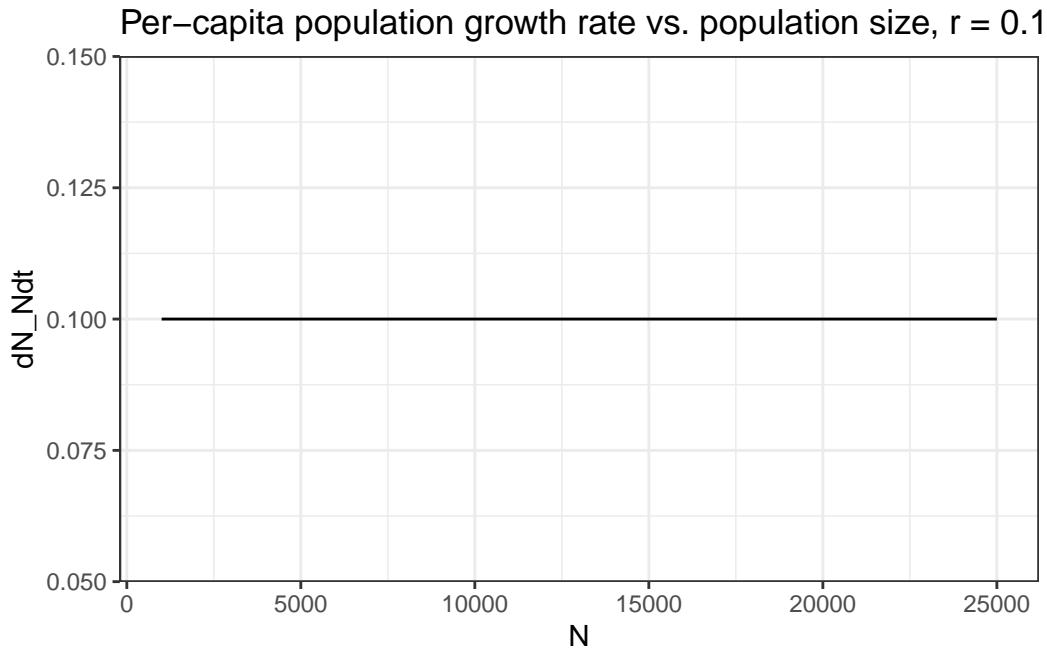
$$\frac{dN}{dt} = rN$$

Now rather than a constant per-capita growth rate r we introduce a function on the right-hand side,

$$\frac{dN}{dt} = N g(N)$$

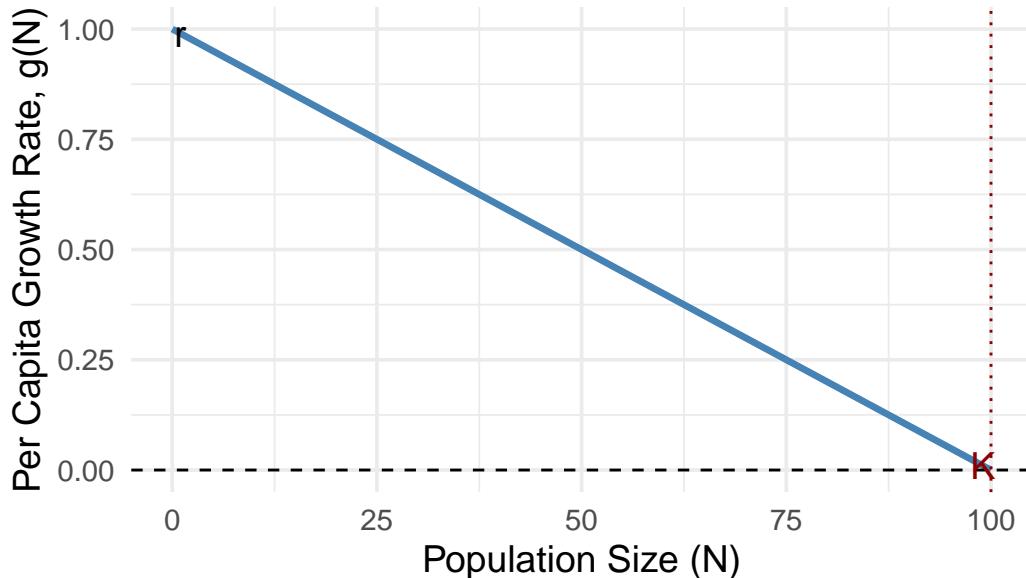
Now the population growth rate is not simply proportional to population size. $g(N)$ still represents the per-capita growth rate, but *it is no longer a constant*. Because this growth rate is now dependent in some way on N , this is called a **density-dependent model**. Exponential growth is a **density-independent model** because r is not dependent on N . Recall that in

the exponential growth model, we said that if we plotted N vs. dN/Ndt , we would get a straight line?



The simplest possible extension to this is that the *per capita population growth rate*, $g(N)$ or dN/Ndt , goes down with N . This suggests that when the population size is higher, the average number of offspring per individual goes down.

Per Capita Growth Rate in Logistic Model

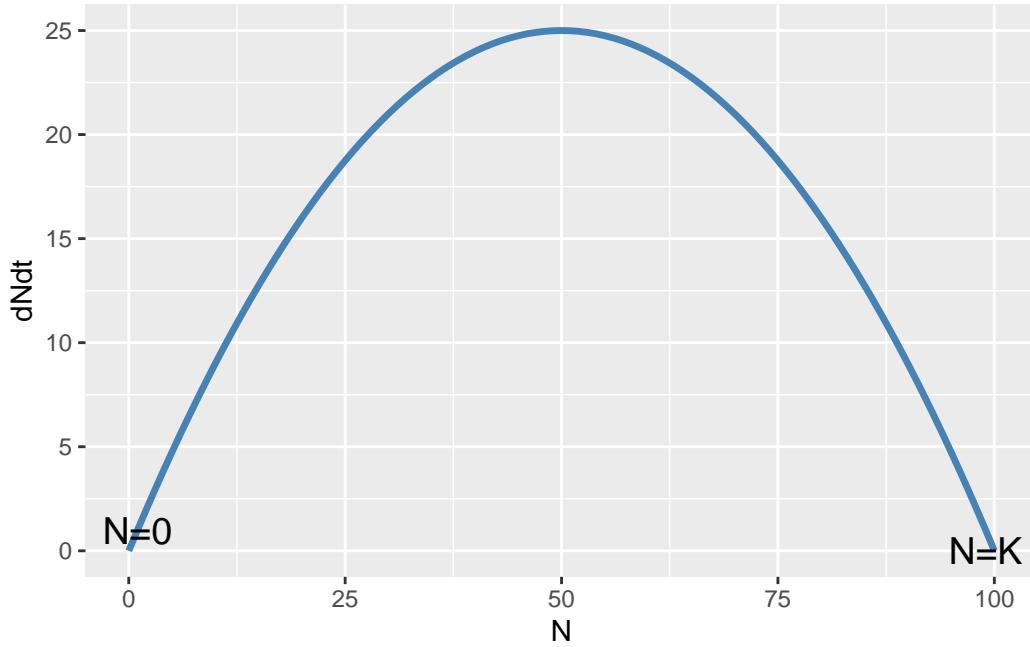


The equation describing this line is,

$$g(N) = r\left(1 - \frac{N}{K}\right)$$

This is the same r as before, but now—as we said previously—the per-capita population growth rate is a function of density as well, and this quantity K . K is a core ecological concept called **carrying capacity**. The intuition behind K is that it's the largest population size the ecosystem can sustain without per-capita population growth becoming negative, i.e., deaths outweighing births.

Before we solve the equation above let's try to intuitively reconstruct the relationship between N and dN/dt —i.e., to multiply the equation for the line above by N . Recall from the exponential model that we are trying to understand three sets of relationships: dN/Ndt vs. N (plotted above), dN/dt vs. N (which we're about to figure out), and N vs. t (which we sketched earlier on the board). **Discuss:** Where are the points when population size is not changing? What is dN/dt at those values? What do we think it is between those values?



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Because $g(N) = dN/Ndt$, if $g(N) = r\left(1 - \frac{N}{K}\right)$, then the equation for the curve above simply multiplies both sides by N :

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

This is the logistic population rate of change in continuous time. We'll pick up next week with stability analyses, integration of the above equation, and discrete-time logistic growth.

Density-dependent population models, continued

Hastings pp81-95

Let's start by putting on the board what we learned last week:

Geometric growth in discrete time— $N_{t+1} = RN$, from which we calculated that $N = N_0 R^t$, and exponential growth in continuous time— $dN/dt = rN$, which we integrated to find that $N(t) = N_0 e^{rt}$. What is the per capita growth rate in each of these models? Answer: in discrete time, it's $R = N_{t+1}/N$, and in continuous time, it's $r = dN/Ndt$. Recall these are both constants! This is basically the only model in which per capita growth is a constant.

We addressed that assumption by making per capita growth conditional on population size, such that $dN/Ndt = r(1 - \frac{N}{K})$. If we multiply both sides by N to get the population growth rate, we get $dN/dt = rN(1 - N/K)$. This is called the logistic model in continuous time. Integrating this equation leads us to:

$$N(t) = \frac{N_0 e^{rt}}{1 + N_0(e^{rt} - 1)/K}$$

If you want to challenge yourself to walk through this integral, it's on p84-85 of the textbook. Before we go any further, let's draw N vs. t , dN/dt vs. N , and dN/Ndt vs. N on the board.

Stability and equilibrium analysis

In this class, our goal is always to connect math to populations. How well does the logistic model describe populations? In some cases, it may describe (and predict!) them quantitatively. But often we don't have the ability to fit this model well, or it fits the data we have but as population dynamics unfold it turns out it wasn't very predictive. What are some ways that we might think a logistic model is fitting well and then learn later we were wrong?

This model may be most useful in making *qualitative* predictions. These are more robust (meaning that they won't change with changes to the model parameters, unlike quantitative predictions). One great way to do this is through equilibrium analysis.

Equilibria are points where the population is *stable*. Mathematically, what does that mean in terms of the quantities we have been calculating and plotting?

If we want to know at what size the population is stable, i.e. $dN/dt = 0$, for any model, we can just set the equation for dN/dt equal to zero, and figure out at what population sizes (N) it solves to 0. Let's try that for the exponential model first:

$$\frac{dN}{dt} = rN = 0$$

This model only has one equilibrium state, when $N = 0$. Does it make sense that an exponential-growth model has no stable population size once $N > 0$?

Let's do the logistic model next:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) = 0$$

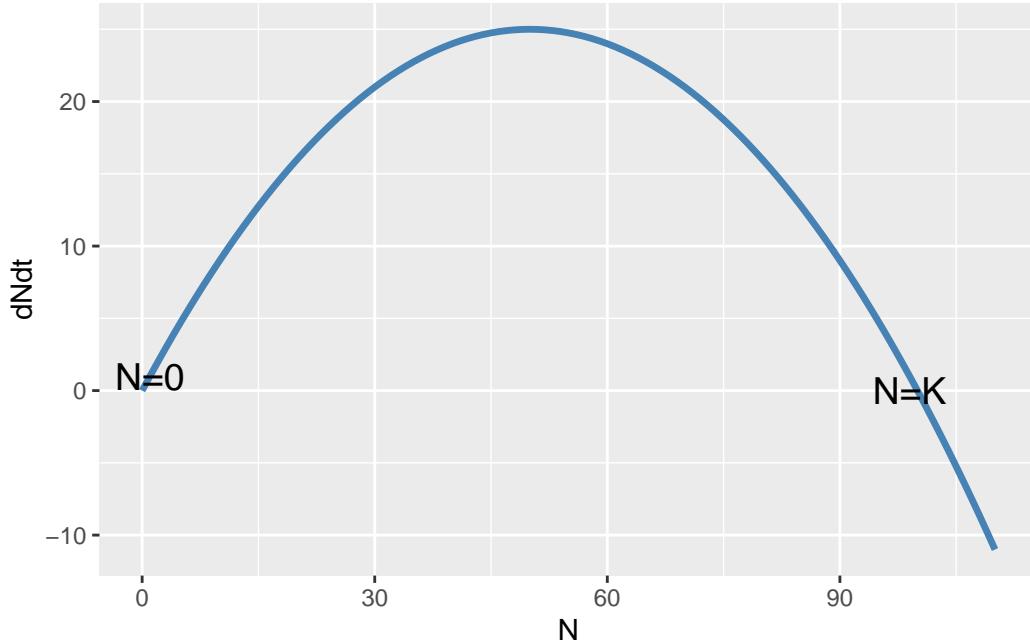
This equation has two solutions, $\hat{N} = K$ and $\hat{N} = 0$. (It's always worth checking if $N = 0$ is a solution; it usually is, because extinct populations are stable!)

In addition to finding this algebraically, we could have figured it out graphically. [How?](#) By graphing dN/dt vs. N and looking for the population sizes at which growth rates are zero.

We're going through this whole exercise to build more intuition about the qualitative predictions of these models. Last week we talked about how the logistic model, qualitatively, predicts rapid *per capita* growth when populations are small, and a leveling-off when populations are big. Equilibrium analysis gives us a different kind of intuition: it helps us understand when populations *are likely to remain where they are*.

Equilibrium analysis has a mathematical meaning: it's when the derivative goes to zero, meaning the system is not changing. But this can happen for a blink of an eye or for a long time. Whether we reach a **stable equilibrium** affects the qualitative behavior we expect. [Intuitively, what do you think is the difference between a stable and an unstable equilibrium?](#)

To find out whether equilibria are stable or unstable, we need to understand the behavior of solutions near the equilibrium point. The most intuitive way to do this is graphically. Returning to our graph:



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If the population is close to $\hat{N} = 0$, what happens to dN/dt ? Does that bring it closer to or further from the equilibrium? [Draw arrows showing that as N increases, dN/dt increases, so small perturbations will drive the system away from that equilibrium, meaning it is unstable.]

If the population is close to $\hat{N} = K$, what happens to dN/dt ? Does that bring it closer to or further from the equilibrium? [Draw arrows showing that as N increases, dN/dt decreases, and as N decreases, dN/dt increases, so small perturbations will drive the system toward that equilibrium, meaning it is stable.]

This conclusion—that the equilibrium $\hat{N} = 0$ is an unstable one, and that $\hat{N} = K$ is a stable equilibrium, is a feature of many models with density-dependence—not just the logistic function. This happens whenever we have the qualitative pattern that *per capita* growth is high when populations are rare, and when we have feedbacks to slow population growth when populations are abundant (i.e., “negative” density dependence.)

Local stability analysis: the graphical explanation

Above we mathematically found equilibria by setting the derivative function $dN/dt = 0$ and solving it. But that didn’t tell us whether the equilibrium was stable or unstable. We can also do that mathematically, but it takes a bit more work. To find an equilibrium we have to set the function, say $G(N)$, equal to 0. To find if the equilibrium is stable, we have to

understand the *slope* of the function near that equilibrium—specifically, whether the slope is negative (stable) or positive (unstable). Keep in mind that these are slope values *at an intercept*, because we’re already at an equilibrium, which means by definition that $G(N) = 0$. The reason that a negative-slope function crossing the intercept creates a stable equilibrium is that, if N goes down a little (below \hat{N}), suddenly the function is positive and brings the population back up. Conversely, if N goes up a little, suddenly the function is negative and brings N back down. The inverse is true for a positive-slope function crossing the intercept (and creating an unstable equilibrium).

Local stability analysis: the mathematical explanation (optional)

The more mathematical way to do this is to actually calculate the slope of the derivative function $G'(N)$ and ask whether it is negative or positive at different equilibria. We can do this for any population model in two steps (finding the equilibria and then testing them for stability). We’re going to walk through this in great detail here because you can build a lot of intuition about stability from the logistic model, which is relatively straightforward. In future models you may not do all the math but this will help you understand the relationship between the population model and the stability of its equilibria.

We begin, again, by setting the derivative equal to 0—for convenience we’re going to call it $G(N)$ and say that the values of N that give equilibria (i.e., $G(N) = 0$) are \hat{N} . So, we’re looking for:

$$G(\hat{N}) = 0$$

We already identified the equilibria for the logistic model earlier ($\hat{N} = 0$ and $\hat{N} = K$). Next, we want to understand the dynamics of $G(N)$ when it is close to \hat{N} . We use a similar approach as we do for derivation: we think about the value of $G(N)$ very close but not exactly at \hat{N} , and try to understand its behavior as we approach \hat{N} . Let’s define a new quantity n , defined as the *deviation from the equilibrium in units of N* : $n + \hat{N} = N$.

We want to understand how n changes with time. That sounds like a derivative! Let’s differentiate both sides of that equation, $n + \hat{N} = N$. Since \hat{N} is a constant, the left- and right-hand sides of the equation above have the same derivative:

$$dn/dt = dN/dt$$

And recall that since we defined $G(N) = dN/dt$ and $x + \hat{N} = N$,

$$dn/dt = G(N) = G(n + \hat{N})$$

We really just want to understand the dynamics of $G(N)$ when $N = x + \hat{N}$. We can approximate the value of the population size equation, $G(N)$, at this value using a *Taylor series*. A Taylor series allows us to approximate any function at a single point. As Hastings (p55) says, “any function $f(x)$ can be approximated near the value x_0 using a *Taylor series* as $f(x_0)$ plus the difference between x and x_0 multiplied by how much the function f changes as its argument, x , changes:”

$$f(x) \approx f(x_0) + (x - x_0) \frac{df}{dx} \Big|_{x=x_0}$$

In our applications, $f(x_0)$ is always an equilibrium point that corresponds to a known value of N . Let’s try to re-write the equation for the Taylor series above in our use case.

$$G(\hat{N} + n) \approx G(\hat{N}) + n \frac{dG}{dN} \Big|_{N=\hat{N}}$$

In words, this equation is telling us that the rate of population growth a little bit away from the equilibrium value can be approximated by the rate of population growth at the equilibrium value plus an extra term, calculated by multiplying the distance from equilibrium by how fast the function is changing when it is close to the equilibrium value.

Let’s substitute in the actual equation for the rate of population change in the logistic model:

$$G(N) = rN(1 - \frac{N}{K})$$

Let’s deal with the easiest part of our Taylor series first. We know that at \hat{N} , the population is at equilibrium, so $dN/dt = G(N) = 0$. (You can also convince yourself of that by substituting 0 into the logistic growth equation above.) This simplifies our Taylor series down to:

$$G(\hat{N} + n) \approx n \frac{dG}{dN} \Big|_{N=\hat{N}}$$

Next we’ll figure out that weird term on the right. What is dG/dN ? Well, that sounds a lot like the derivative of a function called $G(N)$ with respect to N . No problem! We can find the derivative of that function, $rN(1 - N/K)$. Let’s rearrange it to look more like a polynomial:

$$G(N) = rN - \frac{rN^2}{K}$$

Now we can totally take the derivative of this. The derivative of rN with respect to N is just r , since r is a constant. To calculate the second term, let’s separate out N^2 : $d/dN(N^2 \times R/K)$. The derivative of N^2 is just $2N$, so that term becomes $2rN/K$.

$$G'(N) = dG/dN = r - \frac{2rN}{K}$$

Now, we're ready to calculate the Taylor approximation at both equilibria. Let's substitute the equation we just derived for dG/dN :

$$G(\hat{N} + n) \approx n \frac{dG}{dN} \Big|_{N=\hat{N}} \approx n \left(r - \frac{2rN}{K} \Big|_{N=\hat{N}} \right)$$

Let's start with $\hat{N} = 0$. In this case, we get:

$$G(\hat{N} + n) \approx rn$$

This is positive, implying it is an **unstable equilibrium**. Next, we want $\hat{N} = K$:

$$G(\hat{N} + n) \approx n \left(r - \frac{2rK}{K} \right) = n(r - 2r) = n(-r) = -rn$$

This is negative, implying it is a **stable equilibrium**.

Local stability analysis: the mathematical shortcut

You can generalize this procedure of mathematical stability analysis by simply saying that we want to calculate the slope of $G'(N)$ at a small deviation from equilibrium, $n = N - \hat{N}$. We can approximate $dN/dt \approx \lambda n$, where

$$\lambda = \frac{dG}{dN} \Big|_{N=\hat{N}}$$

If λ is positive the equilibrium is unstable, and it's stable if negative. In other words, all you need to do is get the equation for the derivative of the population growth function and evaluate it at \hat{N} . (Hastings, 91: “The rate of return to the equilibrium, or the rate at which the system moves away from the equilibrium, is determined by λ .”) The reason this works is the Taylor expansion we walked through, but in practice you'd mostly use the equation above—or the graphical interpretation—to evaluate stability.

Here's how that would have looked for the logistic model:

$$G(N) = dN/dt = rN(1 - N/K)$$

Restating the equation as $rN - rN^2/K$ and taking the derivative:

$$G'(N) = dG/dN = r - \frac{2rN}{K}$$

Plugging in 0 for N gives you $G'(N) = r$, and plugging in K gives you $G'(N) = -r$.

Extensions to harvested populations

One of the remarkable things about population modeling is that it really underpins a lot of how we manage ocean resources—from marine spatial planning (we’ll get to that in the metapopulations lecture) to fisheries management.

Discuss: What would sustainable fisheries mean in quantitative terms? What do we want the terms we’ve learned about so far to be or not be? Are we trying to maximize or minimize something? If so, what quantity?

Maximum sustainable yield in a logistic model (constant harvest)

Let’s assume we have a fish population that actually follows the logistic growth model. If we imagine subtracting a set quota of fish every year, H , then

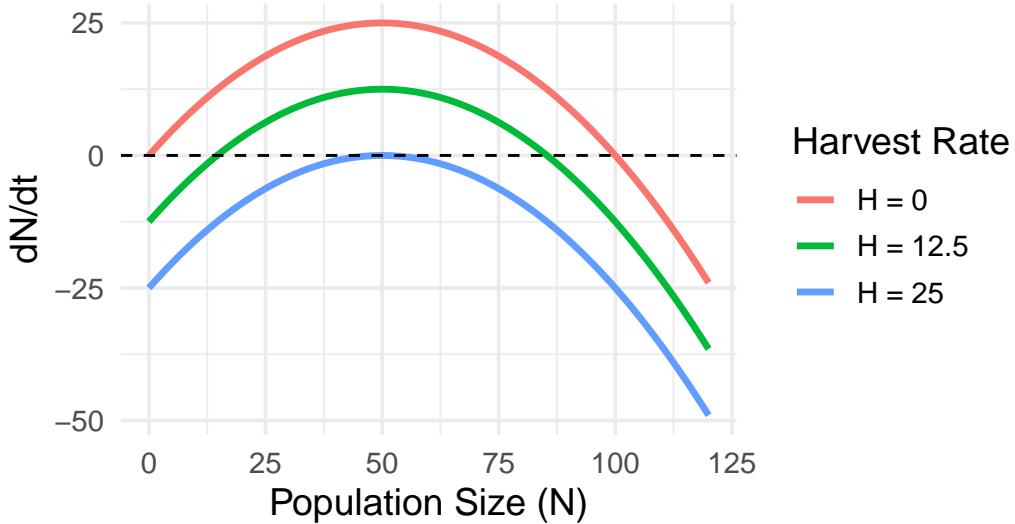
$$\frac{dN}{dt} = rN(1 - N/K) - H$$

How would harvest affect our graph of dN/dt vs. N ?

Start out by drawing the curve with no H and then a moderate H . Discuss the equilibrium points and whether they are stable or unstable. Then add the line for $H = H_{max}$. May want to draw this with H bringing up the x-axis rather than bringing the curve down.

Logistic Growth With Varying Harvest Rates

$H_{max} = 25$ occurs at $N = K/2 = 50$



Is the equilibrium at $H = H_{max}$ stable or unstable? Let's use our rule of thumb previously to figure this out.

$$G'(N) = dG/dN = r - \frac{2rN}{K}$$

Because $H_{max} = K/2$, we can state:

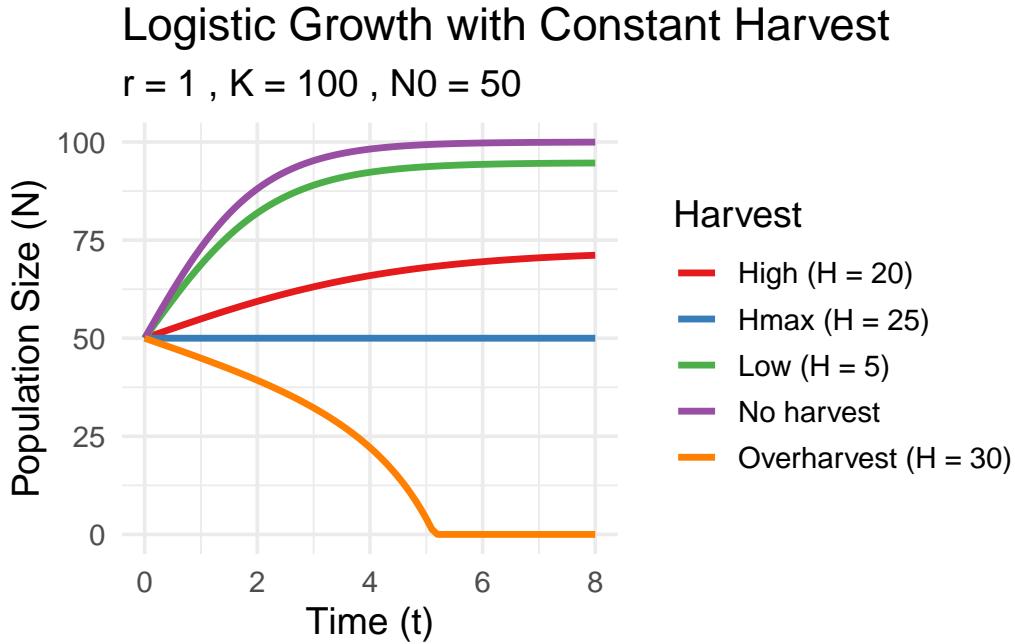
$$r - \frac{2rN}{K} = r - \frac{2r \times K/2}{K} = r - r = 0$$

Zero! We didn't have a rule of thumb for this above. We know that at this point, the first derivative of population size dN/dt or $F'(N)$ is zero (because we're at the x-intercept), and the second derivative dG/dN or $G''(N)$ or $F''(N)$ is... also zero—meaning the slope is flat. In math this is called a “degenerate case” because the system is neither classically stable or unstable. But we can figure out the answer graphically. Let's call $H_{max} = 25$ fish/year and $K = 100$. Then at H_{max} , $N = 50$. What happens if we slightly overshoot—meaning we harvest 26 fish by accident? Then dN/dt becomes negative—in other words, the population's natural rate of increase is less than H_{max} . What happens if we harvest 24 fish? That essentially shifts the curve upwards by 1—so you are back in the land of two equilibria, a stable one at higher N and an unstable one at lower N . This is a *saddle-node bifurcation*: it is stable on one side, and unstable on the other. (We can also see this graphically at the top of the parabola.)

This point is *an optimal harvest level from an economic standpoint* because it maximizes revenue by balancing production (of the fish stock) with returns (of harvest). There is no

mathematical solution that yields greater yearly harvest. However, **it is not stable**, and is extremely sensitive to any level of overharvesting. Roughgarden and Smith (1996) wrote, “Maintaining the stock at the optimal size... is like balancing a marble on top of a dome.” **What are some other reasons why this might not be the most realistic or wise approach to fisheries management?**

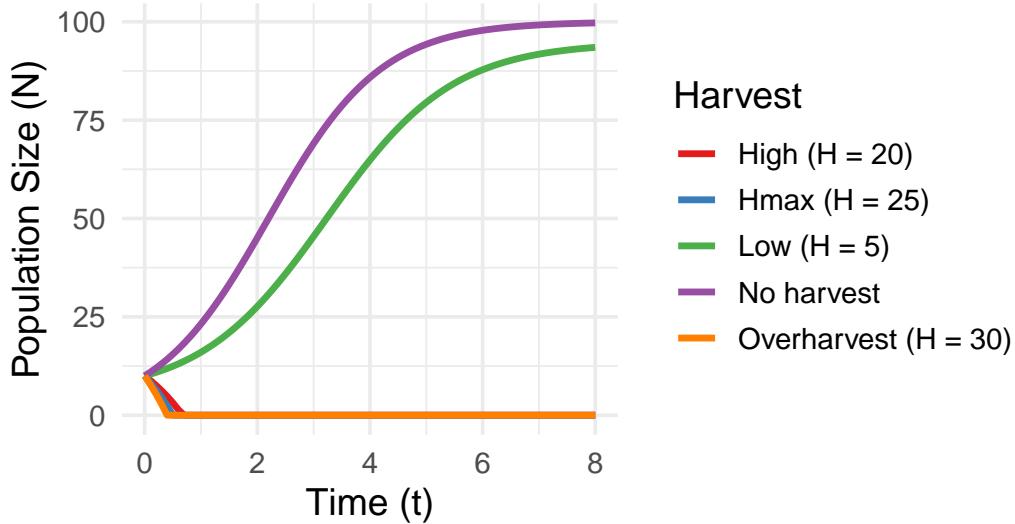
To emphasize this point, here are some plots of N vs. t in a logistic-growth, constant-harvest scenario with different levels of H . Let’s start by assuming we are already at $K/2$ (i.e., $N_0 = K/2$):



What if we draw the same curves with $N_0 = 0$?

Logistic Growth with Constant Harvest

$$r = 1, K = 100, N_0 = 10$$



Alternatives to MSY management (constant effort)

Are there more robust ways to achieve sustainable yields than setting harvest quotas equal to the maximum dN/dt ? An alternative to a constant harvest rate (measured in fish per unit time) is a constant effort model (still measured in units of fish per time, but now a dynamic equation). Here, harvest is proportional to population size and **effort** (the intensity of fishing, e.g., hours on the water, number of nets deployed, etc.)

Instead of

$$\frac{dN}{dt} = rN(1 - N/K) - H$$

Where H was a constant rate, we now have:

$$\frac{dN}{dt} = rN(1 - N/K) - qEN$$

Where N is the population size, q is a catchability coefficient (more on this later), and E is effort. Wait—but shouldn't this still be a rate? Let's work through the units and intuition of these different parameters.

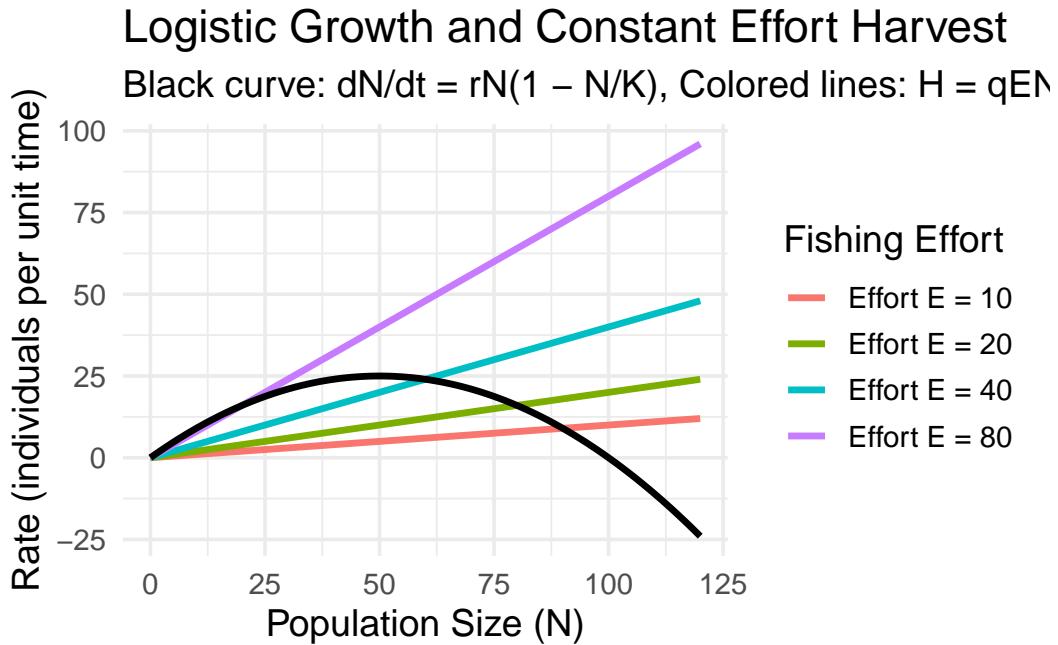
The unit of N is individuals. The unit of E is effort; something like boats, days, permits, traps, etc. **For this to end up in the same units of individuals per time, what are the units of q ?**

q is measured in $1 / (\text{effort} \times \text{individuals} \times \text{time})$. Here, it's a scaling constant that translates the fishing effort into the number of fish that will actually be caught.

So q is a constant here. Since this is a “constant effort” model, E is also a constant! It tells us that regardless of how many fish are in the ocean, the fishing industry will do the same thing to try to catch them. Is this a more or less realistic model than the constant harvest model, above?

But because N is not a constant, harvest here (qEN) is now a dynamic equation. What form would you expect this equation to take?

Let's draw it on top of our now-familiar curve for dN/dt vs. N in the logistic model. For moderate levels of E , where are the equilibria? Which are stable and which are not?



For moderate levels of effort, aside from the trivial equilibrium of $N = 0$ (no fish = no growth), there is only one other equilibrium, and it is stable. If population size exceeds harvest, then the population will grow up to the point where the diagonal crosses the curved line. If harvest exceeds population growth (i.e., if you go further up the constant effort line), then population size will go down, and effort will also go down. Let's explore this mathematically by writing the equation for this model and setting it equal to 0.

$$0 = rN(1 - N/K) - qEN = rN - rN^2/K - qEN = N(r - rN/K - qE) = N(r(1 - N/K) - qE)$$

What are the solutions to this equilibrium? As we said above there is one where $N = 0$. To find the other, we start with

$$qE = r(1 - N/K)$$

and solve for N:

$$qE/r = 1 - N/K$$

$$N/K = 1 - qE/r$$

$$\hat{N} = K(1 - qE/r)$$

When does this yield a stable equilibrium? Well, let's take the derivative of (dN/dt) and plug in our equilibrium value, \hat{N} .

$$G(N) = rN(1 - N/K) - qEN = N(r - qE) - N^2(r/K)$$

$$G'(N) = r - qE - 2N(r/K)$$

Plugging in \hat{N} ,

$$G'(\hat{N}) = r - qE - 2(K(1 - \frac{qE}{r}))(\frac{r}{K}) = r - qE - 2r(1 - \frac{qE}{r}) = r - qE - 2r + 2qE = qE - r$$

Great! But now ... is $qE - r$ positive or negative? **What is the intuition behind the difference between these two numbers?** Recall that r is the intrinsic growth rate or the maximum per capita growth rate, which dN/Ndt approaches when N is small. qE is in the same units and represents the harvest rate per capita.

So, under what circumstances is this a stable equilibrium? It's when $qE < r$, meaning that the per capita harvest rate never exceeds the population's intrinsic growth rate.

Let's go back to our graph of constant effort and draw a really high effort rate. **Does this ever have a stable equilibrium?** You can see that it does not graphically, because it never intersects the growth function when it has a negative slope (meaning that $G'(\hat{N})$ would be negative).

So you know, this “constant effort” model has a name in fisheries: the Schaefer model. As Marc Mangel wrote in the Theoretical Ecologist’s Toolbox (p215), “The Schaefer model involves a single variable $N(t)$ denoting the biomass of the stock, logistic growth of that biomass in the absence of harvest, and harvest proportional to abundance.” So—just like the MSY concept in logistic growth—this model is actually being used in natural resource management.

Discuss: What else might cause overfishing or collapse of a harvested population that isn't captured here?

Other forms of density dependence in continuous time

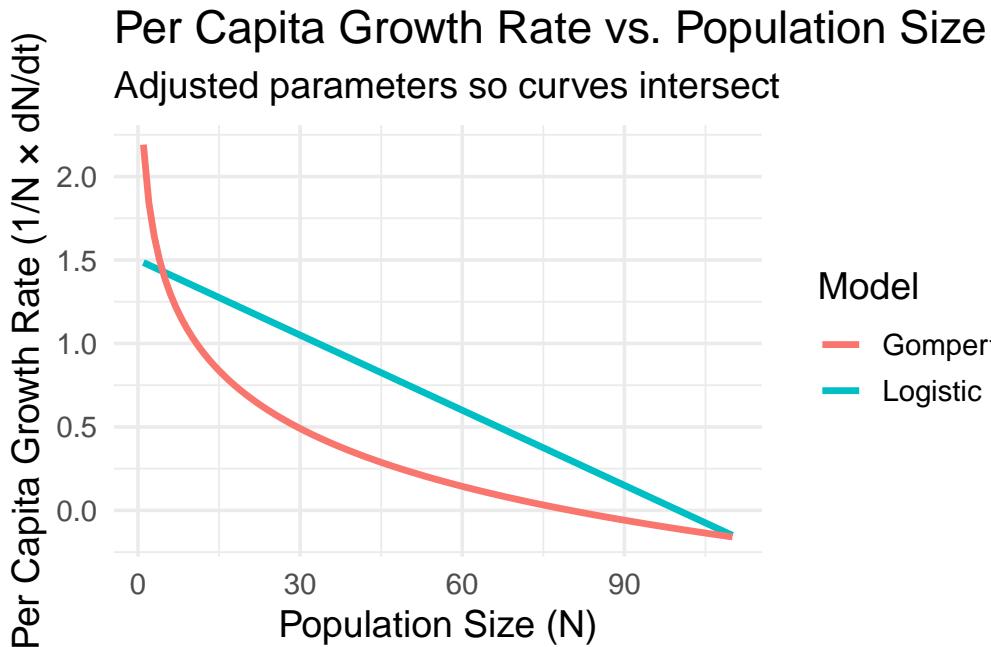
We've been working a lot with plots of dN/dt vs. N . But recall that we usually think about three plots: N vs. t , dN/dt vs. N , and dN/Ndt vs. N . We're going to revisit the latter. Recall that this was a straight, horizontal line in the exponential, continuous-time model, and it was a straight, sloping line in the logistic, continuous-time model. This represents an assumption that density dependence is linear: i.e., that as N increases, the density-dependent term ($1-N/K$) decreases linearly from 1 (at $N=0$) to 0 (at $N=K$). This implies that per capita growth slows down at a constant rate as populations increase.

Gompertz model

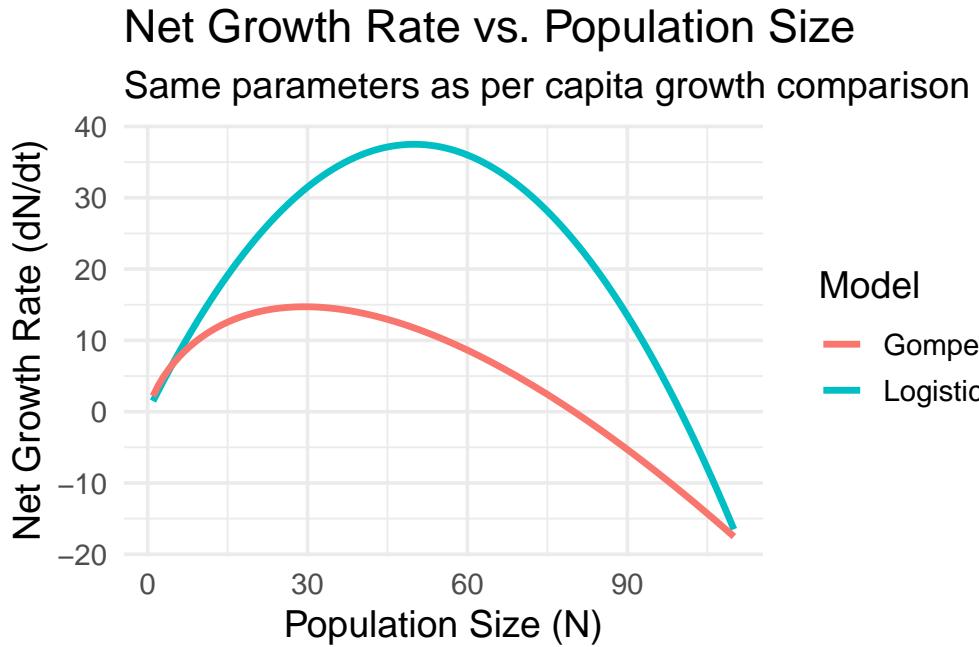
This is an easy thing to modify, because in reality, we might expect this relationship to be nonlinear: maybe per capita growth is not super sensitive at low N , and then drops steeply at high N . Let's try this equation instead:

$$dN/Ndt = r \ln(K/N)$$

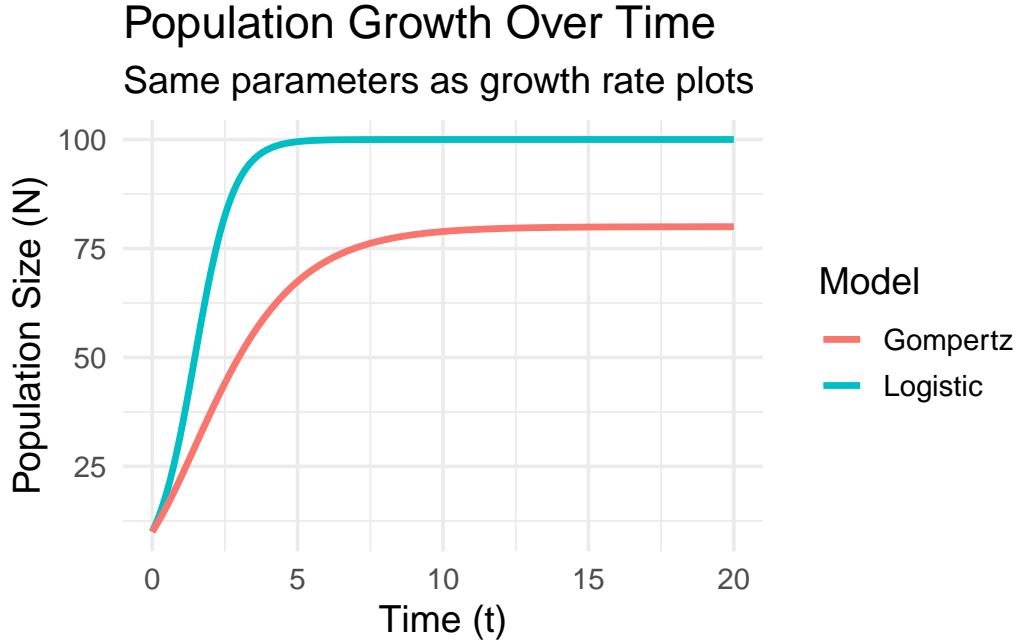
(Because $\ln(A/B) = -\ln(B/A)$, you could also restate this as $-r \ln(N/K)$, if you want to compare it more directly to the slope we had before with K in the denominator.)



We said earlier that the Gompertz model was going to start off with gradual population growth and then show steeper density dependence at high N . Let's plot dN/dt vs. N to explore this.



And finally, N vs. t .



Note that the shape of these curves relative to one another is totally dependent on the parameter values. One K may be higher than the other, depending on parameters. The thing to

remember about the Gompertz model is basically just that the relationship between per capita growth rate and population size is nonlinear, which may fit some data and some models better. If you work in fisheries and you hear someone mention a Gompertz model, just understand it is a density-dependent, continuous-time model that has a slightly different formulation than the logistic.

Positive density dependence

All of the density dependence we've been talking about so far is technically called *negative density dependence*. It's confusing to remember which is which, but think of it this way: is the relationship between population size and average offspring (per-capita population growth rate, dN/Ndt) positive or negative in the logistic model?

There's another way that density can interact with per-capita population growth rate. Think about abalone in California. All seven of our abalone species are endangered (six are critically endangered). These were massively depleted by humans because they are really easy to access and harvest. Disease, warming, heatwaves, and kelp loss have also negatively impacted these species.

Abalone are broadcast spawners. They have separate sexes, so the eggs and sperm need to meet in the water. If there are too few of them, this won't happen and we'll see a *recruitment failure*—when reproduction fails to lead to a new generation of an ecologically meaningful size.

How would this affect the plot of N vs. dN/Ndt in the logistic growth model?

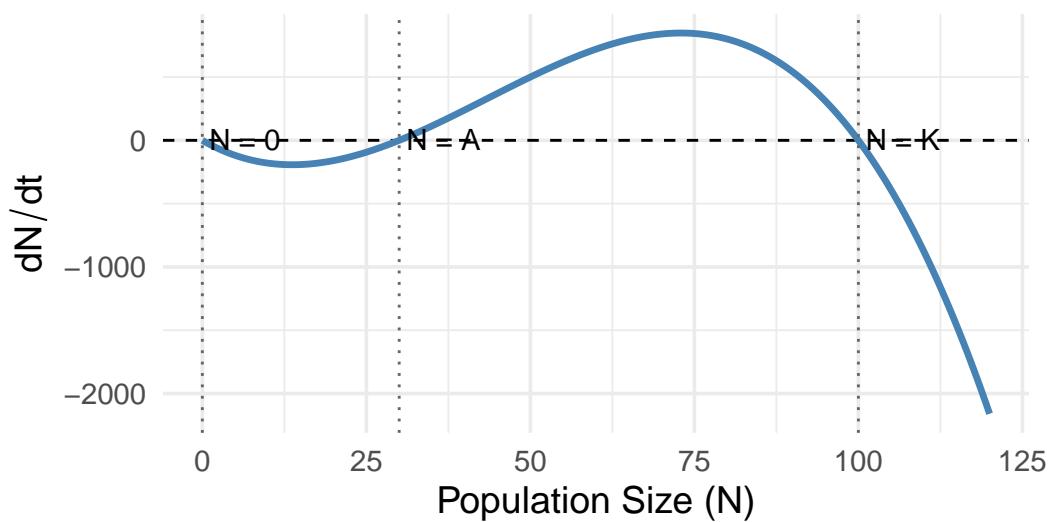
We can model this effect by introducing a new parameter into the *continuous-time* logistic growth equation, A (this stands for **Allee effect**, another word for this form of positive density dependence.) Then the population growth rate is given by

$$dN/dt = rN(N - A)(1 - N/K)$$

Let's start by finding the equilibria of this model. Because it's a product of three terms, we can say from looking at it that it will be equal to zero if any one of the three terms is zero. The first equilibrium is when $rN = 0$; because r is a constant, that means $\hat{N} = 0$. The second is when $N - A = 0$, so we also have $\hat{N} = A$. Finally, if $(1 - N/K) = 0$, we get $\hat{N} = K$.

To figure out if these equilibria are stable, let's graph the equation above.

Growth Rate with Allee Effect: $\frac{dN}{dt} = rN(N - A)$

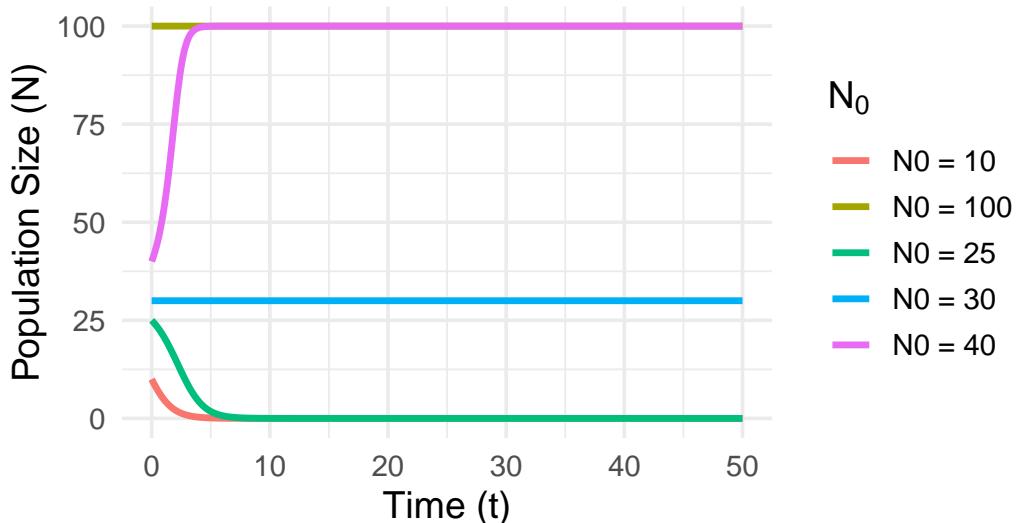


Graphically, which equilibria are stable and which are unstable?

Take a couple minutes to think and draw: What do you think the graph of N vs t will look like for a few different values of N_0 ?

Population Trajectories under Allee Effect

Different initial population sizes relative to Allee threshold



Time lags and density dependence

One criticism that would be very valid of all the models we have discussed so far is that they are too “neat.” You all plotted data of an actual system this week, and saw that it is almost certainly much more dynamic than these smooth curves. The textbook goes into more detail about criticism of the logistic model, which mostly centers around it being very difficult to quantitatively prove, partly because it’s hard to know if a stable equilibrium has been reached when looking at real data, and partly because our ability to estimate the exact parameters (of any density-dependent model—logistic, Gompertz, etc.) is limited.

Delayed logistic

(Hastings pp 92-96) Most of the rest of the course will be adding different forms of complexity to better approximate real systems. Probably the next simplest case is a population that does not reach a single stable equilibrium, but instead oscillates around K . This is common in microbes and insects, especially in laboratory studies.

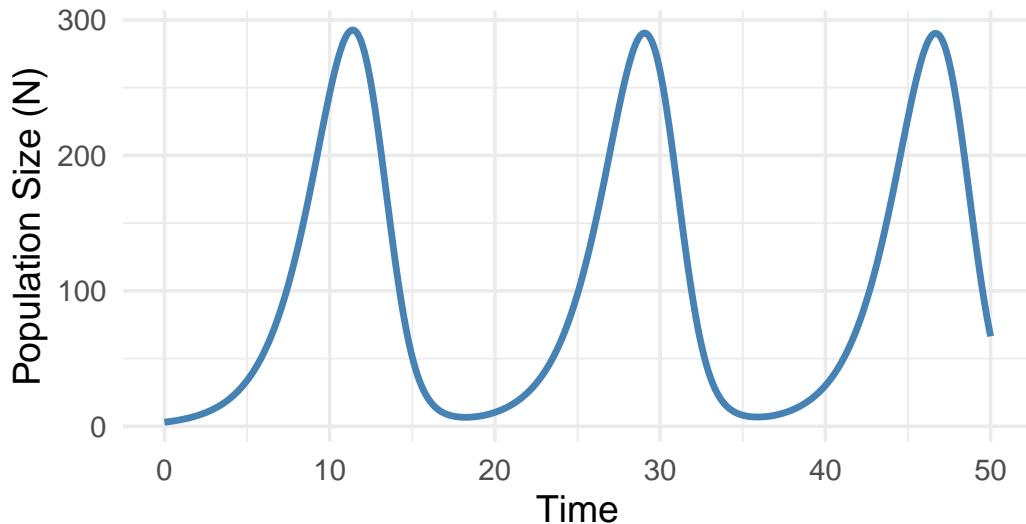
The analogy in the textbook is a thermostat in a room: even though the mean air temperature is at a given setting, in practice the continuous temperature probably repeatedly dips and warms. We can model this relatively simply by introducing a time delay in the logistic model. This implies that there is a lag between when population size changes, and when population growth rate changes. We call that lag T , and define

$$dN/dt = rN_t(1 - N_{t-T}/K)$$

You can see here that the effect of density dependence ($1-N/K$) is lagged T amount behind t .

Delayed Logistic Population Growth

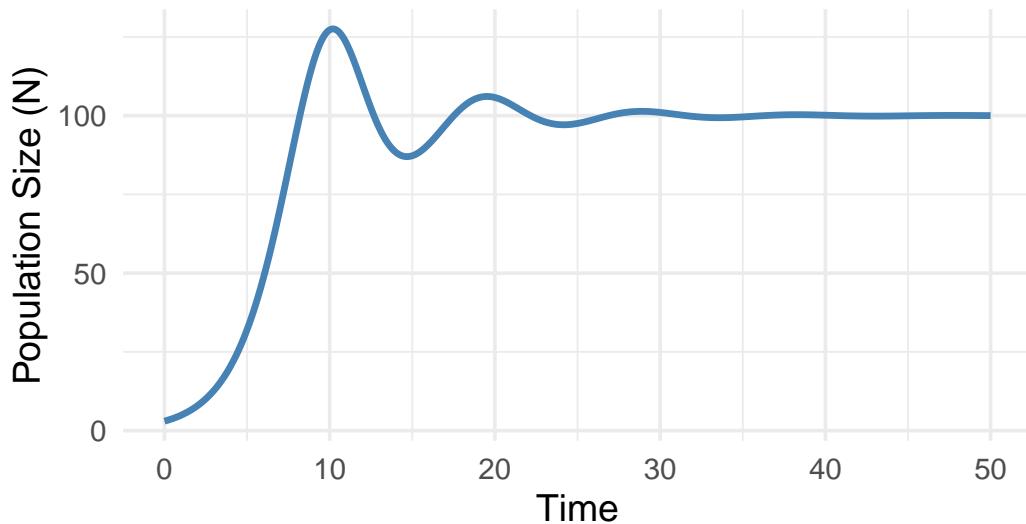
Delay T = 4 , r = 0.5



This is a really fun equation to play around with, because you can see that the predicted dynamics change with r and T (and, specifically, their product; you get oscillations when $rT > \pi/2 \approx 1.57$, and sustained oscillations at even greater values.) If I shrink T I get damped oscillations:

Delayed Logistic Population Growth

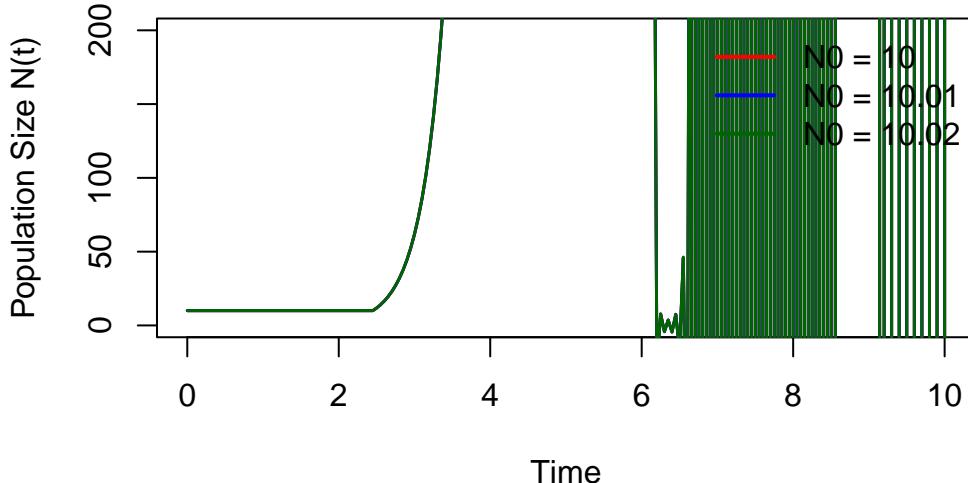
Delay T = 2 , r = 0.5



And if rT is large I get outcomes that are highly sensitive to initial conditions—even though we haven't introduced any randomness or stochasticity! All we've done is slightly change

initial conditions or parameter values, and run a deterministic simple model, but one with time lags.

Chaos in Delayed Logistic Model ($r = 4$, $T = 2.5$)



Have you ever heard of something where tiny changes in initial conditions lead to wildly different outcomes? People call this the *butterfly effect*: a butterfly flaps its wings and some time later there's a tornado. Mathematically, this means the system is **chaotic**. Even though the system is deterministic, not stochastic, tiny changes in some variables can lead to huge differences.

The delayed logistic model can approximate some, but not all, population dynamics. What species do you think it would describe well? Which would it describe poorly?

Crucially, it is missing:

- The effect of different generations and histories of reproductive success (i.e., age structure)
- More complex lagged effects
- The effects of seasonal reproduction

Density dependence in discrete time

(Hastings 96-101)

Let's return to discrete time and explore the dynamics of some discrete-time models that also include density dependence. The first equation we wrote down in this class was:

$$N_{t+1} = F(N_t)$$

And I promised you that we'd spend a lot of the class talking about the forms that F can take. The first form we looked at was the simplest,

$$F(N_t) = RN_t$$

$$N_t = N_0 R^t$$

Where the way you get from population size at time t to population size at time $t+1$ is just multiplying by a constant, R . Let's write down some options with density dependence. **Discuss:** Qualitatively, what would a discrete-time model for density dependence look like? What would be on the right-hand side of $F(N_t)$?

Ricker model

We're starting with this model because we know all the parameters in the equation, although the equation itself is new to us:

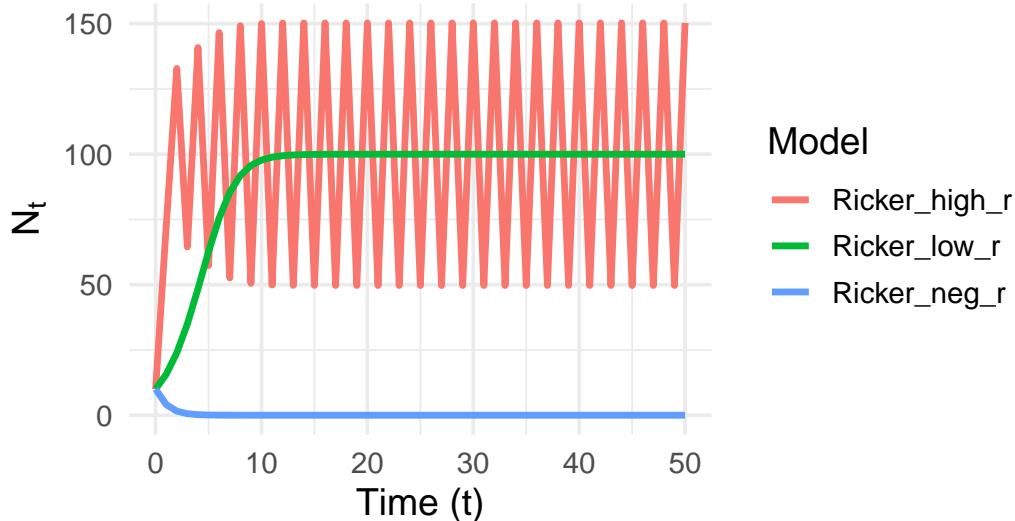
$$N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})}$$

Recall how we discussed above that for a discrete-time model to have density dependence, in this equation, N_t would have to be multiplied by something that isn't a constant (and is, in fact, a function of N)? Here we go! And notice how similar this is to the continuous-time logistic model. **Why might we exponentiate that term? When you raise e to a power, can it ever be negative?**

Most people start with graphs of N_t vs. N_{t+1} but I always like to look at a population trend image so we'll do that first.

Ricker Model Population Trajectories

Initial $N_0 = 10$, $K = 100$



First return plots

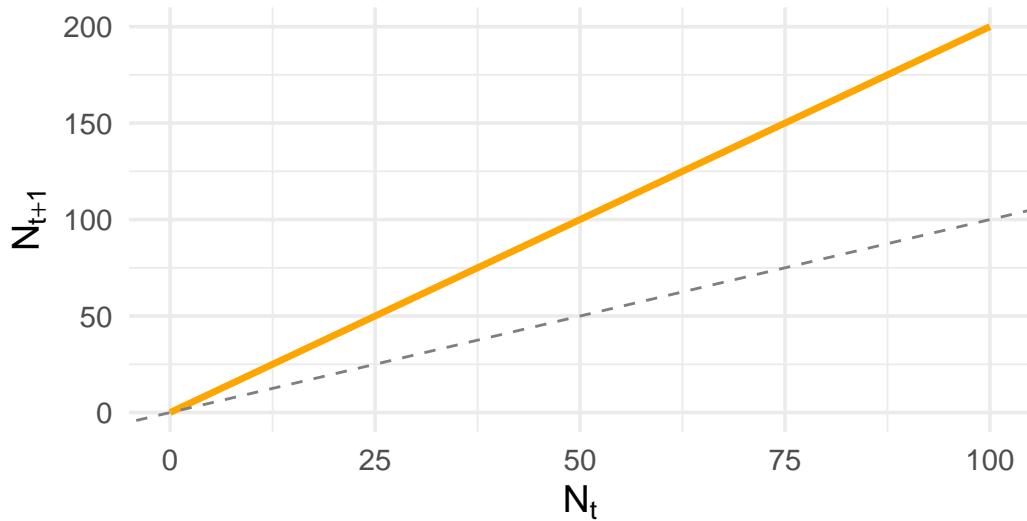
We've been looking at three classes of graphs, but today we're going to add in a fourth one: N_t vs. N_{t+1} . These are called "first return" or "next-generation" plots, and they're really common in discrete-time models. This shows how the population at time t determines the population at $t + 1$; in other words, given its current value, where will the population go? To orient ourselves to these figures let's quickly plot one for geometric growth, $N_{t+1} = RN_t$ (or $F(N) = R^t N_0$). Take a few minutes and try to draw this figure yourself.

What graph did we see much earlier in the class that looks like this one? This plot is highly analogous to dN/dt vs. N in the exponential growth continuous time case. They both describe how the current population size affects the rate of change, and they both give us the direction and speed of population change.

Take a moment to think: Where are the equilibria of this model? How would you know? Here, we can find equilibria graphically when the function crosses the "identity" (1:1) line. Does the geometric growth model have any equilibria?

Geometric Growth: $N[t+1]$ vs $N[t]$

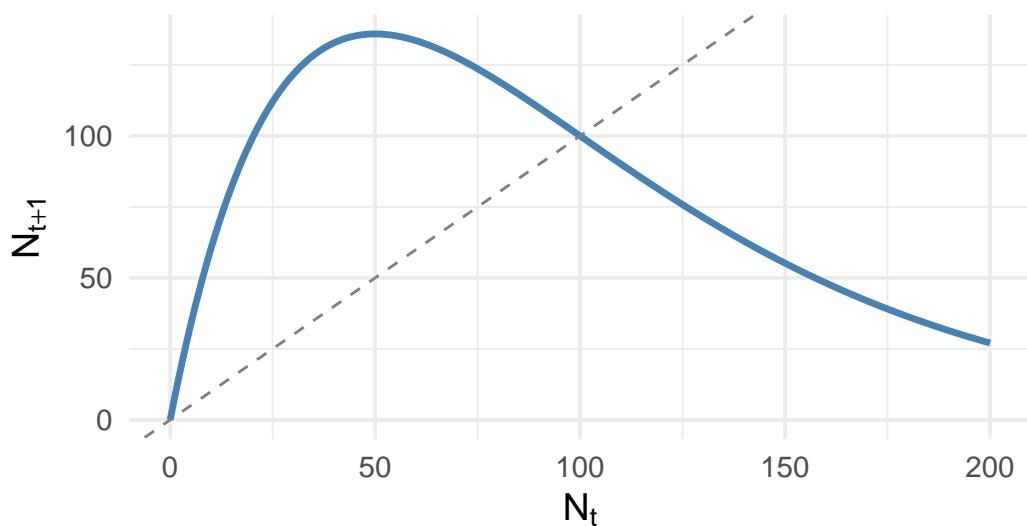
$R = 2$



Keeping in mind all the properties of the dN/dt vs. N plot of the logistic continuous-time model above (the upside-down parabola), let's graph the first-return plot for the Ricker model.

Ricker Model: Next Generation vs. Current Population

$r = 2$, $K = 100$



From the Ricker model formula, what is its growth rate when rare?

Now let's ask all of our usual questions: does this have any equilibria? What does it mean for population size, per capita growth, etc.?

We solved for equilibria above by setting $dN/dt = 0$. Here, we want to set $N_t = N_{t+1} = \hat{N}$.

$$\hat{N} = \hat{N}e^{r(1-\frac{\hat{N}}{K})}$$

This has a trivial equilibrium at $\hat{N} = 0$. But dividing both sides by \hat{N} and taking the log, we get:

$$0 = r(1 - \hat{N}/K)$$

This simplifies to $\hat{N} = K$. What other model had equilibria at population sizes of 0 and K? If I were better at drawing you could see that on the graph above as well. Your next question, now that we have found the equilibrium for the Ricker model, might be: But is it stable? Even though this is a discrete-time model, you can still do this by taking the derivative of this equation:

$$N_{t+1} = N_t e^{r(1-\frac{N_t}{K})}$$

And asking about its behavior at \hat{N} . Let's take the derivative of this equation. We're going to take advantage of the **product rule**, which says that for any u and v, $dG/dN = u'v + uv'$. In other words, when we want the derivative of a product, we take the derivative of each, multiply it by the other, and sum them. Here, $u' = 1$ (the derivative of N with respect to N). v' is:

$$v' = \frac{d}{dN} e^{r(1-N/K)}$$

How do we take this derivative? Hopefully this is triggering some vague memories from calculus. You need to remember two things. First, the *chain rule*, which applies to composite functions—like $f(x) = g(h(x))$. Then, $f'(x) = g'(h(x)) \times h'(x)$. In other words you multiply the derivative of the outer function (keeping the inside intact) by the derivative of the inner function. Let's work through this for an exponential function, $f(x) = e^{g(x)}$.

The second thing you need to remember is that the derivative of e to the something is just ... itself! $d/dx e^x = e^x$. So, we can separate this into:

$$v' = \frac{d}{dN} e^{r(1-N/K)} = e^{r(1-N/K)} \times \frac{d}{dN} r(1 - N/K)$$

Now we just have to take the derivative of $r(1 - N/K)$, which we've done before. We multiply it out into $r - rN/K$, and when taking the derivative with respect to N, this turns into $-r/K$. So our whole v' turns into $-r/K \times e^{r(1-N/K)}$. Recall that we started with $G(N) = N_t e^{r(1-\frac{N_t}{K})}$ and said that $dG/dN = u'v + uv'$ (the product rule). So putting it all together (recall that here, $u' = 1$), we get:

$$dG/dN = e^{r(1-N/K)} - r/K e^{r(1-N/K)} \times N = e^{r(1-N/K)}(1 - rN/K)$$

This is the derivative of the Ricker model in discrete time. Remember, we did all this to understand whether the equilibrium $\hat{N} = K$ is stable or unstable. Let's substitute that in. $e^{r(1-N/K)}$ turns into 1, and so does N/K . So we get that $dG/dN = 1 - r$.

Stability analysis of discrete-time models

In continuous time, what was our stability criterion with respect to this second derivative at the equilibrium value? Stability in continuous time is defined by the sign of the derivative near the equilibrium. If it's negative, it's stabilizing, and if it's positive, it's destabilizing. Think back to our plots of dN/dt vs. N ; if the function crosses the $dN/dt = 0$ line (meaning that, at least momentarily, population is at equilibrium) with a positive slope, the dynamics pull the system away from that point. The reverse is true if it crosses with a negative slope.

The mathematical rule of thumb

But now think back to our first-return plot. When did we define an equilibrium? When $N_{t+1} = N_t$. Previously we were interested in $dG/dN = 0$, meaning when functions crossed the x-intercept. Now we're interested in when functions cross the identity line, meaning that $G'(N) = 1$. This is also the criterion for stability in *all discrete-time models, not just the Ricker model*: if $|f'(\hat{N})| < 1$.

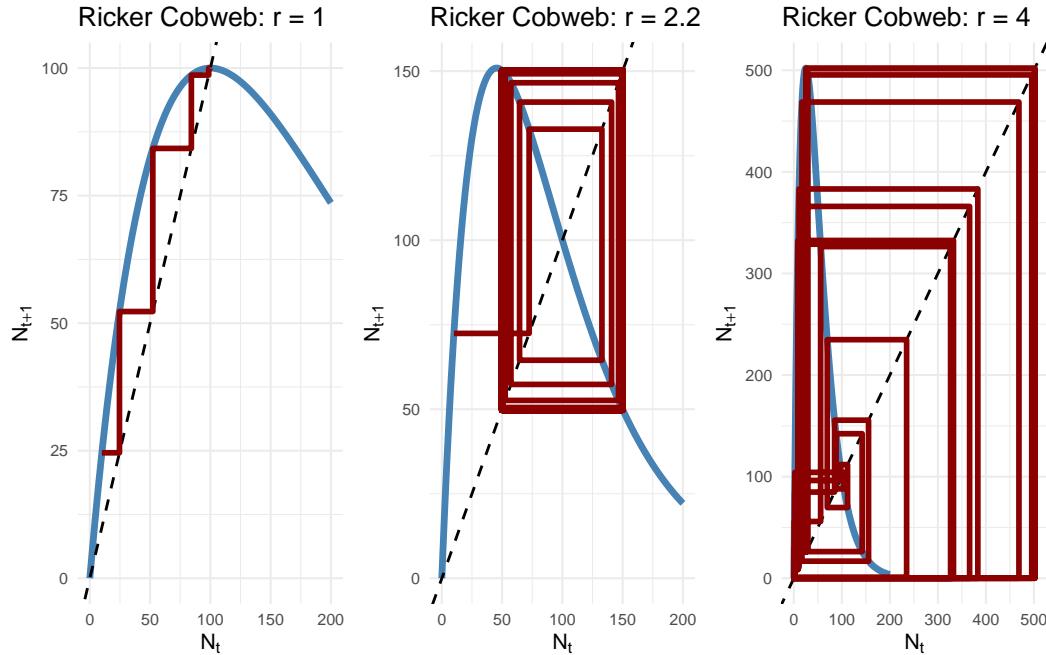
Revisiting the second derivative of the Ricker model at $\hat{N} = K$, $dG/dN = 1 - r$: What values does r have to take on for this to be stable? In other words, for what r is $|1 - r| < 1$? Answer: r must be between 0 and 2.

The graphical explanation

Let's try to build some graphical intuition for stability in discrete-time models, which have more complex behavior than continuous-time ones. We're again going to trace population dynamics from one moment to the next, but this time in the first-return plot. Let's start with a value of N a little above 0. Then we're going to:

- Go vertically up to the curve. This gives us the next population size (at the x-value we picked, what's the y-axis value?)
- Now let's re-consider that value to be our new x. How do we get from y to x on this plot? Go horizontally toward the 1:1 (identity) line. That translates the y you found (last time step's N_{t+1}) into an x (this time-step's N_t).
- Repeat!

Drawing plots is getting harder in this class, but let's start with a low value of r , which means the peak of the Ricker curve is on the identity line. (Because this curve has a long tail we're going to stop drawing the axes on the same scales.) We know where the equilibria are: the question is, does the dynamics of the system pull us toward or away those two points?



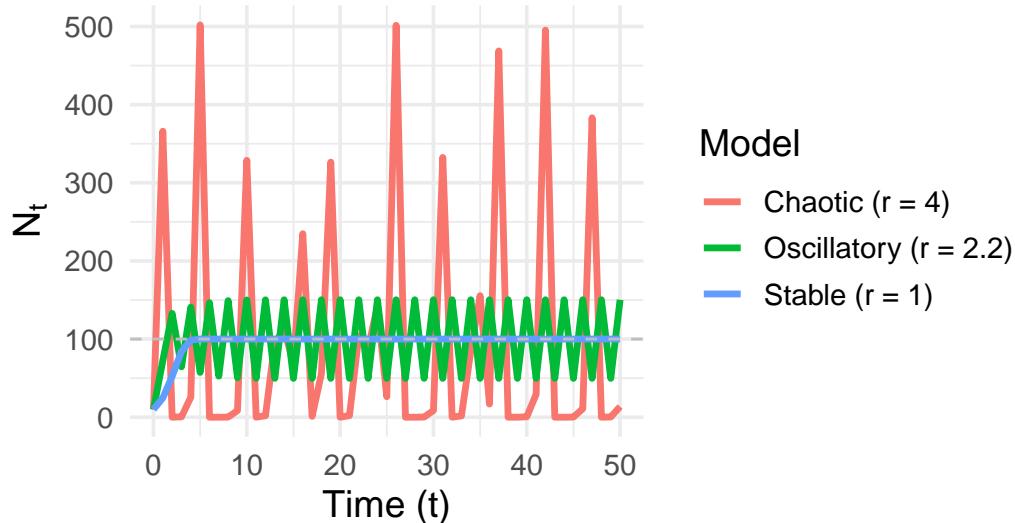
We can see that $\hat{N} = 0$ is always unstable because we are always drawing away from it, and the equilibrium $\hat{N} = K$ is very stable for low r . Let's draw out these diagrams for higher values of r . How on Earth do we interpret these cobweb diagrams? The second one eventually exhibits regular bouncing between the same population sizes. **What did we call that behavior earlier?** The third one never stabilizes and goes all over the place. **What did we call that behavior earlier?**

We know that the Ricker model equilibrium at $\hat{N} = K$ is stable for $0 < r < 2$. It turns out that r controls the steepness of the N_{t+1} vs N plot near the equilibrium point. (Remember that the second derivative was just $1 - r^2$? That is the slope of the N_{t+1} vs N plot at the equilibrium! It only depends on r .) Thus, if r is small (and likely stable), the curve is not very steep when it crosses the identity line. We could have actually guessed whether the plots above would lead to stability without doing the cobweb diagrams!

To check our intuition, let's graph the exact same parameter values in N vs t space:

Population Trajectories for the Ricker Model

$K = 100$, $N_0 = 10$



This is also consistent with our mathematical condition for stability in the Ricker model above. When r gets too large, we see sustained oscillations and then chaos.

Reflect and then share: The only thing varying between these curves is r . Why would the value of r , biologically speaking, have such a big impact on population dynamics? Why would larger values of r lead to more complex behavior in a discrete-time model? What are some real-world populations that might exhibit this behavior?

Chaos in ecology

That simple models in discrete time could yield chaotic dynamics at realistic values of r was a surprising discovery (see May, 1974). We now suspect that many systems have chaotic dynamics, particularly plankton systems (lots to read about this if you're interested.) **Reflect and then share:** If chaos is common in simple population models, what does that mean for the predictability of the real world?

Age and stage structure

Discuss: Up to this point we've been assuming all individuals in a population are the same. What are some ways in which that might not be true? What might vary among individuals, and how might that variation affect population dynamics?

The loggerhead sea turtle scenario

Loggerhead sea turtles, *Caretta caretta*, are large marine reptiles found in the Atlantic, Pacific, and Indian Oceans as well as the Mediterranean. This species has a complex life cycle with very different behavior and reproductive activity by life stage. Females mate every 2-3 years and then nest on beaches close to where they themselves hatched. They do not tend to their eggs, which hatch after several months. Hatchlings then make their way to the water, where they disperse into the open ocean. As they grow larger they often reappear in coastal habitats, frequenting lagoons and estuaries. Females do not reach sexual maturity until they are around 35 years old. Loggerheads can live more than 80 years and are often over a meter long.

As you can see, modeling loggerheads as a population of identical individuals who all reproduce at the same rate is probably a bad assumption. Also, loggerhead populations are generally declining worldwide. Their different life stages face very different threats. Adults are often killed by boat strikes, fishing gear entanglements, or marine debris. Habitat degradation is common in coastal areas, which is particularly harmful to species like loggerheads that return to the beaches where they hatched. Turtle sex is determined by the temperature during incubation, so climate change will likely alter the sex ratio of this species. Human activity on or near beaches poses a risk to eggs (which can be destroyed easily) and hatchlings (which may not reach the water, especially if they are disoriented by artificial light).

Matrix refresher

A **matrix** is a rectangular array of numbers. For example, a 2×3 matrix has 2 rows and 3 columns:

$$A = \begin{bmatrix} 1 & 4 & 2 \\ 3 & 0 & 5 \end{bmatrix}$$

We usually denote a matrix with uppercase letters (e.g., A , B), and its elements with lowercase letters and subscripts, like a_{ij} for the element in row i and column j .

- A matrix with m rows and n columns is called an $m \times n$ matrix (rows always go first!)
- A one-dimensional matrix is called a **vector** (this should sound familiar from computing)
- A **column vector** is a matrix with size $n \times 1$
- A **row vector** is $1 \times n$

For example, a population vector tracking three age classes might look like:

$$\mathbf{n} = \begin{bmatrix} n_0 \\ n_1 \\ n_2 \end{bmatrix}$$

Here, we aren't saying anything about *how to get from the matrix to a single number*. If we wanted to state **n** as the sum of the three age classes here we would just do that. Rather we're saying that this matrix *holds* entries for each age class. We're going to use matrices to track age-structured populations, because they're a tidy way to hold information about multiple ages (or stages) without transforming it (like summing it or averaging it, which we don't necessarily want to do—which is why we're moving away from calculating a single N).

Now, let's refresh matrix operations. You can add or subtract matrices to/from one another **only if they have the same dimensions**. You add corresponding elements (matrix elements with the same position):

If

$$A = \begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix}, \quad B = \begin{bmatrix} 5 & 6 \\ 7 & 8 \end{bmatrix}$$

Then:

$$A + B = \begin{bmatrix} 1+5 & 2+6 \\ 3+7 & 4+8 \end{bmatrix} = \begin{bmatrix} 6 & 8 \\ 10 & 12 \end{bmatrix}$$

Subtraction works the same way:

$$A - B = \begin{bmatrix} 1-5 & 2-6 \\ 3-7 & 4-8 \end{bmatrix} = \begin{bmatrix} -4 & -4 \\ -4 & -4 \end{bmatrix}$$

The above is called **matrix addition or subtraction**. Mathematically, you aren't supposed to just add or subtract scalars (single values); i.e., $A+5$ is an illegal operation because a matrix is an array of numbers and a scalar is not. You can do this operation in lots of programming languages though, and in practice it typically adds the scalar elementwise (separately to every element of the matrix, i.e., adding 5 to every value in A.)

Matrix multiplication is a little more complicated, so we'll split this into three parts: *matrix-scalar*, *matrix-vector*, and *matrix-matrix multiplication*. You can multiply a matrix by a single number (scalar) by multiplying **every entry** in the matrix:

If

$$A = \begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix} \quad \text{and} \quad k = 5,$$

then:

$$kA = 5 \cdot A = \begin{bmatrix} 5 \cdot 1 & 5 \cdot 2 \\ 5 \cdot 3 & 5 \cdot 4 \end{bmatrix} = \begin{bmatrix} 5 & 10 \\ 15 & 20 \end{bmatrix}$$

This operation scales the entire matrix up or down. In this class, we'll be mostly using *matrix-vector multiplication*. If A is a 3×3 matrix and \mathbf{n} is a 3×1 column vector:

$$A \cdot \mathbf{n} = \begin{bmatrix} a_{00} & a_{01} & a_{02} \\ a_{10} & a_{11} & a_{12} \\ a_{20} & a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} n_0 \\ n_1 \\ n_2 \end{bmatrix} = \begin{bmatrix} a_{00}n_0 + a_{01}n_1 + a_{02}n_2 \\ a_{10}n_0 + a_{11}n_1 + a_{12}n_2 \\ a_{20}n_0 + a_{21}n_1 + a_{22}n_2 \end{bmatrix}$$

Each new entry is a **linear combination** of the population across age classes. In other words, for square matrices, we take the i th element of the column matrix (i.e., i th row) and multiply each entry in the i th *column* of the matrix by that value. Then we *add all those values together*. For n -by- n square matrices multiplied by a n -by-1 column vector, after you do the addition for each element, you get back a n -by-1 matrix.

Age structure

Hastings pp16-20, Caswell 8-18

If your goal was to conserve loggerhead turtles, in addition to chronicling their population dynamics enough to know they are declining, your next most-pressing question would probably be: **which of these life stage-specific threats is driving population decline, or would be most valuable to protect to help the species?**

Loggerhead sea turtles have a pretty complex life cycle so we're going to introduce these models with a simpler example and come back to turtles later. To make this as easy as possible, we're going to assume that per capita birth rate and survival rate are not affected by the number of individuals (*no density dependence*). However, they ARE affected by age.

In the discrete-time, geometric growth case, how did we calculate R from counts of individuals observed from one time step to the next?

In our simple example, let's assume that:

- Our hypothetical organism lives for up to three years. We're going to call the individuals in their first year of life (0-364 days old) the “age 0 class”, individuals in their second year of life the “age 1 class” (just like humans: you are 1 until you turn 2), and so on. All age classes can reproduce, but their rates may differ. No individuals survive past 3, so there is no age class 3.
- The population has two sexes, but we are only tracking and quantifying females. (This is a not-uncommon approach in population dynamics.)

- Age 0 individuals have, on average, f_0 offspring per year (per capita). Age 1 individuals have, on average, f_1 offspring per year (per capita). Age 2 individuals have, on average, f_2 offspring per year (per capita). These f 's stand for *fecundity* or *fertility*, which are basically technical terms for average offspring per year.
- p_0 is the probability that a 0-year-old survives to become a 1-year-old. p_1 is the probability that a 1-year-old survives to become a 2-year-old. (We don't need to specify a survival rate for age 2; why?)
- N_t is the total number of individuals at time t , and it is a single value (scalar). $N_t = \sum n_t$, where $n_t = n_0(t) + n_1(t)$. Note that these are lowercase because they are *not* total population sizes and/or because they are vectors—none of them are the same as “big N”.

$n_0(t)$ is the number of offspring of 0-year-olds in year t plus the number of offspring of 1-year-olds in year t . How would we calculate this, i.e., turn this statement into an equation?

$n_1(t)$ is the number of 0-year-olds from time $t-1$ that survive to time t . How would we calculate this?

$n_2(t)$ is the number of 1-year-olds from time $t-1$ that survive to time t . How would we calculate this?

Conventionally we put $t+1$ on the left and t on the right (rather than $t-1$ and t). We could also denote these $n_{0,t}$ but we put t in parentheses because having everything in the subscript gets awkward when we are in $t+1$ land and beyond.

$$n_0(t+1) = n_0(t)f_0 + n_1(t)f_1 + n_2(t)f_2$$

$$n_1(t+1) = n_0(t)p_0$$

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

Work out what the population size is at $t+1, t+2, t+3, t+4$ if the population at N_t has (A) 10 age 0 individuals, no age 1 individuals, and 5 age 2 individuals or (B) no age 0 individuals, 10 age 1 individuals, no age 2 individuals. Hint: A table with rows for the age classes and columns for the time steps will help.

The equations above can be written, much more conveniently, in matrix form. As a group, try writing these down in matrix form, with population sizes at $t+1$ on one side and population sizes at t on the other.

We start by just spelling out the vectors on both sides:

$$\begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \end{bmatrix} = \begin{bmatrix} (n_0(t)f_0 + n_1(t)f_1 + n_2(t)f_2) \\ n_0(t)p_0 \\ n_1(t)p_1 \end{bmatrix}$$

We want to factor the right-hand side into a matrix multiplied by something. If we factor out the vector of population sizes, we get:

$$\begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \end{bmatrix} = \begin{bmatrix} f_0 & f_1 & f_2 \\ p_0 & 0 & 0 \\ 0 & p_1 & 0 \end{bmatrix} \begin{bmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \end{bmatrix}$$

The above is a convenient way to summarize the age-structured population dynamics. We can summarize this even more compactly by defining the matrix in the middle as \mathbf{L} , which stands for Leslie matrix (one of the first people to utilize this model in ecology). Then we can state,

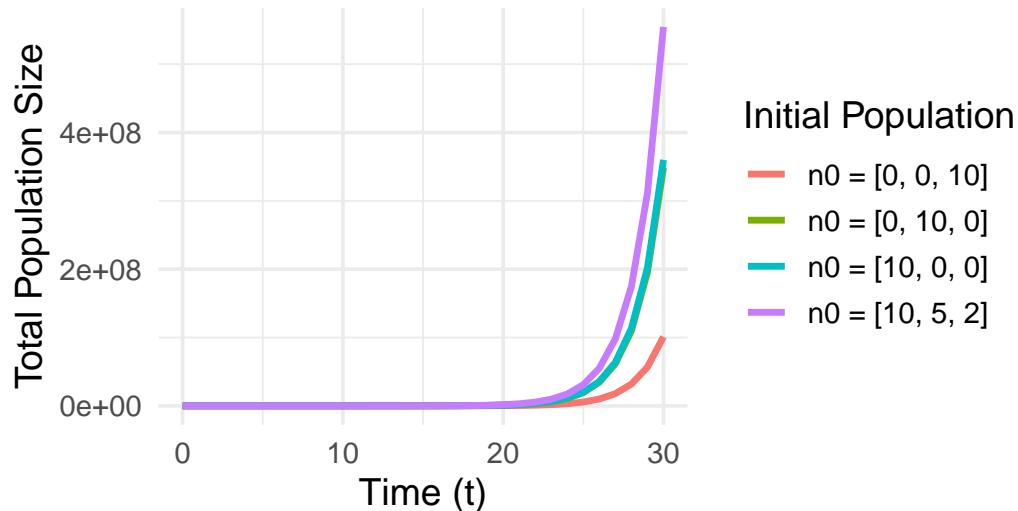
$$n(t+1) = \mathbf{L}n(t)$$

Matrix population models are generally classified by the form that \mathbf{L} takes, and this is the simplest one—where \mathbf{L} never changes. Nonetheless this sets us up to ask all kinds of questions about population dynamics! Your first one might be, will this age-structured population still exhibit exponential growth? It *looks* like it should, but recall that \mathbf{L} is a matrix—not a scalar—and n is a vector. This model DOES tell us that *birth and death rates* are constant, but does that itself lead to exponential growth?

Matrix models are so popular in population dynamics because they can be used to make projections of abundance across ages. Let's look at some examples.

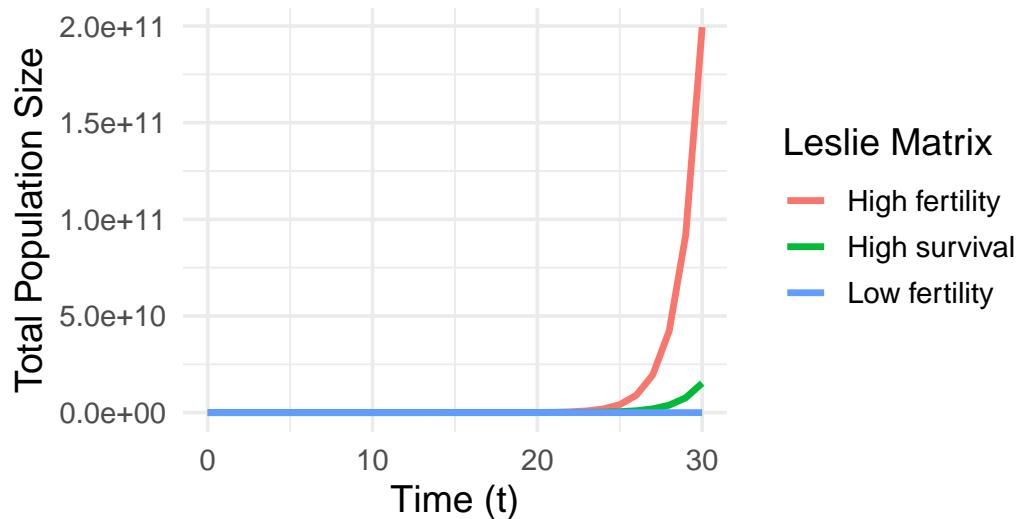
Population Size Over Time

Matrix model: $\mathbf{n}(t+1) = \mathbf{L} \times \mathbf{n}(t)$



Population Size Over Time for Different Leslie Matrices

All simulations use $\mathbf{n}_0 = [10, 5, 2]$



Several observations here. First—yes, this model does lead to exponential growth, even with age structure. However, both the initial population sizes and the Leslie matrix parameters affect the rate of exponential growth. Let's think more about the properties of this matrix:

$$\begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \end{bmatrix} = \begin{bmatrix} f_0 & f_1 & f_2 \\ p_0 & 0 & 0 \\ 0 & p_1 & 0 \end{bmatrix} \begin{bmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \end{bmatrix}$$

A few things to notice about the Leslie matrix:

- Birth rates, or fecundity, are always in the first row.
- The subdiagonal contains survival fractions, or probabilites.
- The other entries are all zero.
- n-by-n Leslie matrices have n eigenvalues and n eigenvectors.

These things hold for **all age-structured population models, regardless of the number of age classes, or whether we make b or s conditional on other stuff.** (They are not true for stage-structured models, which we'll get to later.) What additional stuff could b or s be conditional on? They could be driven by the environment,

$$n(t+1) = \mathbf{L}_t n(t)$$

Or by the population itself (i.e., density dependence).

$$n(t+1) = \mathbf{L}_n n(t)$$

You can imagine turning some or all of the elements of \mathbf{L} into functions of population size and the environment. You could certainly make an argument that both birth and survival have a density dependence, either positive (Allee effects) or negative (logistic growth). We're not going to go that far in this class. Matrix population modeling is a whole class and field unto itself, adhering closely to Hal Caswell's phenomenal book on the topic. It also requires linear algebra techniques that not everyone came into this class with. But I very highly recommend that book if you are interested in learning more. We are going to unpack a few more properties of the simplest (exponential growth) model, and then discuss stage structure.

Dominant eigenvalues and eigenvectors

One thing we might want to do, similar to when we studied geometric growth in discrete time without age structure, is get a general function for $n(t)$ as a function of the initial population size $n(0)$. This allows us to explore age structure mathematically without stepping through every generation one at a time. Without age structure, we had $N(t+1) = RN_t$ and solved this to find that $N(t) = R^t N_0$. Similarly, here, we have $n(t+1) = Ln(t)$ and can deduce that $n(t) = \mathbf{L}^t n(0)$. (Convince yourself of this by looking at the equations above.)

From here, we want a simple expression for $\mathbf{L}^t n(0)$ in terms of the parameters of the Leslie matrix that we can use to understand this model better. In particular, for large values of t, it

would be nice to not have to figure out what L is raised to a large exponent. To simplify this, we will now take advantage of a property of n-by-n Leslie matrices, which is that they have n eigenvalues and eigenvectors. We will denote these λ and \vec{n} . If this doesn't sound familiar to you from linear algebra, or even if it does, here's how they are defined: for a n-by-n matrix M, there are at most n (and for Leslie matrices, *exactly* n) sets of scalars and vectors for which the following is true:

$$\mathbf{M}\vec{\mathbf{v}} = \lambda\vec{\mathbf{v}}$$

Remember, we can't just divide both sides by v, which is a column vector. In this class we won't get into actually *finding* eigenvalues and eigenvectors, but we will use them to gain inference into age- and stage-structured models.

Here, you need to know a little trick of eigenvectors. For a set of eigenvectors, e.g., $\vec{\mathbf{v}_1} = \begin{bmatrix} 1 \\ 0 \end{bmatrix}$ and $\vec{\mathbf{v}_2} = \begin{bmatrix} 0 \\ 1 \end{bmatrix}$, you can state any arbitrary vector x as $\mathbf{x} = a_1\vec{\mathbf{v}_1} + a_2\vec{\mathbf{v}_2}$, where a_1, a_2 are constants you can solve for computationally.

We care about this rule because it makes the equation above, $n(t) = \mathbf{L}^t n(0)$, much more tractable. Let's call the eigenvectors of L $\vec{\mathbf{v}_1}, \vec{\mathbf{v}_2}, \vec{\mathbf{v}_3}$ and the eigenvalues $\lambda_1, \lambda_2, \lambda_3$. Recalling that $n(0) = [n_0 + n_1 + n_2]$, we can say that

$$n(0) = a_1\vec{\mathbf{v}_1} + a_2\vec{\mathbf{v}_2} + a_3\vec{\mathbf{v}_3}$$

Substituting this in gives us

$$n(t) = \mathbf{L}^t n(0) = \mathbf{L}^t(a_1\vec{\mathbf{v}_1} + a_2\vec{\mathbf{v}_2} + a_3\vec{\mathbf{v}_3}) = \mathbf{L}^t a_1\vec{\mathbf{v}_1} + \mathbf{L}^t a_2\vec{\mathbf{v}_2} + \mathbf{L}^t a_3\vec{\mathbf{v}_3}$$

And recall that above we defined the eigenvalue as the λ for which $\mathbf{M} \mathbf{v} = \lambda \mathbf{v}$? We can therefore substitute:

$$n(t) = \mathbf{L}^t n(0) = a_1\lambda_1^t\vec{\mathbf{v}_1} + a_2\lambda_2^t\vec{\mathbf{v}_2} + a_3\lambda_3^t\vec{\mathbf{v}_3}$$

Now, all of a sudden, we have the entire right-hand side of this equation expressed in terms of constants except for t. All we need to do is raise λ to t. **As t gets large, what single value in this equation drives the population size?**

It's the biggest $|\lambda|$ —the **dominant eigenvalue**, which is often denoted λ_1 . As time goes on, $n(t) \approx a_1\lambda_1^t\vec{\mathbf{v}_1}$. This tells us that a single eigenvalue drives the long-term population growth (or decline) rate, and encodes a combined effect of birth and death. **When $\lambda < 1$, the population is declining exponentially/geometrically; when $\lambda > 1$, it's increasing.**

Assuming you could calculate the eigenvectors, eigenvalues, and coefficients, what kind of biological questions could you explore with this model?

Stable age distribution

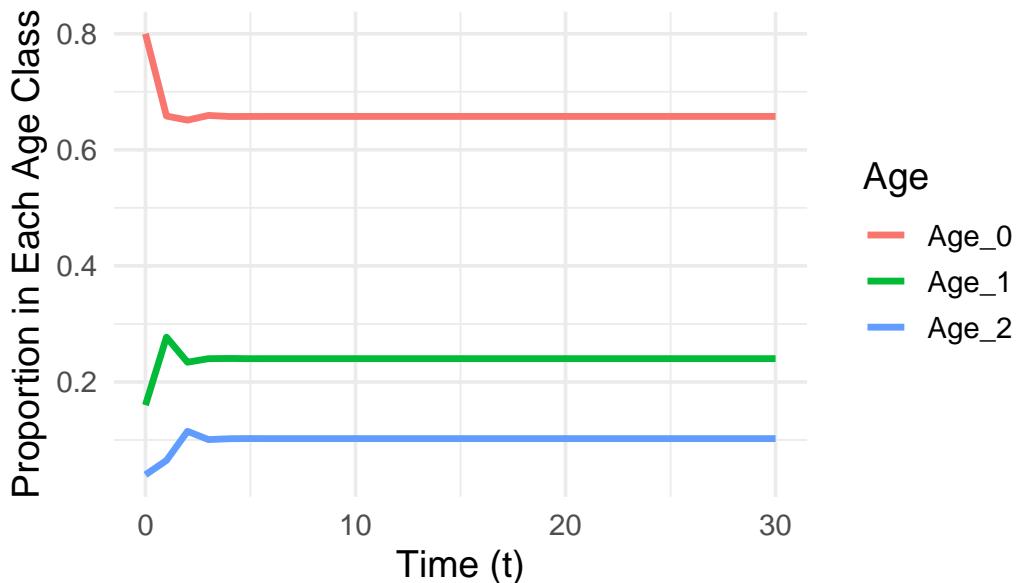
We talked about the intuition behind the dominant eigenvalue: it determines long-term population change and approximates the combined effect of birth and death. What's the intuition behind the associated eigenvector, \vec{v}_1 ?

It turns out that in a scenario like the one we've been exploring—with constant birth and death rates given by \mathbf{L} , that do not change over time—the population approaches a *stable age distribution*. This is actually a corollary of the population having a unique, constant growth rate that is not dependent on time or population size. For this to be the case, each age class must also have a constant growth rate—i.e., must make the same *per capita* contribution to the population every year. The growth rate would not be constant from one year to the next if the relative contributions of, for example, age 0 and age 1 individuals changed.

This is NOT THE SAME as a stable population size; as we saw in the plots earlier, these populations will exhibit exponential growth or decline. However, as they grow away from the initial conditions, they will move toward a constant *ratio of age classes*. **This is the stable age distribution, and it is given by \vec{v}_1 .**

Again, while this model doesn't actually describe many real-world populations, it can be helpful to delve into the stable age distribution to understand which life stages dominate long-term dynamics and how deviations from the stable age distribution arise and affect long-term dynamics. The Hastings textbook goes into detail on how this stable age distribution arises and demonstrates mathematically why it's stable; I'll skip this but feel free to look it up.

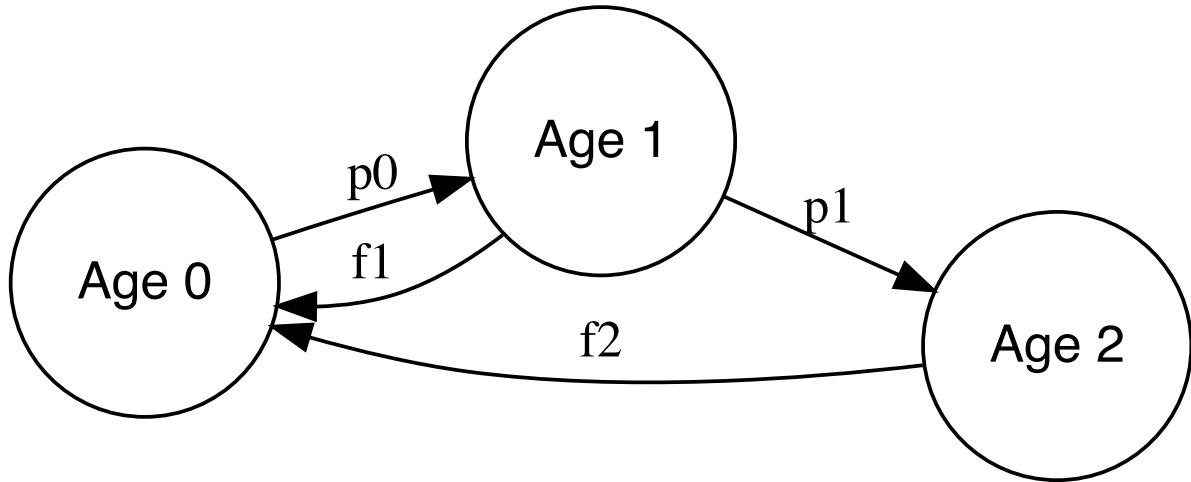
Convergence to Stable Age Distribution



Stage structure

After all this, we still aren't quite ready to build a model of the loggerhead sea turtle. That's because we've been talking about age structure, but with turtles (and many species), what really matters is *stage structure*—how many individuals are at each life stage. These aren't the same thing. Recall how turtles can be reproductive adults for decades, but their habitat use changes a lot early in life? Not only are life stages important, but turtles stay at them for multiple years, and different durations depending on the stage. We could build a giant matrix for every possible age of turtles, but we also often don't *know* their age, only their stage. (This is true for many surveyed populations).

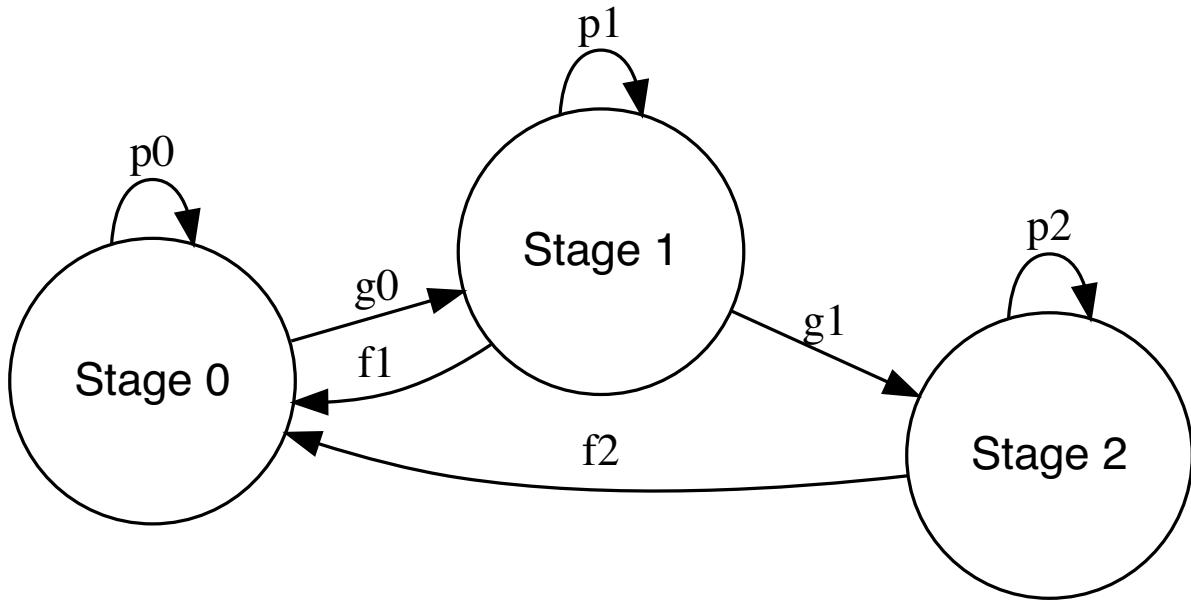
To model stage structure we introduce a little more complexity to our matrix models (Caswell pp56-). The easiest way to start understanding this is graphically. Let's sketch a diagram of the population we described above.



This is a graphical representation of the population model we wrote down in our simplest example. **What key change do we need to make to transition to a stage-structured model?**

In a stage-structured model, individuals don't transition states (the big circles) in every time step. Some of them will move on to the next stage, but a proportion of them will stay at the same stage. (In Caswell's book, he calls these "size classes", because that's often how we measure them—especially in natural resource applications, like fisheries and forestry.) To describe this, we need to introduce another set of parameters: g_0, g_1 , etc., which represent the probability an individual *survives and grows to the next stage*. (We still also have p_0, p_1 , etc. in this model; those now represent the probability that an individual *survives and stays at the same stage*.) Note that these don't sum to 1, because there are a bunch of individuals that die in every time step. In all of our discussions of stage-structured models, we'll assume that individuals can't skip stages; to get from stage 0 to 2, they have to go through 1 first.

Try adapting the figure above to include this additional complexity, for a population with three stages but a lot of ages. Start by re-labeling the circles stages, not ages, and then think about how to add or change arrows.



Now do you see the advantage of stage-structured models? This could be an organism that lives for 50 years, but so long as we can identify the life stages *that have different birth, death, growth, or other vital rates*, we can vastly simplify the model. In the textbook there's an example of an actual stage-structured model for killer whales. They have four life stages. Stage 0 lasts for less than a year, so there is no probability of staying in that stage. Killer whales only reproduce in stages 1 and 2. Try drawing a life cycle graph of this killer whale population model.

Now let's move onto the matrix representations of these models. We can still state that $\mathbf{n}(t+1) = \mathbf{An}(t)$. The only difference from the age-structured example above is that the matrix is slightly different (see below) and \mathbf{n} is now a vector of *stage* abundances (not age).

How do we get this matrix? First of all, it will be a n-by-n matrix, where n is the number of stages. You can actually populate the entire matrix from the diagrams we've drawn. The element $a_{i,j}$ is given by the arrow in our life cycle graph from stage j to stage i. (The direction is important here; it's $j \rightarrow i$, not $i \rightarrow j$.) For the three-stage example, try filling in ****A.****

$$\begin{bmatrix} a[1, 1] = p_0 & a[1, 2] = f_1 & a[1, 3] = f_2 \\ a[2, 1] = g_0 & a[2, 2] = p_1 & a[2, 3] = 0 \\ a[3, 1] = 0 & a[3, 2] = g_1 & a[3, 3] = p_2 \end{bmatrix}$$

This is, again, a Leslie matrix. It still has fecundities in the first row. Now, the subdiagonal contains transition probabilities (individuals that survive and grow to the next stage) and the diagonal contains probabilities of surviving and staying at the same stage. We are now, at last, ready to build a stage-structured population model of loggerhead sea turtles! Crouser et al. 1987 actually did this—a large improvement over previous, age-structured models of

loggerheads. Do you think it was reasonable for them to fit a model without density dependence or environmental effects—i.e., a constant growth rate model—to this population? Why or why not?

They estimated a λ around 0.945; Does this mean the population was increasing or decreasing? They then calculated the stable age distribution (dominant eigenvector), the relative reproductive contributions of each age class at the stable age distribution, and then simulated how λ would change if mortality at each life stage either increased or decreased drastically (representing human impacts or conservation measures). They found that the most sensitive life stages were juveniles and subadults: reducing mortality on those would tip the population into a growth phase, and increasing mortality on those would cause rapid collapse. This and a follow-up paper, Crowder et al. 1994, demonstrated that a popular conservation strategy for sea turtles—protecting nesting beaches and hatchlings—was much less effective than reducing at-sea mortality of juvenile and subadult sea turtles. This set of studies was extremely influential and led to the widespread adoption of “turtle excluder devices”.

Metapopulations

As this course has progressed we've chipped away at the unrealistic assumptions in our simplest models. Because per capita population growth is unlikely to be constant, we introduced negative density dependence (logistic model) and positive density dependence (Allee effects). We also modeled the effects of time lags, both in the continuous-time delayed logistic model and in the discrete-time Ricker model, and saw how complex dynamics can quickly arise in those models. Next, we tackled the assumption that all individuals in a population are identical, and saw how we can track population dynamics across age or stage classes separately, allowing them to have different rates of fecundity, growth, and death.

The next assumption we will tackle is that populations are homogenous and perfectly mixed across *space*. Just as individuals (or groups of individuals) have different vital rates at different ages and life stages, individuals or populations may have different vital rates in different *places*. What are some reasons why this might be the case?

The simplest way to build this into population models is to say that rather than a single population where all individuals (of the same age / stage) are identical and can reproduce with one another, we say that there is *a set of those populations*—a **metapopulation**, or a “population of populations.” We call each place occupied by one of those populations a “patch.”

The biggest difference between metapopulation models and population models is that the latter describes *abundance*, or N , and the former describes *persistence*. Metapopulation models are commonly applied to understand the relationship between changing habitat and local extinction, or “extirpation.” We don’t apply them to think about how many individuals are in

a patch (we can use conventional population models for that) but rather to understand what proportion of an available landscape or seascape is being occupied by any population.

Hastings only spends one page on this, so I'm instead using the introduction to metapopulations from Gotelli (Chapter 4) as well as Marissa Baskett's ESP121 notes here.

The simplest model of patch dynamics

Every patch has two states: empty or occupied. A patch becomes empty due to local extinction, and it becomes occupied due to immigration. The quantity we are interested in tracking is p , the fraction of occupied patches (ranges from 0 to 1). In this simplest model, let's say that all patches have the same rate of extinction (e) and immigration (i). Then:

$$\frac{dp}{dt} = \text{immigration} - \text{extinction}$$

In words, the *rate of change of p over time* is driven by the immigration rate minus the extinction rate. [Draw a metapopulation on the board and define p .] We define the extinction rate as e and the immigration rate as i (some textbooks use m , which can also mean mortality, which is why I'm using i). Immigrants come from an occupied patch, and can only go into an unoccupied patch. Extinctions can only happen in occupied patches. Thus, we can write this equation as:

$$\frac{dp}{dt} = ip(1-p) - ep = p(i(1-p) - e)$$

Equilibria and stability

Remember how in our first population model, we said that the rate of population change over time was equal to births minus deaths? This is an analogous model, except rather than continuous turnover of individuals, there is continuous turnover of occupied patches. Just as logistic (well, all) population models are stable when births equal deaths, metapopulation models are stable when immigration equals extinction. **How would we find the equilibrium where immigration equals extinction in this case? Take a few minutes to solve the below.**

$$0 = p(i(1-p) - e)$$

We find two equilibria: $\hat{p} = 0$, i.e. extinction, or $\hat{p} = 1 - e/i = \frac{i-e}{i}$. Let's analyze these equilibria for stability. Once again, if $dp/dt = G(p) = 0$ it tells us about equilibria, and whether $G'(p)$ is positive or negative tells us about stability. So let's take the derivative of this equation.

$$G'(p) = \frac{d}{dp} ip(1-p) - ep = \frac{d}{dp} ip - ip^2 - ep = i - 2ip - e$$

Substituting in our first equilibrium, $\hat{p} = 0$, gives us $i - e$. Remember that the equilibrium will be stable if this value is negative. When is it negative? When is it positive? When is it zero? Is it a good thing or a bad thing if the equilibrium at $\hat{p} = 0$ is stable?

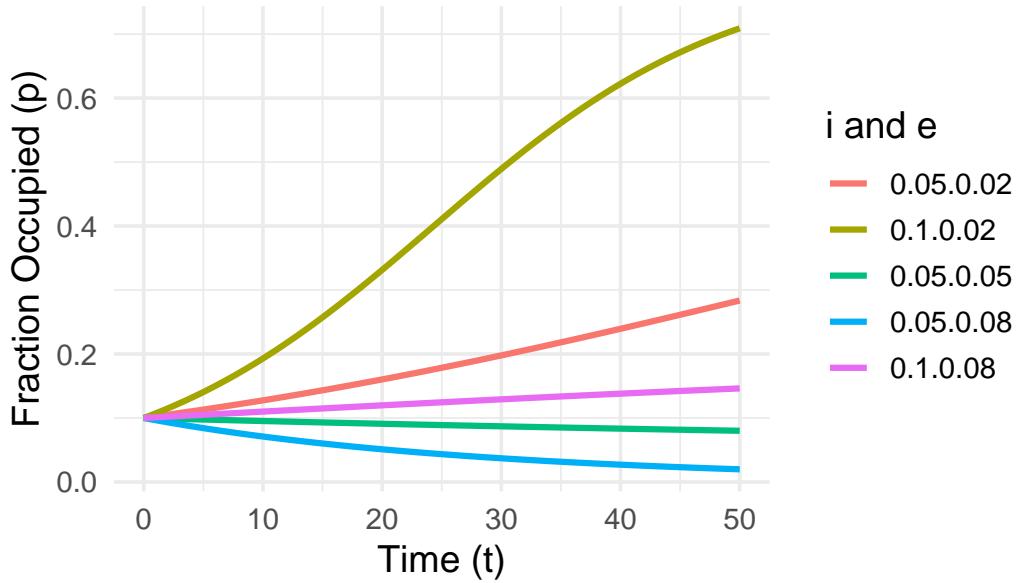
Now let's do the equilibrium at $\hat{p} = \frac{i-e}{i}$.

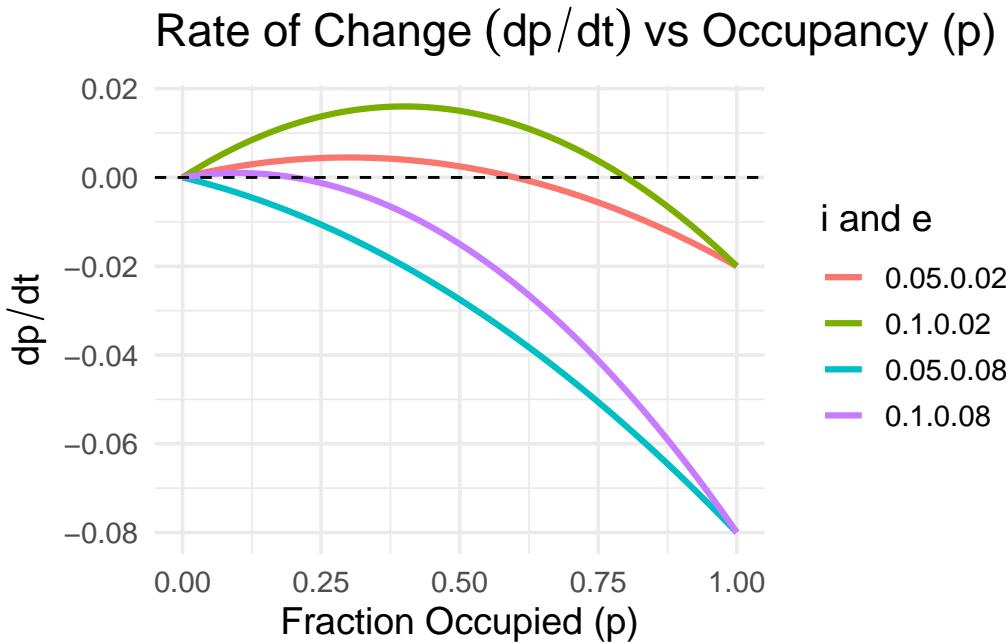
$$i - 2i(1 - e/i) - e = i - 2i + 2ie/i - e = -i + 2e - e = e - i$$

This is stable (negative) when $i > e$. We could have guessed this by thinking more deeply about the $\hat{p} = 1 - e/i$ equilibrium condition: for it to lead to persistence, we'd need $p > 0$, or $\frac{i-e}{i} > 0$; this can be simplified to $i - e > 0$, or $i > e$. This should make intuitive sense. Note that this condition doesn't mean that p goes to 1; it goes to a value determined by the ratio of extinction to immigration (aka colonization).

Finally, let's draw metapopulation dynamics and see the parallels with logistic population growth.

Metapopulation Dynamics (p vs t)





Case study: marine reserves

Now that we've seen how metapopulation dynamics in this simple model are analogous to logistic growth—where the fraction occupied, p , eventually stabilizes, and dp/dt goes to 0—let's add in some more complexity to resemble a marine ecosystem. To do this, we'll build from a paper entitled "Role of marine reserves in recruitment to reef fisheries: A metapopulation model" (Man *et al.* 1995 *Biological Conservation*). They start with our same definitions as above, where p is the proportion occupied; extinction is e , and the proportion of occupied patches decreases at a rate ep ; and propagules move from occupied patches to empty ones, giving an immigration rate $ip(1 - p)$. (Note that the paper uses m where we use i ; I chose this notation because m also can mean mortality, so I think the paper's notation is confusing.) Thus, again,

$$dp/dt = ip(1 - p) - ep$$

Man et al. make three key modifications to make this model more realistic for marine reserve planning and harvested populations. First, not all patches are equal. Some proportion of them, q_1 , are marine reserves (no fishing or other human uses), and another proportion (q_2) is fished; $q_1 + q_2 = 1$. This is the main management lever of the fishery; managers can increase or decrease q_1 . (This might sound simplistic, but it is actually a common management strategy in many parts of the world, especially data-limited settings. If you're curious about some ways this can work, read more about "territorial use rights for fishers".) In their model, exploitation (fishing) affects e , but not m . Thus they define a new e_1 (unfished) and e_2 (fished) and assume

that e_2 is much, much bigger. (Remember last week we talked about early marine reserve theory using the “scorched earth hypothesis”—that everything dies outside of the protected area?)

Next, they also divide up tracking persistence into p_1 and p_2 . Being natural resource managers, they’re really curious about p_2 : how can you keep a viable population in the exploited areas just by turning the dial of “how much habitat is protected”? They do assume that individuals are equally likely to go from any occupied patch into any other occupied patch, fished or unfished, so there is just one i value to track here. Let’s try to derive our two equations for dp_1/dt and dp_2/dt .

Looking at our differential equation for dp/dt without any marine reserve extensions, we see there are three parts: $-ep$, which deals with extinction from occupied patches; ip , which tells us the rate at which individuals immigrate from occupied patches; and $1 - p$, which scales that down so that only empty patches are being colonized. For marine reserves, adapting $-ep$ is straightforward; we just have $-e_1 p_1$. Adapting ip is also straightforward; i is still a single constant that applies to offspring produced everywhere (in either patch type), so this just becomes $i(p_1 + p_2)$. How do we adjust the term $(1 - p)$ to represent *only available patches that are in marine reserves*? Fortunately, we defined a quantity for this! To figure out what proportion of patches in marine reserves are unoccupied, we just take $q_1 - p_1$. So this becomes

$$dp_1/dt = i(p_1 + p_2)(q_1 - p_1) - e_1 p_1$$

And the exact same equation for exploited patches, because the production of offspring is the same everywhere (the first term, $i(p_1 + p_2)$); we scale that down by what proportion of exploited patches are occupied, $q_2 - p_2$; and then subtract out the extinction rate in this patch type.

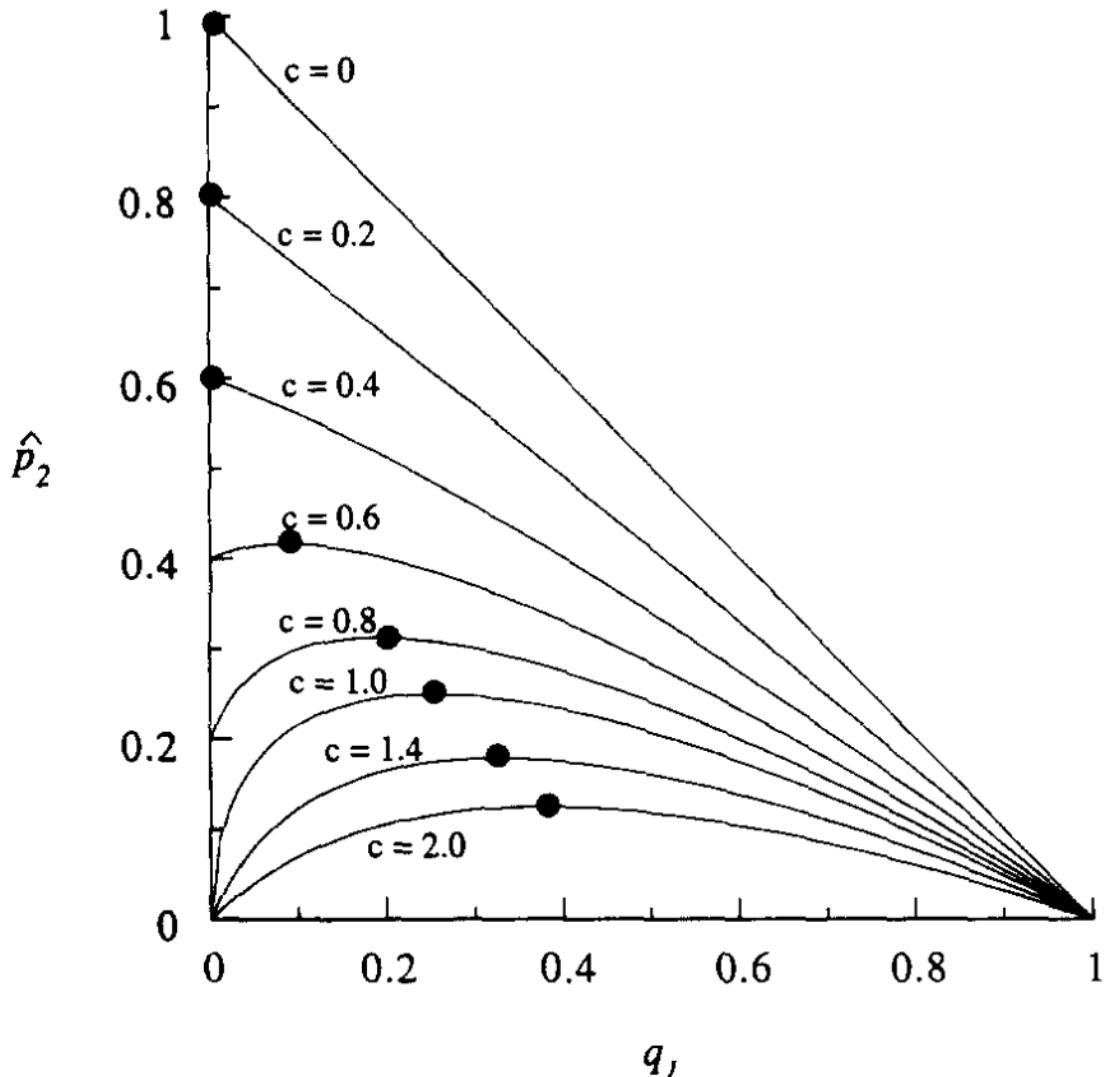
$$dp_2/dt = i(p_1 + p_2)(q_2 - p_2) - e_2 p_2$$

They then make a third assumption, which is that $e_1 = 0$. In other words, for harvested populations, none of them die in marine reserves. **Do you think this is true?** (They also rearrange some terms in the dp_2/dt equation which isn’t important here.) The authors add that ideally these equations would include a time lag between the recruitment process of larvae or juveniles, i , and the process of “aging into the fishery”, which is when they start counting p . They note that is computationally intractable, which I’m sure it was in 1995, but it isn’t now!

Let’s find the equilibrium value for \hat{p}_1 with the simplified equation, $dp_1/dt = i(p_1 + p_2)(q_1 - p_1)$. When does $dp_1/dt = 0$? What does that tell us about the long-term dynamics of this system?

Modeling the benefits of marine reserves to fisheries

In the paper they find the equilibrium value for \hat{p}_2 ; we won't go through the math for this. But I do want to highlight how these fairly simple equations can inform strategic decisions about marine spatial planning. The best way to do this is a figure from the paper, which I'll attempt to re-draw.



This implies that if fishing mortality (e_2 or c) is low, there's no reason for any habitat protection. The highest occupancy rate in harvested areas occurs when zero habitat is protected. But as fishing mortality increases, the marine reserves start to serve a role in producing "spillover" to

the harvested areas—and you see that for very high fishing mortality rates, *if no habitat was protected, this model predicts total extinction outside of marine reserves.*

Now, there are a lot more extensions that would make this model more realistic. *If you really wanted to know how much habitat to protect to maximize fisheries benefits, what else would you need to know?*

As an interesting coda, whether marine reserves increase fish biomass *in total* is still a huge area of debate. *Why do you think this has been so difficult to prove?*

The marine reserve population modeling literature is large, and the early classics are well worth a read, including:

- Botsford, Hastings, and Gaines 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters.*
- Guichard *et al.* 2004. Toward a Dynamic Metacommunity Approach to Marine Reserve Theory. *BioScience.*

Spatial population modeling

Metapopulation models don't quantify abundance, just persistence throughout the patch network (so they also don't track individual patches). Let's say we want to track actual abundance, but still incorporate some spatial structure to our population models. It turns out that you're already able to do this—and it's a chance to start blending together the modeling approaches we've been learning. Let's work through the equations on our own. We assume:

- Discrete time, logistic growth dynamics
- Two adjacent patches, indexed A and B
- Three age classes. Age 0 is recruits; they don't do anything except age and die (at a constant rate, s_0). Age 1 is juveniles; they don't reproduce but are highly mobile. Age 2 is adults; they don't move, but they do reproduce *at a patch-specific rate*, f_A and f_B (you can think of this as an environmental effect, although for now let's just leave it as a constant).
- Movement happens between patches at a fixed rate, d , which stands for diffusion.

Together, let's write down a system of equations for the three age classes each year ($n_0(t+1)$ and so on).

If we have time, discuss and try extending these equations to additional complexities, such as density dependence (possibly with a patch-specific carrying capacity), more than two patches, fishing mortality, etc.

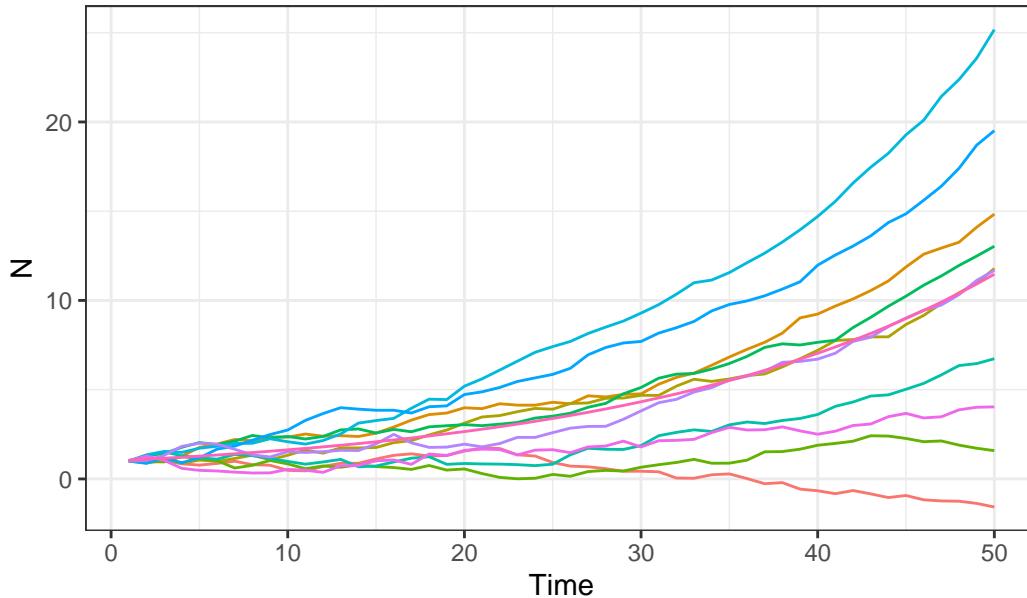
<<< HEAD # Stochasticity in population dynamics

When this course was approved by the UCSC Registrar, stochasticity was listed as an important topic I planned to cover. I was subsequently surprised to learn that this topic is not explored in any of the introductory population modeling texts I was using. Many of you are familiar with the concept of stochasticity as “noise” or “variation” in data, but what does it mean to introduce it into theoretical models? To answer this question we turn to Marc Mangel’s “The Theoretical Biologist’s Toolbox” (chapter seven).

Up to now, we have only learned about **deterministic models**. This means that for any combination of parameter values and initial conditions, *there is only one possible outcome*. This is true even in models that result in chaos! We call the dynamics chaotic because tiny differences in parameter values or initial conditions lead to hugely divergent outcomes, but *they are still deterministic—just with a very high sensitivity that makes qualitative predictions impossible*.

Stochastic models are fundamentally not this way. In stochastic dynamics, even the simplest models can have multiple outcomes. This is probably a better description of nature, where we can take the exact same management action and see a range of different outcomes. Let’s explore this in the simplest possible way, by revisiting our model of exponential growth in discrete time: $N_t = R^t N_0$. Now, we add a simple error term, $N(t + 1) = RN(t) + z(t)$. Note that because it is a function of time, z is different in every time step! It’s not a constant. The simplest definition of z is that it is normally distributed with a mean of 0 and a variance of σ^2 , where σ is a standard deviation parameter that you could set (for a simulation) or estimate from data. Let’s plot how that affects the exponential model.

Stochastic Exponential Growth

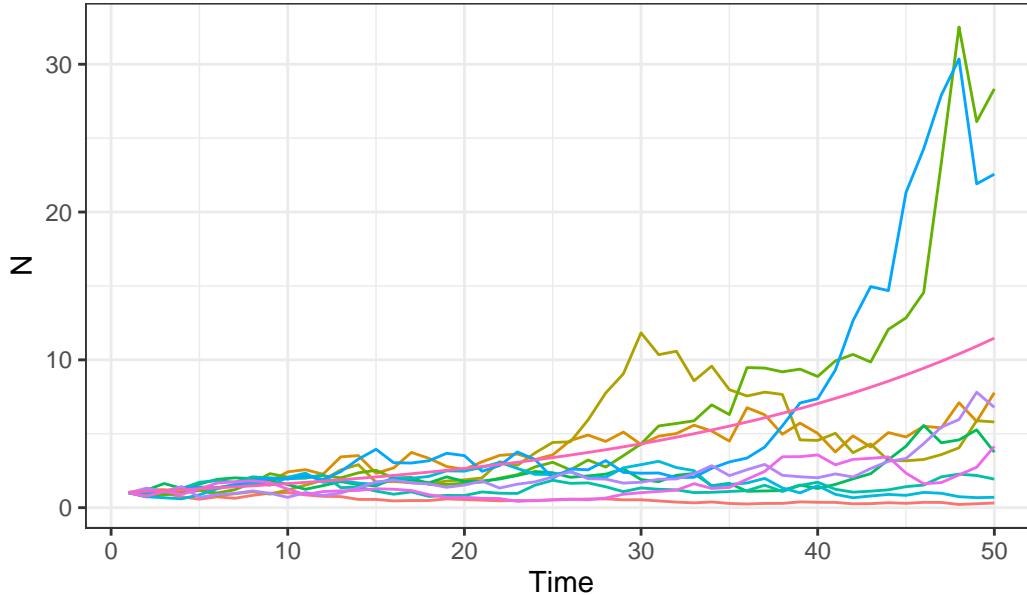


In this most simple case, the deterministic trajectory is predicted to be the same as the average of the stochastic trajectories. However, this is just a product of how simple exponential growth

is (i.e., the first derivative of this model is linear). If that were not the case, we could not get back the deterministic trajectory just by averaging the stochastic ones.

In the plot above we added a super simple error term to the end of the equation. We could also add it *inside* of the growth rate, such that there is random fluctuation in per-capita growth from one time step to the next (rather than stochasticity in population size): $N(t+1) = (R+z)N_t$. Let's re-generate the above plot with the same parameter values but this form of stochastic dynamics instead.

Stochastic Exponential Growth



This form of stochasticity—which modifies per capita growth rather than overall population size—leads to much greater fluctuations in predicted dynamics. Which form of stochasticity is “right”? As with other decisions in this class, the answer is partly based on biology (where do you actually think stochasticity enters the system?) and partly on your data (which more resembles the system you are trying to model?) Mangel goes into depth on other kinds of stochasticity that are more useful in modeling real-world systems, including Brownian motion (a continuous-time form of stochasticity that accumulates over time, meaning that uncertainty builds as the system evolves forward).

One really common use of stochasticity in population biology is in **population viability analysis**. This is a method for figuring out the probability of a population persisting with a positive growth rate in a given time frame, usually in the context of human impacts and/or management interventions (similar to our loggerhead sea turtle case study). These models are often developed for megafauna with small population sizes. I'm going to introduce you to one developed for Southern Resident killer whales, a population of orcas that lives off of BC / WA. This population receives massive research and public attention, for many reasons including that they are declining due to a host of human impacts (most notably declining Chinook salmon,

their major prey; noise disturbance; and contamination by PCBs which bioaccumulate and cause increased mortality) plus inbreeding. The Southern Resident killer whale population is *small*: <80 individuals. A huge amount is known about each individual whale: its age, sex, parentage, etc.

Lacy *et al.* 2017 (Scientific Reports) developed a ridiculously detailed population model of these killer whales. They have actual, historical values of demographic parameters every year, so they can use not just the rates but fit an environmentally-driven function, and they also included individual variation in many rates (e.g., probability of reproductive success).

Try to imagine what you would need to know to understand if this tiny population of orcas will be around in 80 years. A lot of your questions would center around binomial outcomes: will an orca survive to the next year or not? Will a reproductive female have a calf or not? What sex will that calf be? Will it be a good year for salmon or a bad year? Etc.

So in this PVA (and most PVAs), the researchers used stochastic—not deterministic—approaches. They set up a very complicated population model with variation across environmental conditions, sexes, age classes, and sometimes individuals. Then they simulated it forward but with many of the rates drawn from probability distributions. Their 10,000 model trajectories were hugely divergent: the estimated little r was -0.002, but the standard deviation was 0.045 (which obviously covers the difference between recovery and extinction).

We're going to pause our discussion of stochasticity here, because it's veering into statistical modeling, and there are other courses at UCSC to learn about autoregressive processes (take the time-series class!) and Bayesian statistics (where you can simultaneously model underlying processes and variation introduced by different processes, including data collection; also a class worth taking). Suffice it to say that if one issue you have had in this class is that all of the models look much "neater" than your data, or if issues of small sample sizes and binomial outcomes (like with killer whales) arise, you may still be able to use these mechanistic models to understand your study system, with some extensions that capture sources of stochasticity.

Interacting populations

We've already started to write down equations for multiple age classes or life stages; multiple patches and populations; and multiple forms of population growth. Now and for the next few weeks, we're going to consider some models of multiple interacting species.

First, I think it's worth interrogating—why do we need multispecies models at all? What can they capture that we couldn't represent with single-species models? Try to come up with a list of ecological processes that we can't simplify down to exogenous effects on single populations.

Core feature of multispecies models are:

- We are representing populations that are interacting, and

- Those populations are from different species *with different relevant traits*.

So by extension, our goal here is to understand: what happens when populations of species with different traits interact?

There are many kinds of species interactions. I will broadly group these as: interactions that reduce population growth for both species (we start with these); interactions that reduce growth in one population and increase it in the other; and interactions that increase population growth for both species (we will mostly ignore these).

The sections of these notes about Lotka-Volterra models are drawn from A Primer of Ecology (Gotelli, 4th Ed.).

Lotka-Volterra competition

Let's start with a population of species 1 that is growing logistically:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \left(N_1/K_1\right)\right) = r_1 N_1 \left(\frac{K_1 - N_1}{K_1}\right)$$

So far this is just regular logistic growth with a bunch of bonus subscripts. But let's say that we want to reduce population growth by an extra term related to another population of another species, N_2 . **Where in this equation should we put this?**

Let's have it slow down the rate at which species 1 approaches carrying capacity:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \left(N_1/K_1\right)\right) = r_1 N_1 \left(\frac{K_1 - N_1 - f(N_2)}{K_1}\right)$$

There are lots of formulations for $f(N_2)$ that we could write down that would be reasonable. The simplest is just to call it a constant α that scales the population size of the other species. If we include that and factor out K_1 , we get:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \left(N_1/K_1\right)\right) = \left(\frac{r_1 N_1}{K_1}\right) (K_1 - N_1 - \alpha N_2)$$

And we can write the same for the other population,

$$\frac{dN_2}{dt} = \left(\frac{r_2 N_2}{K_2}\right) (K_2 - N_2 - \beta N_1)$$

Let's think a little more about α and β —the “competition coefficients”. In words, what is the relative effect of Species 1's population size *vs.* the population size of Species 2 if $\alpha = 0.5$? 1? 4?

When N_1 increases, this slows down dN_1/dt . We've been calling this *negative density dependence* ([who remembers why it is negative?](#)) You could also call it, equivalently, *the strength of intraspecific competition*.

Conversely, α is the *strength of interspecific competition*. It tells you, relative to the effect of adding another individual of Species 1, what the effect is of adding another individual of Species 2. When $\alpha > 1$, Species 2 inhibits Species 1 more than Species 1 inhibits itself. Be sure you understand what happens to this system of equations if $\alpha = 1$! Note, also, that α and β don't need to be the same number (and usually aren't).

Equilibria and state-space plots

Can we find the equilibrium population sizes for these equations? Let's set each equal to 0.

$$0 = \left(\frac{r_1 N_1}{K_1} \right) (K_1 - N_1 - \alpha N_2)$$

$$\hat{N}_1 = (K_1 - \alpha N_2)$$

$$\hat{N}_2 = (K_2 - \beta N_1)$$

[What is the intuition behind these equilibria in words?](#)

The next thing we might want to do is understand how the dynamics of each population influences the other at different population sizes. Let's unpack that graphically. We're going to use plots a little like the "first return" plots from the delay logistic model, where we plotted N_t vs. N_{t+1} , but here it'll be N_1 vs N_2 .

First we're going to draw those axes. This is called a *state-space plot*. Any point on this graph represents a combination of abundances of the two species. We use this graph to represent the state of our two quantities of interest at the same time. As both populations change in size, we can trace a path on this plot (do this as a demonstration).

Now we're going to draw the *isocline* for Species 1: the line along which its population is at equilibrium. (Notice how the equation for \hat{N}_1 is the equation for a line? What are the x- and y-intercepts on the N_1 vs N_2 plot?) Be sure to label the line $dN_1/dt = 0$.

Another way to think about this is by rearranging the equilibria so just K is on one side. That gives the intuition that in a single-species model, carrying capacity is "filled" by just individuals of that one species. In this Lotka-Volterra model, each species' carrying capacity is "filled" by individuals of both species: $K_1 = \hat{N}_1 + \alpha N_2$. N_2 obviously is not a constant, but realize that in this model, \hat{N}_1 isn't either! There is a wide range of equilibrium values of Species

1 depending on how many individuals of Species 2 there are (as well as other parameters, of course).

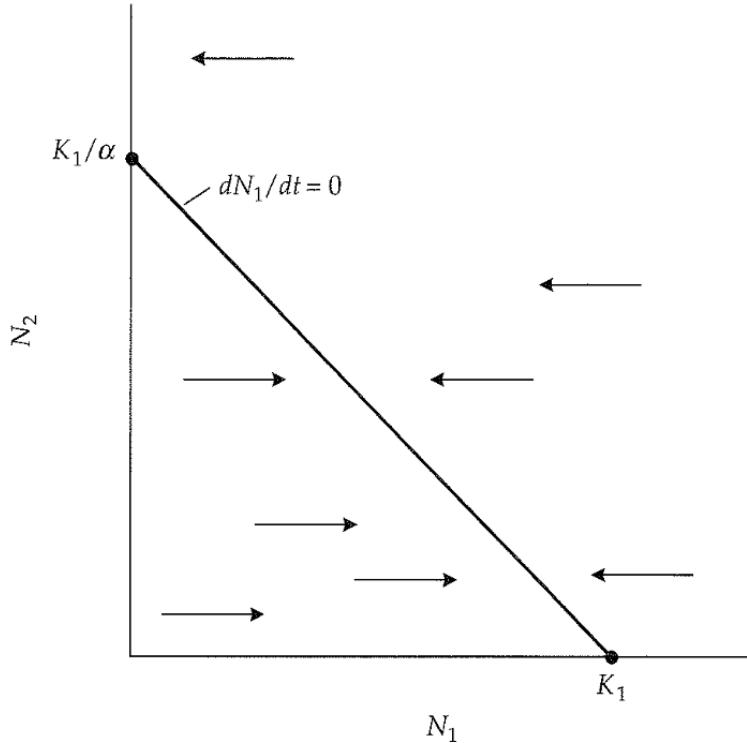


Figure 5.3 The linear isocline for species 1 in the Lotka–Volterra competition model. The isocline defines the combination of abundances for which species 1 shows zero growth. For points to the left of this line, the population of species 1 increases, indicated by the right-pointing horizontal arrow. For points to the right, the joint abundance of species 1 and species 2 exceeds the isocline for species 1, so its population decreases, indicated by the left-pointing arrows.

To the left of the isocline for Species 1, the joint abundance of N_1 and N_2 is less than K_1 , so Species 1 will increase (draw horizontal arrows) and $dN_1/dt > 0$. To the right of the isocline, the joint abundance of N_1 and N_2 is greater than K_1 , so Species 1 will decrease. When we are drawing these graphs, pay very close attention to which species you are plotting, and note that the arrows are parallel to the axis of the species we're focusing on (so right now we're drawing horizontal arrows for the species on the horizontal axis).

On a separate plot, let's plot the isocline of Species 2. What are the x- and y-intercepts? What happens below and above the isocline?

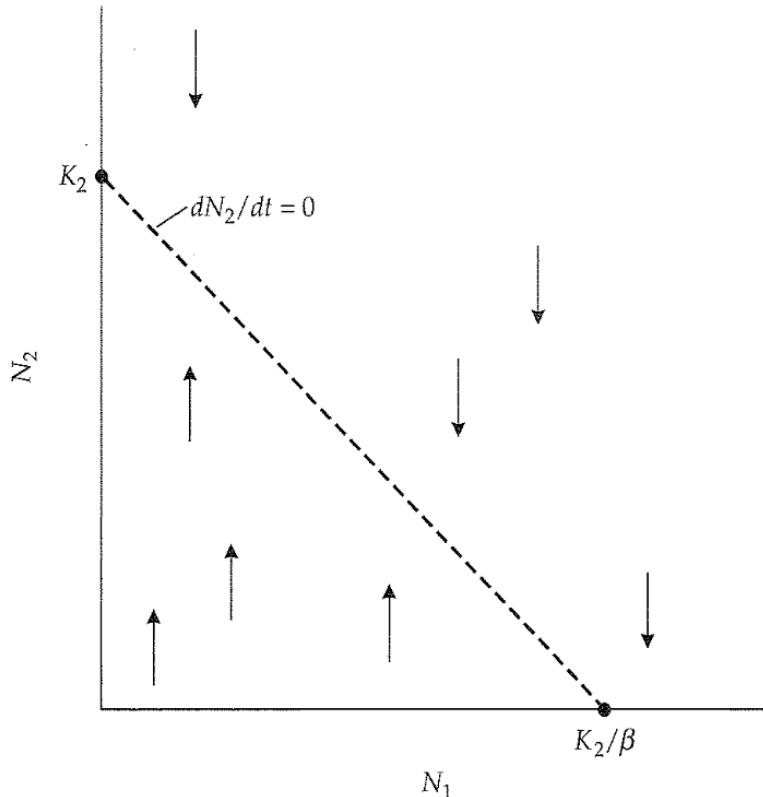


Figure 5.4 The isocline for species 2 in the Lotka–Volterra competition model. Note that the arrows point vertically for species 2, because its abundance is measured on the y axis of the state space graph.

You may have realized by now that there are an infinite number of these lines that we can draw, depending on the values of the two interspecific competition coefficients and the two carrying capacities. However, all of these fall into four qualitative outcomes. Let's plot the two isoclines on top of each other and explore those outcomes.

In the first case, $K_1/\alpha > K_2$, and $K_1 > K_2/\beta$. Take a moment to try drawing those lines yourself on the state-space graph. Once you draw the isoclines, for each species (it helps to use different colors), draw the horizontal and vertical arrows representing their population growth rates in different parts of the state space.

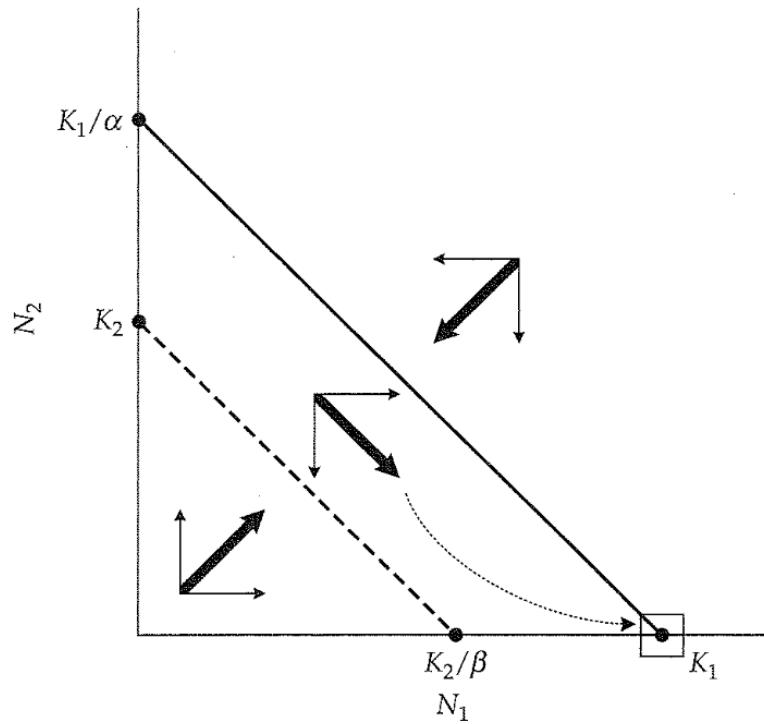


Figure 5.5 Case 1: Competitive exclusion of species 2 by species 1. The thin arrows show the trajectories of each population, and the thick arrow is the joint vector of movement. Competition results in the exclusion of species 2 and an equilibrium for species 1 at carrying capacity. The box indicates a stable equilibrium point.

The top right portion of this state space is easy. We are beyond the isoclines for both species, and both will decline until we hit an isocline (we'll talk more about what happens at that point later.)

Now, think about the bottom left of this state space (when both populations are at low abundance). We are below both isoclines, so both will grow. But what happens when we hit the isocline for Species 2? We're still in the positive population growth rate space for Species 1, so it is just going to keep growing—pulling the system into an area where the growth rate of Species 2 is negative.

We call this case **competitive exclusion** (of Species 2 by Species 1) because *no matter where you start in the state space, Species 2 will go extinct.*

The second case is if we flip these lines and the isocline of Species 2 is always above Species 1. This system will now tend toward the equilibrium where Species 2 goes to K_2 and Species 1 goes to zero. **Draw arrows to show this.**

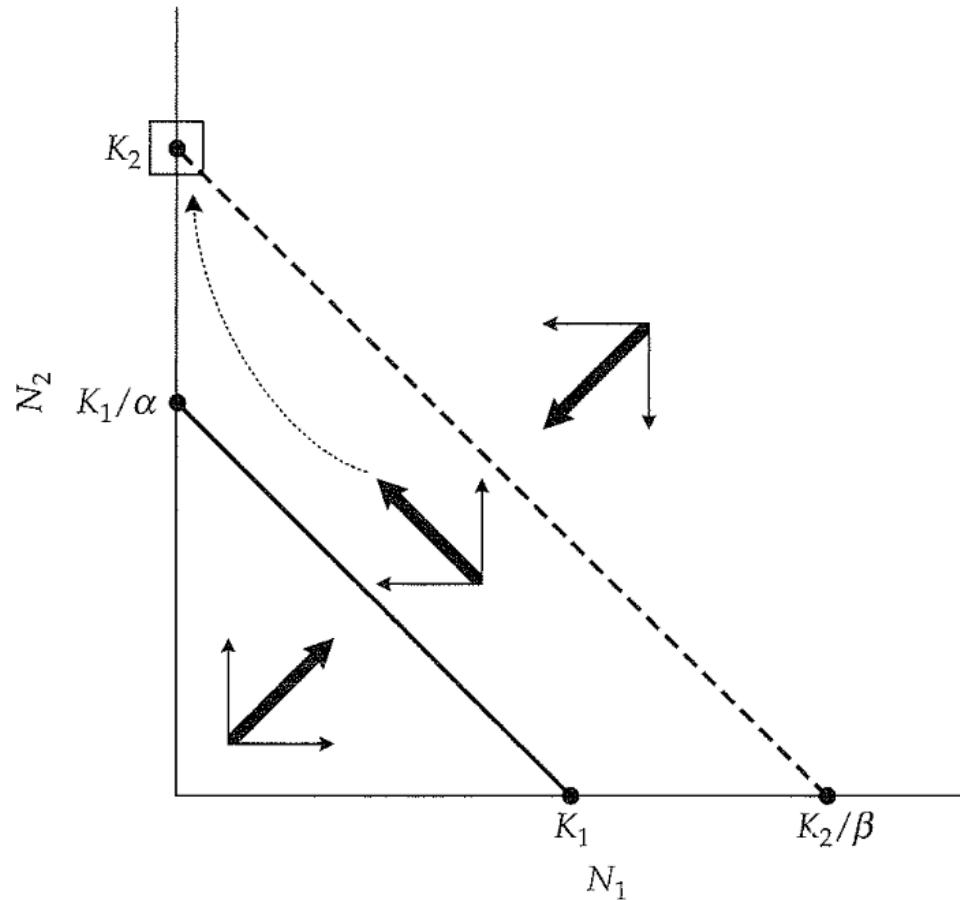


Figure 5.6 Case 2: Competitive exclusion of species 1 by species 2.

The next cases are where things get really fun, because the isoclines are going to cross. What does it mean ecologically for the system of two populations for isoclines to cross?

Let's start by drawing our isocline for Species 1, and the horizontal arrows. Now, the isocline for Species 2 is going to have a shallower slope. Draw this, and the horizontal arrows. Do you think the point where the lines cross is stable or unstable?

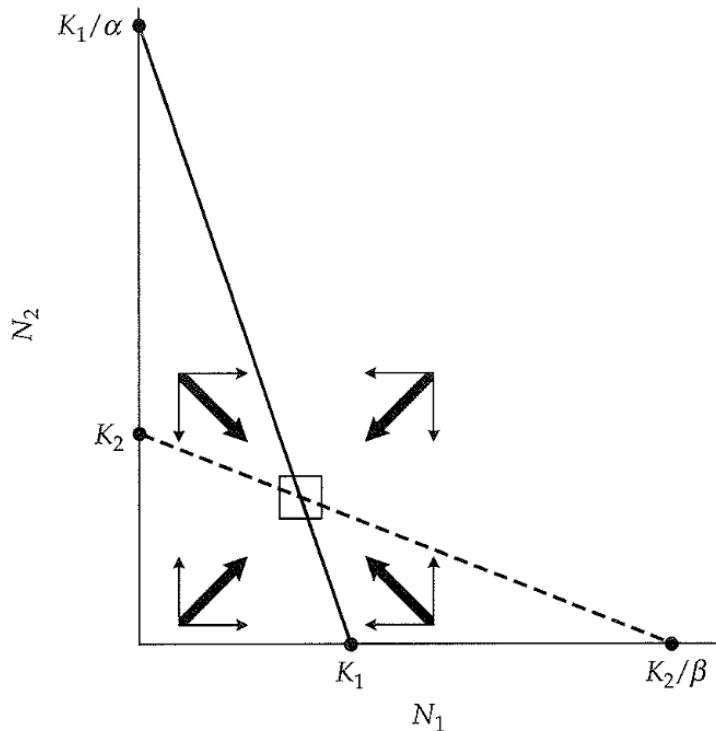


Figure 5.7 Case 3: Coexistence in a stable equilibrium. The two isoclines cross, and the joint vectors point in towards the equilibrium point. The equilibrium is stable because if the populations are displaced, they will always return to their equilibrium sizes.

Our final case is when the Species 1 line is shallower than the Species 2 line. Draw that state-space figure. This is an unstable equilibrium, and the “winner” is hard to predict: it depends on initial conditions and growth rates.

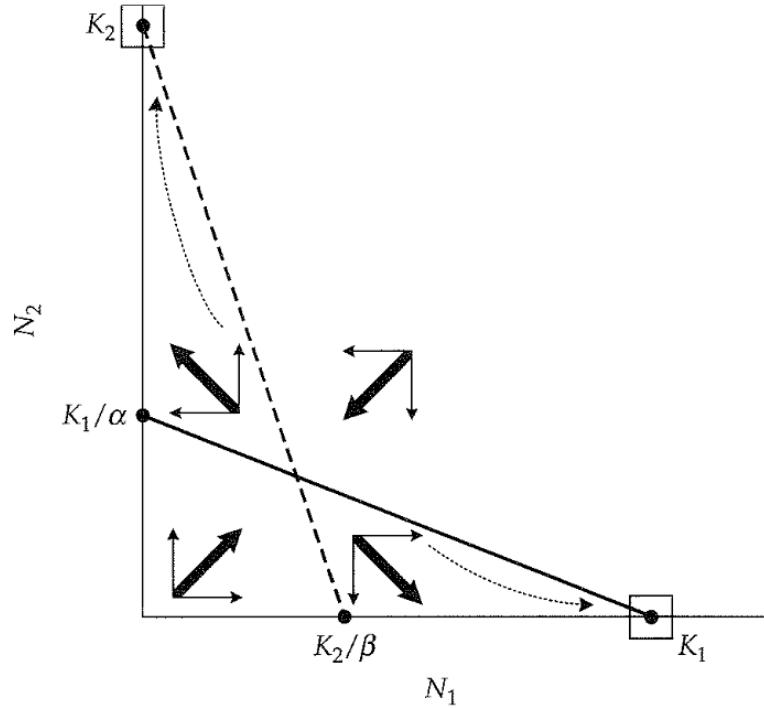
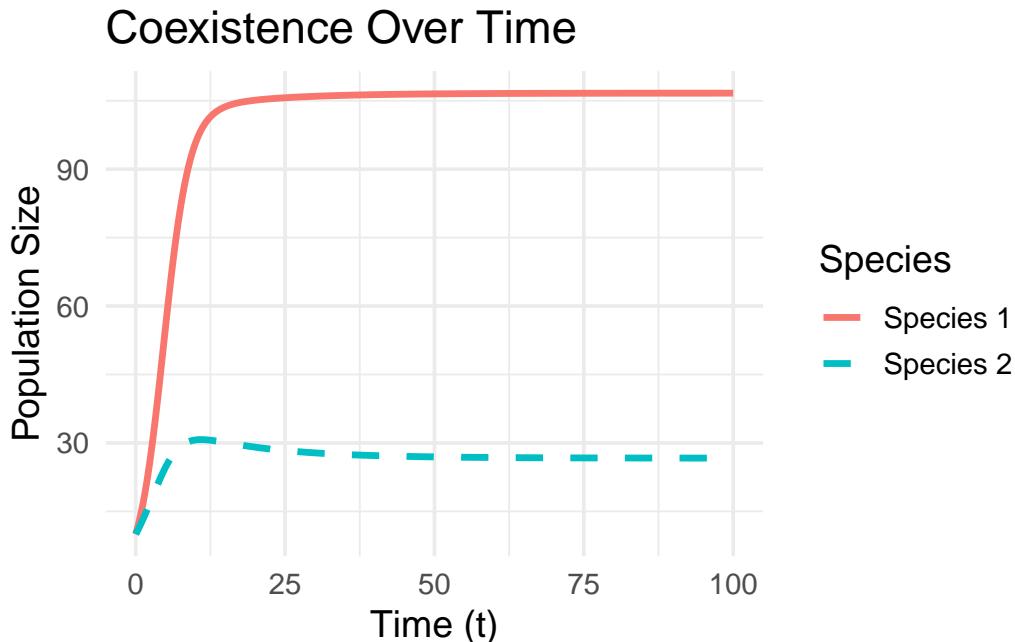


Figure 5.8 Case 4: Competitive exclusion in an unstable equilibrium. The two isoclines again cross and form an equilibrium point. However, the joint vectors point away from this equilibrium. If the populations are displaced, one species or the other will win in competition, depending on the starting abundances.

Population trends over time in Lotka-Volterra competition



Criteria for coexistence

By now you hopefully understand qualitatively that there are four possible outcomes anytime two species interact: one wins, the other wins, they coexist stably, or they have an unstable equilibrium where one is likely to outcompete the other but it's hard to guess which. The more interesting question is maybe *when you expect each of these outcomes*, which we will answer next.

Is there a way to guess the outcome of Lotka-Volterra competition without drawing these graphs? Just like with the other models we've discussed, the answer is yes! The key insight here is to think about what happens if we end up on the state-space diagram where one population is at really low abundance and its competitor is at high abundance. Does it have a chance of increasing then (i.e., a positive per capita growth rate)? If so, then we can argue that it will persist in that scenario.

The mathematical criterion describing that situation is:

$$\frac{dN_1}{N_1 dt} = r_1 \left(\frac{K_1 - N_1 - \alpha K_2}{K_1} \right)$$

Remember, we're looking for this quantity to be above 0. Because r_1 is always positive, that means that we can just look for the right-hand term to be positive as well:

$$\frac{K_1 - \alpha K_2}{K_1} > 0$$

Which we can rearrange to state the criterion for Species 1 to successfully invade: $K_1/K_2 > \alpha$. This suggests an intuitive proportionality between the carrying capacity of Species 1 and the competitive strength of Species 2.

The analogous inequality holds for the persistence of Species 2 ($K_2/K_1 > \beta$). If we invert both sides of this, we can directly compare it to the first inequality! **Using just these two inequalities, write down mathematical conditions for the four outcomes we found graphically earlier.**

These sets of inequalities can be interpreted in a number of ways. One is by asking: What happens to stable coexistence as α and β approach 1? Remember that those parameters tell us how much an individual of one species inhibits the other, so when they are close to 1, it means they affect each other about as much as they affect themselves. As these species get really similar, the ratio of carrying capacities that allows coexistence becomes vanishingly small. This led to the *principle of competitive exclusion*, which is that species with identical resource use cannot coexist.

This idea—that very similar species are unlikely to coexist—has received a lot of attention in theoretical ecology. In nature, there are lots of similar species, which has been difficult to explain with models. In the next few sections of these notes we'll introduce some other attempts to explain the biodiversity we see in nature with simple models of coexistence. **Besides this Lotka-Volterra criterion—that species should inhibit others at a rate different from that at which they inhibit themselves—what other mechanisms for coexistence have you heard of?**

Lotka-Volterra predation

Competition is a major focus of terrestrial community ecology, where people are often studying birds, plants, insects, and other taxa that frequently and intensely compete with one another. In the oceans, species interactions are more likely to be consumptive: marine stuff tends to eat other marine stuff. To model those interactions, we need to adapt the models above to represent predator-prey dynamics.

The Lotka-Volterra analog calls the predator population P and the prey or “victim” population V. We can say generically that $dV/dt = f(V, P)$. But what is f here? Well, it depends on what we think drives the abundance of V. Maybe we think that in the absence of predators, V would increase exponentially (this is the simplest case):

$$\frac{dV}{dt} = rV$$

But this exponential increase is offset by losses that occur when predators are present. We write down a form for this where losses are proportional to *the product* of the number of predators and the number of prey,

$$\frac{dV}{dt} = rV - \alpha VP$$

This is not the same α as before. Now, it is measuring the effect of a single predator on *per capita* growth of prey, dV/Vdt . We call this **capture efficiency**. (Its units are victims / (victim times time times predator).) When we multiply this by V (αV), it gives us the rate of prey capture by a single predator as a function of prey density—also known as the **functional response**.

We also think that predator growth rates are affected by both predators and prey, $dP/dt = g(P, V)$. For the sake of simplicity we say this predator is specialized only on this prey source and its population can only grow when the prey population is present.

$$\frac{dP}{dt} = \beta VP - qP$$

Here βVP indicates random encounters of predators and victims, and β represents **conversion efficiency**—the effect of a single victim on the per capita growth rate, dP/Pdt , of the predator. (This is analogous to catchability in the constant harvest model.)

Setting the victim equation equal to zero, we find the following equilibrium solution:

$$\hat{P} = \frac{r}{\alpha}$$

Wait a minute; why is the victim equilibrium—where that population is not changing in size—defined in terms of the predator population? In this simplest formulation of a predator-prey model, a specific number of predators maintains the victim population at zero growth. Doing the same for predators, we find

$$\hat{V} = \frac{q}{\beta}$$

Again, we find that a threshold number of victims maintains the predator population at a fixed size. Let's plot these two isolines in state space, now with victims on the x-axis and predators on the y-axis.

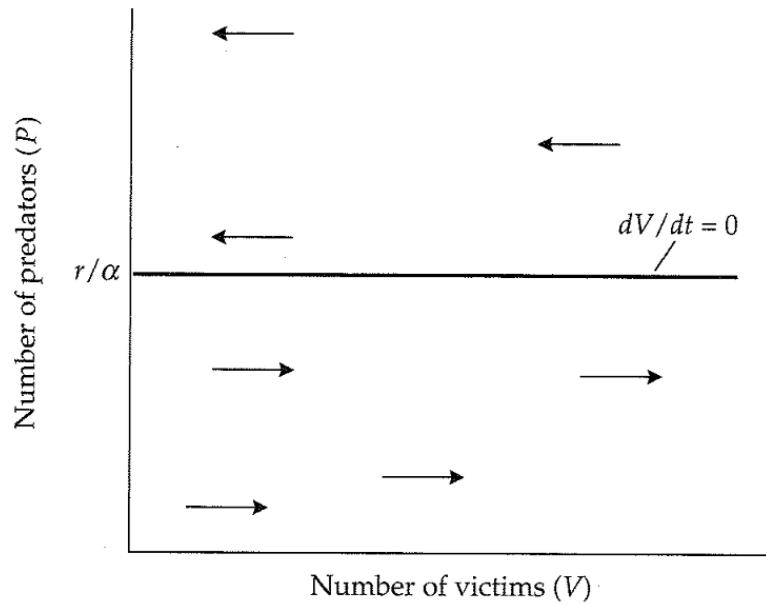


Figure 6.1 The victim isocline in state space. The Lotka–Volterra predation model predicts a critical number of predators (r/α) that controls the victim population. If there are fewer predators than this, the victim population increases (right-pointing arrows). If there are more predators, the victim population decreases (left-pointing arrows). The victim population has zero growth when $P = r/\alpha$.

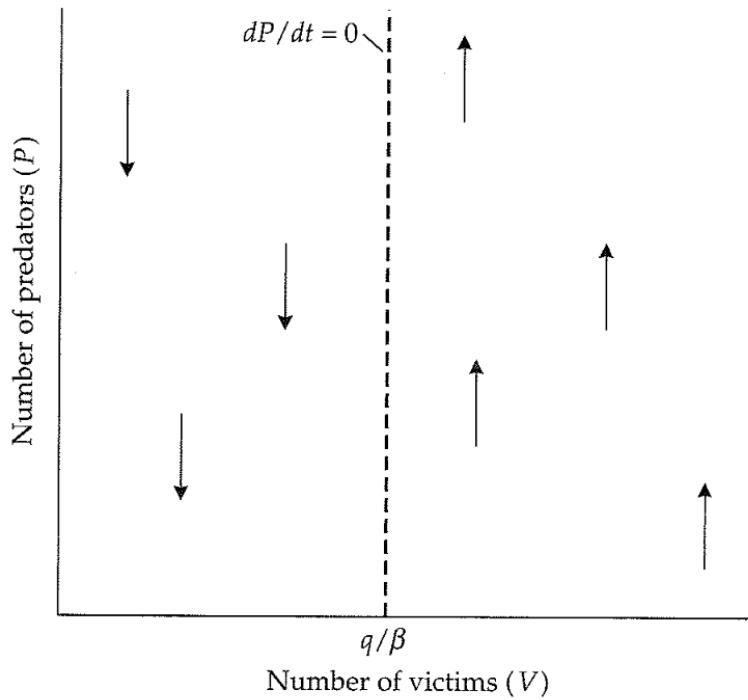


Figure 6.2 The predator isocline in state space. The Lotka–Volterra predation model predicts a critical number of victims (q/β) that controls the predator population. If there are fewer victims than this, the predator population decreases (downward-pointing arrows). If there are more victims, the predator population increases (upward-pointing arrows). The predator population has zero growth when $V = q/\beta$.

Now we put this all together to jointly map predator and prey populations:

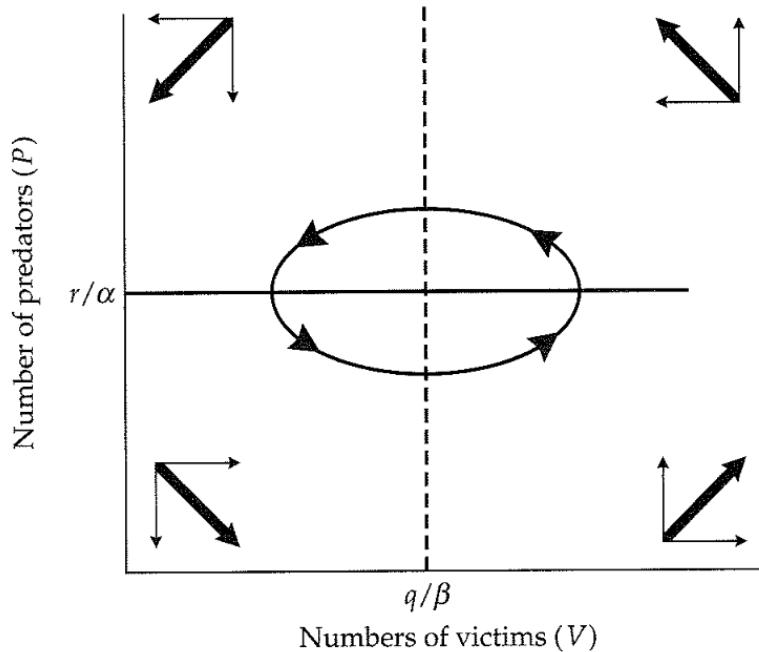


Figure 6.3 The dynamics of predator and victim populations in the Lotka–Volterra model. The vectors indicate the trajectories of the populations in the different regions of the state space. The populations trace a counterclockwise path that approximates an ellipse.

Unlike the competition model, there is only one possible outcome of combining these isoclines. The intuition behind what this means for population dynamics is clearer if we look at an actual plot of population sizes over time.

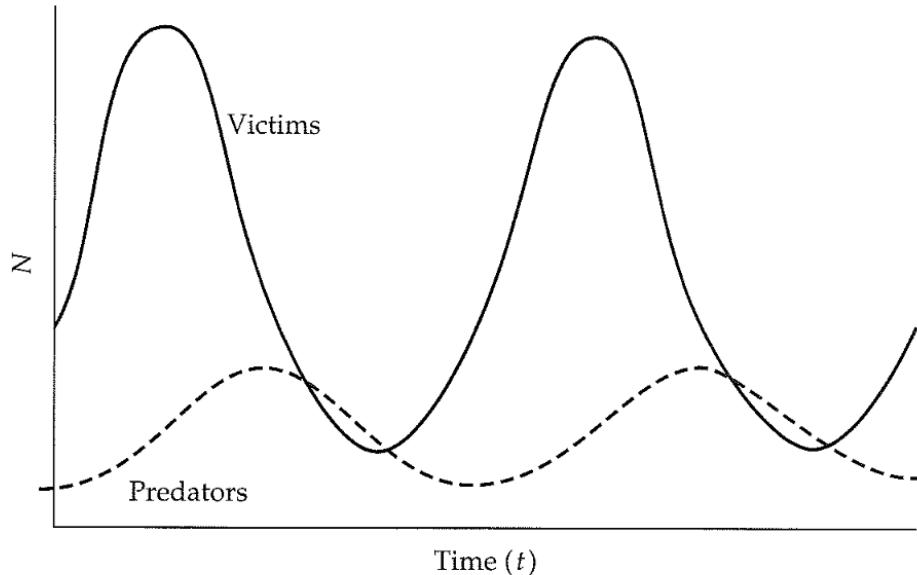


Figure 6.4 Cycles of predators and victims in the Lotka–Volterra model. Each population cycles with an amplitude that is determined by the starting population sizes and a period of approximately $2\pi/\sqrt{rq}$. The predator and victim populations are displaced by one-quarter of a cycle, so that the predator population peaks when the victim population has declined to half its maximum, and vice versa.

At first, prey experience low predation and grow quickly. As the prey population increases, predators also increase, albeit with a slight lag. They then deplete the prey population which quickly declines. As predators decline in turn, prey are released from predation and can increase, starting the cycle over again.

Unlike the Lotka–Volterra competition model, where there are multiple qualitatively different outcomes and the parameters are hard to estimate, here we actually see predator-prey cycles in nature not infrequently—with canonical examples that include moose and wolves on Isle Royale, for example. There are lots of extensions of the Lotka–Volterra predator-prey model (see Gotelli) to add complexity, such as a victim carrying capacity.

Alternative models for coexistence

R*

There are many other models that make predictions of species coexistence besides Lotka–Volterra. One group of those focuses less on extensions of density-dependent growth, and more on the idea that coexistence is limited by competition for resources. Actually, this is a different way of thinking about quantifying population growth, where populations grow purely

as a function of resource availability (where resources are broadly defined and can include abiotic and biotic pools) and mortality. Sound familiar? Ecosystem models or “box models” are often *consumer resource models* at heart. You learn these in biological oceanography, but today we’ll put an ecological twist on them.

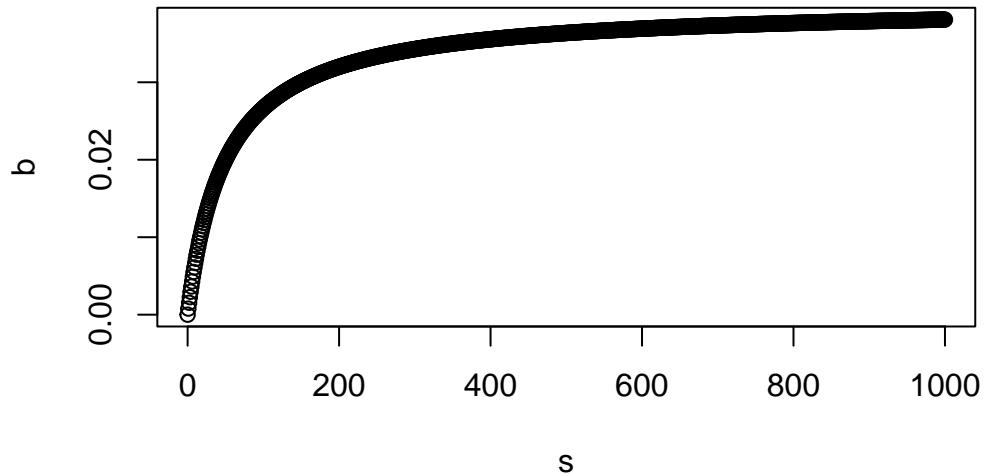
Lotka-Volterra competition doesn’t give rise to coexistence very easily. Recall that there were many scenarios in which the equilibrium state was reached when one species outcompeted the other. Yet in nature, we see many species coexisting. One early explanation for this was *niche diversification*; broadly, we have immense biodiversity on Earth because each species has a different *environmental niche*. It follows from the principle of competitive exclusion that two species with identical niches cannot coexist. (For a nice summary of this, see Hutchinson’s “Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?”)

Niche diversification or *differentiation* seems intuitive when looking at animals and plants. Fish have different foraging strategies, plants often partition habitat at small scales, and so on. There is also evidence for this happening in time, which is called the *storage effect* (when species use resources and habitats in different seasons or times of day, for example). Yet it’s hard to argue that there are as many distinct environmental niches as there are species of phytoplankton (G.E. Hutchinson called this, famously, “the paradox of the plankton”). He argued that in some systems, *equilibrium is never reached*, especially among fast-growing, short-lived organisms such as plankton.

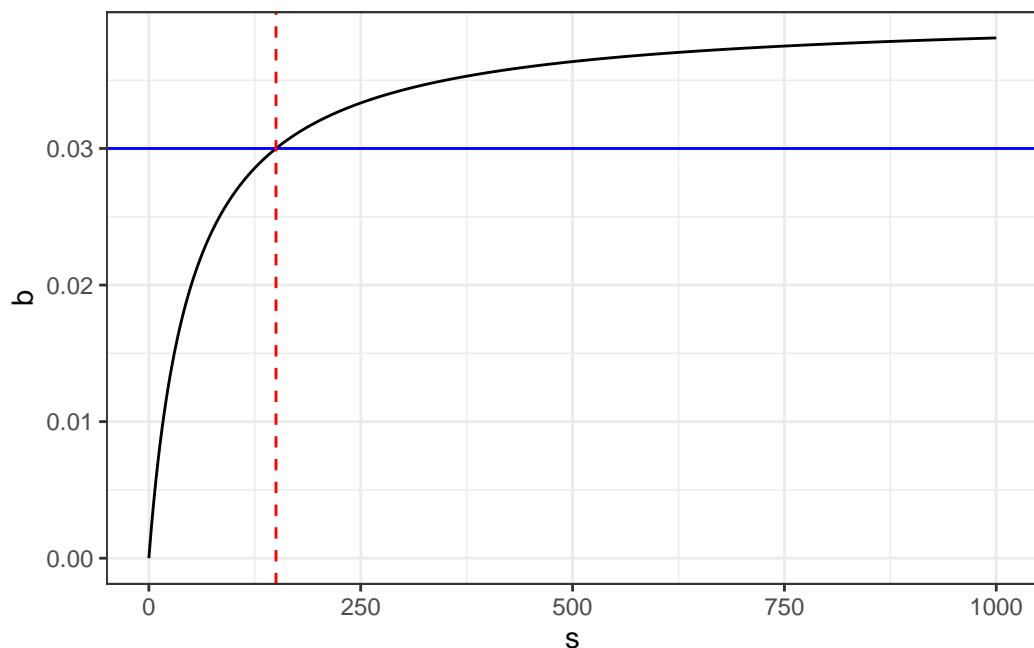
This theory is appealing because niches are hard (maybe impossible) to measure, but resources are easy—and these consumer-resource models are all about temporal variability in resource density. Here, a resource is anything in the environment a species uses that gets depleted as a population grows. We denote those resources R , which I understand is super confusing since that represented discrete-time average growth earlier! We say that a single population on a single resource will grow according to the Monod equation,

$$b = r \frac{R}{K_S + R}$$

Where K_S is a half-velocity constant: the value of R when $b = 0.5r$. This implies that in the absence of mortality,



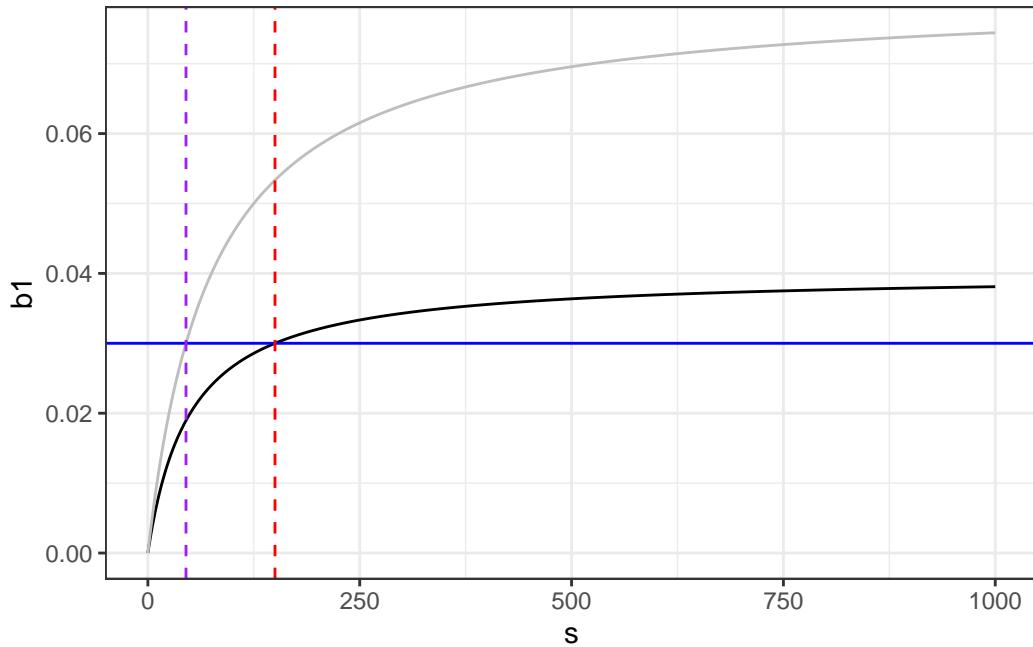
But we know that there is some mortality rate. Let's say this is fixed at m . Then, any resource level below where a line at m intersects the curve above would be insufficient for this population; in other words, it needs a minimum resource concentration for b to be equal to or greater than this value R^* .



Where on this plot is dN/dt positive? Negative? Zero?

You can probably see here that R^* is an equilibrium: $b = d$. Is R^* stable or unstable? If you have $R < R^*$, the population declines, which allows the resource to recover; then R^* will increase. If $R > R^*$, the population will use up the resource until it is depleted to R^* .

Let's add another consumer with its own curve of birth rate as a function of resource availability, but with the same value of m . (As you have probably already realized, m is a lot like a sinking rate in a NPZ model.)

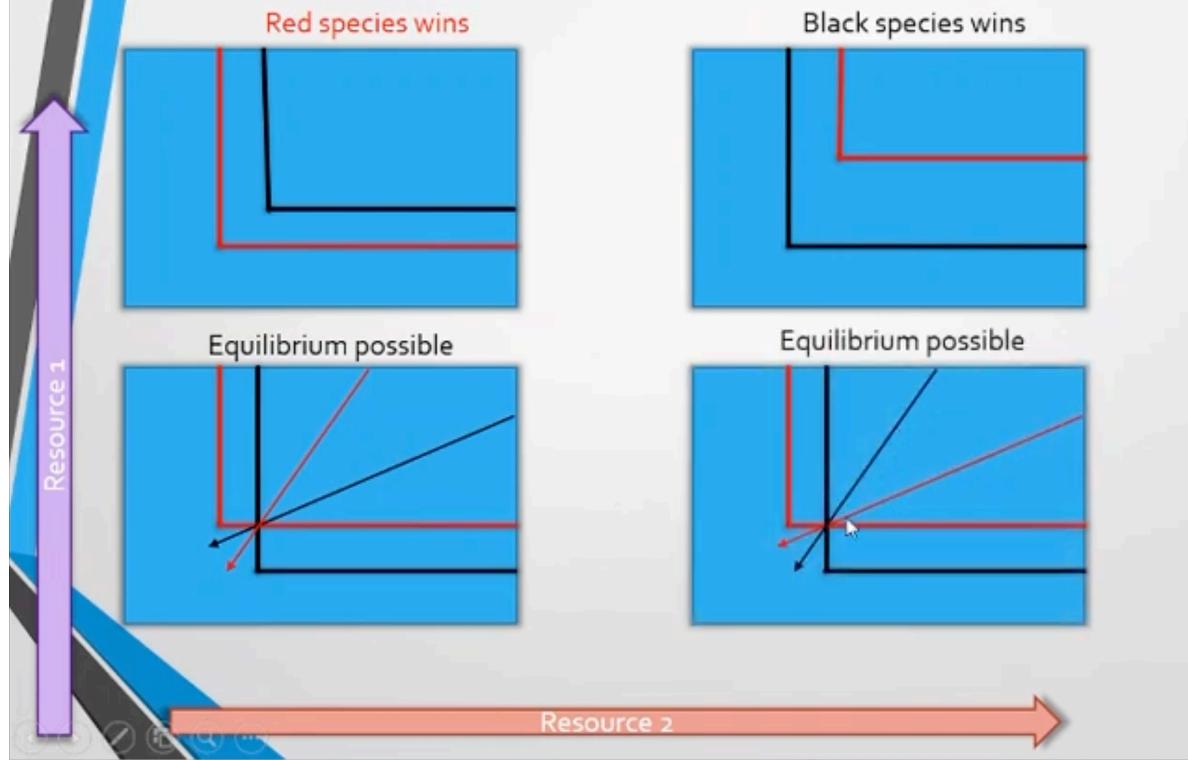


Label both R^* values on the plot for both species. [What is the outcome of this two-consumer, one-resource model?](#) In this scenario, the species that can have a positive growth rate at a lower resource concentration will always win. (Re-draw the lines crossing, which I can't seem to do on a computer, and discuss what that implies at artificially high resource concentrations.)

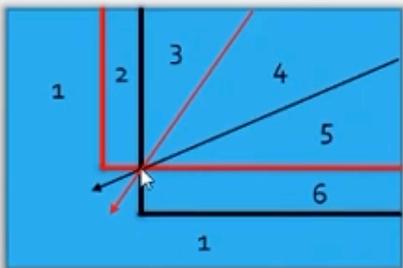
What if we introduce a second resource? Now, we need to put a resource on each axis. Just like in the Lotka-Volterra models, we're going to draw species' isoclines on these plots: the lines at which their growth is zero (birth = death). We actually did that above, when we drew a line at R^* . If we do that for a species' R^* values *on both axes*, we get an isocline that looks like a right angle.

Let's assume, for simplicity, that Resource 1 and Resource 2 come into the system at an equal rate. Then we can draw (images courtesy of Brian O'Neill, University of Wisconsin)...

R^* - 2 consumers, 2 resources



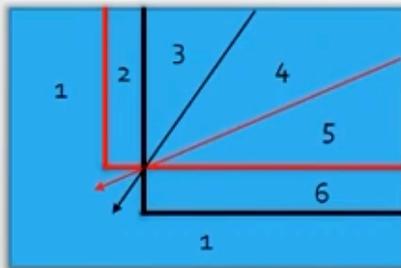
R^* - 2 consumers, 2 resources



- Resource supply point location
 - 1 – insufficient resources to support either species
 - 2 – Red species wins
 - 6 – Black species wins
 - 3 – Red species wins
 - Red draws resources to left of black ZNGI
 - 5 – Black species wins
 - Black draws resources below red ZNGI
 - 4 – Stable equilibrium
 - Each species consumes resource that limits itself most



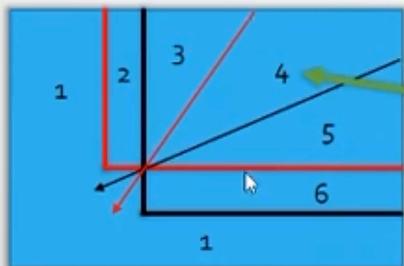
R* - 2 consumers, 2 resources



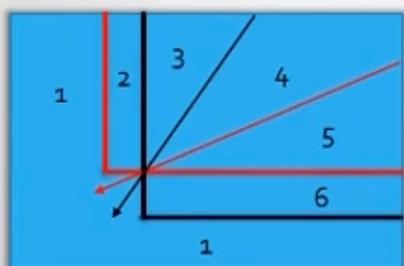
- Resource supply point location
 - 1 – insufficient resources to support either species
 - 2 – Red species wins
 - 6 – Black species wins
 - 3 – Red species wins
 - Red draws resources to left of black ZNGI
 - 5 – Black species wins
 - Black draws resources below red ZNGI
 - 4 – **Unstable equilibrium**
 - Each species consumes resource that limits other species most



Coexistence



- Is it possible?
- Requires interspecific competition to be weaker than intraspecific
 - If intra stronger
 - Species will be self limited and not completely take over other species
 - If inter stronger
 - If species gains upper hand, it won't be stopped by itself



Many interacting species

Food web models

You hopefully learned in an introductory ecology about food web models. These are intuitive maps of what eats what in an ecosystem. These are a central concept in community ecology, anchoring our understanding of how energy flows through ecosystems and how species affect each other. Food webs historically emphasized bottom-up processes: producers do photosynthesis, primary consumers eat producers, secondary consumers eat primary consumers, apex predators eat everything.

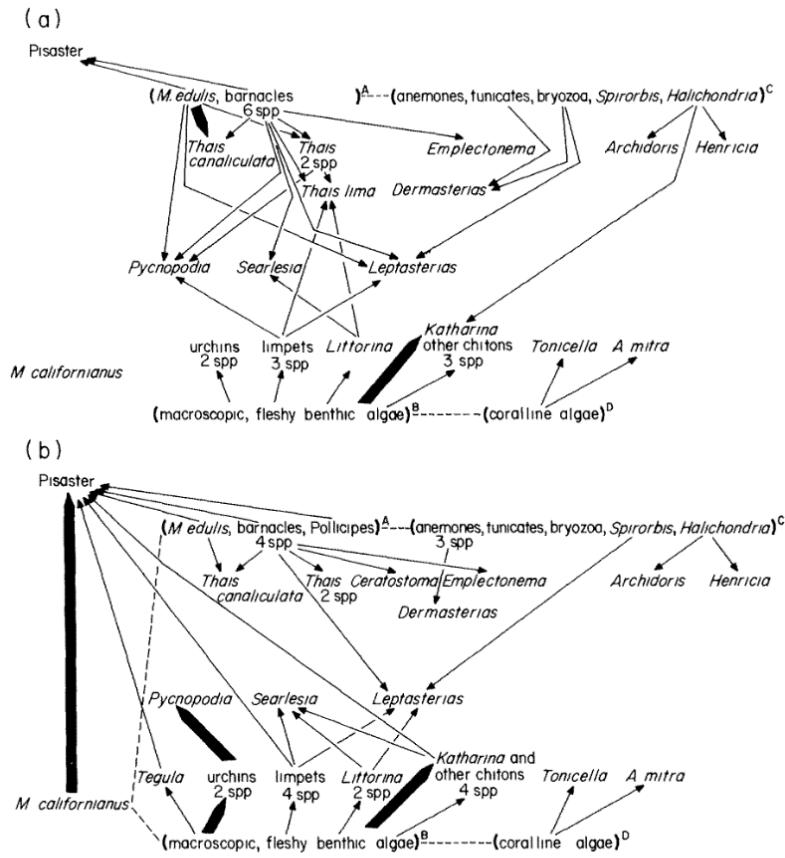


FIG. 2. Two eastern Pacific rocky intertidal food webs. (a) Torch Bay, Alaska (b) Cape Flattery area, Washington. The topological positions of species common to both is identical. Symbolism is the same as in Fig. 1.

Trophic cascades

However, it has always been clear that populations at higher trophic levels can influence lower trophic levels as much as the reverse. A canonical example of this is a *trophic cascade*, when predators indirectly mediate other species interactions (see Ripple et al. 2016 TREE). One common consequence of a trophic cascade is the elimination of a predator leading to a decline in lower trophic level diversity, essentially because the predator was maintaining high biodiversity by interfering with competition. In Bob Paine's iconic experiments removing *Pisaster* (a top predator sea star) from an island's rocky shores, the community declined from 15 species to 8, because mussels outcompeted every other similar species with which it had previously coexisted under the predation pressure of *Pisaster* (Paine 1966).

This is where we'll end our discussion of models of interacting species. I could easily teach another entire course on community ecology, exploring the many mathematical models that

aim to theoretically predict the diversity and coexistence we see in ecosystems. But this veers quite far away from population dynamics, which is what you signed up to learn. So we return to some special topics in population dynamics to wrap up this course.

Resilience, stability, and tipping points

Textcolor{green}{{Take a moment to reflect, and then share: What does “resilience” mean in the context of population dynamics?}}

Much of classical ecological theory brought principles from physics and chemistry to bear on modeling populations, with a major focus on quantifying equilibria and stability. Yet the degree to which stability is a feature of ecosystems—and what it would look like in nature for an ecosystem to be “stable”—is widely debated. Notably, the conditions for stability are essentially always violated in the present day. The idea that species can be in equilibrium with their environment hinges on the environment not changing, which is never true now. Plus even in an unchanging environment it’s likely that ecosystems are frequently in transient states.

In 1973, CS Holling wrote a seminal paper (cited more than 27,000 times as of the writing of these notes) confronting this flaw in ecological models: that they are unrealistically simple and their dynamics often lead to global instability or global stability—neither of which seem very plausible. He argued that instead, thinking of the phase plane of interacting species, there are likely to be regions that lead to stable equilibria—a “domain of attraction”—and regions that lead to extinction of one species. (We did see some phase plane plots that were not globally stable or unstable, but those were decided by chance initial conditions, not by fundamentally different dynamics in different parts of the phase plane—which is what Holling argued for.)

Fundamental to this issue is the question, how complex is a real state-space plane of an ecosystem? Can we develop models that suggest multiple “domains of attraction” exist? Early theoretical ecological models suggested that there are “alternative stable states”, which means multiple domains of attraction (see May, 1977). [Draw ball-and-cup diagram and label domain of attraction and stable and unstable equilibria.](#)

What features are we looking for these models to capture in order to be more “realistic”? Holling gives the example of an alpine lake in Italy for which we have historical data for about 4,000 years. The lake ecosystem persisted essentially unchanged even as the land around it shifted from grassland to forest (post-glaciation) and the construction of Roman highways. Then suddenly, shortly after 171 BC, the entire aquatic ecosystem altered to a eutrophic and high-productivity state, from which it did not rebound. Holling wrote, “The whole sequence of environmental changes can be viewed as changes in parameters or driving variables, and the long persistence in the face of these major changes suggests that natural systems have a high capacity to absorb change without dramatically altering. But this resilient character has its limits, and when the limits are passed, as by the construction of a Roman highway, the system

rapidly changes to another condition.” Draw two cases of “conditions” (x-axis) vs. ecosystem state (y-axis): a downward-sloping line and a steep drop-off like in the lake example.

Holling proposed new definitions for stability and resilience as the two defining features of ecosystems:

- **Resilience** determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist. Resilience tells us
- **Stability** is the ability of a system to return to an equilibrium state after a temporary disturbance. The more rapidly it returns, and with the least fluctuation, the more stable it is.

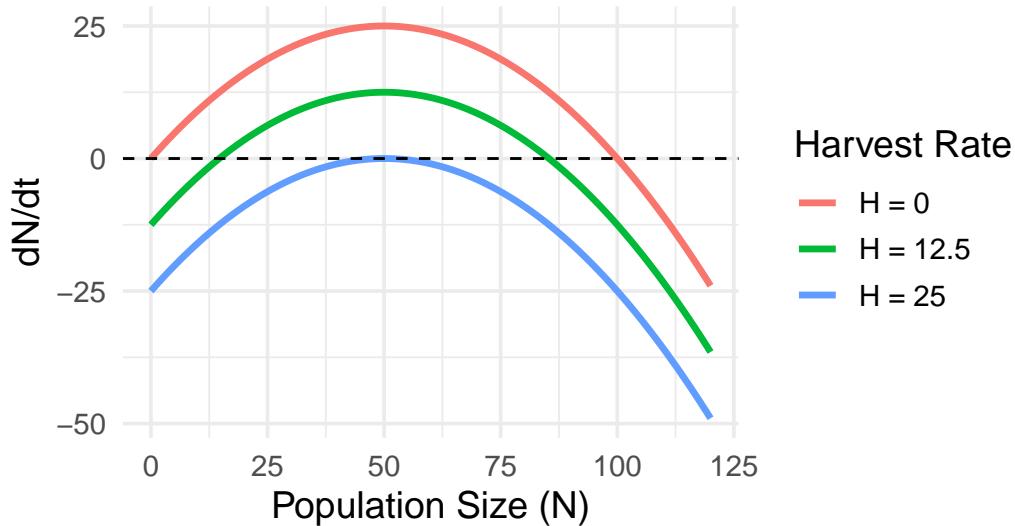
This implies two measurements for stability: its displacement from a historical baseline, and its return time. Holling proposed measuring resilience as the size and depth of the domain of attraction in the state-space plane (how big is the cup?) Also note that the term “equilibrium” is nowhere to be found here! The point is that we look for resilience instead.

An example using constant harvest of a density-dependent population

We didn’t use these words at the time, but we actually—in a single species!—found a case like the lake one above when we looked at the constant-harvest (MSY) model in a logistically growing population. Recall when we drew,

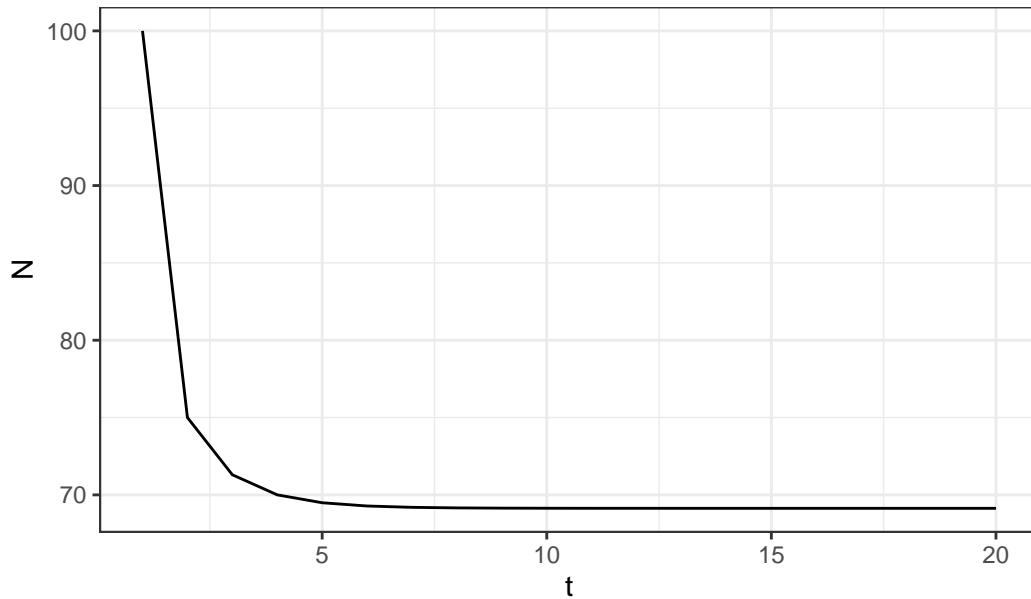
Logistic Growth With Varying Harvest Rates

$$H_{\max} = 25 \text{ occurs at } N = K/2 = 50$$



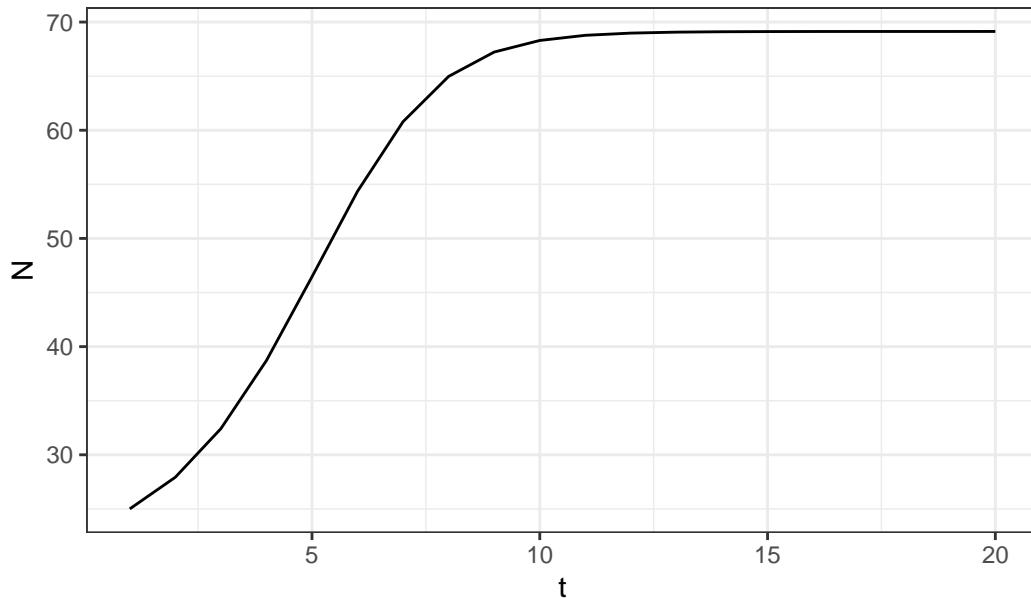
Now for the population where $H = H_{\max}$, let's actually draw its population size through time, starting out at K and introducing constant harvest. (Ignore the actual values in terms of K and H ; I generated these plots with a Ricker model so they aren't at the exact theoretical points as in the continuous-time logistic, but they're just here for illustration.)

Initial population size = K ; Maximum harvest

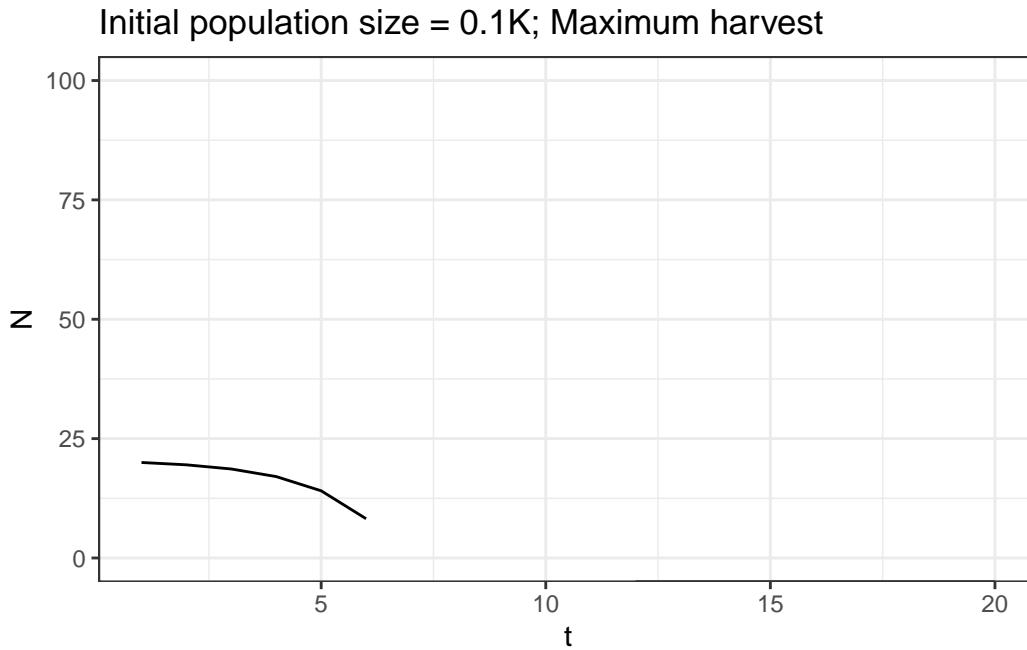


What happens if the population starts at a smaller population size?

Initial population size = $K/4$; Maximum harvest

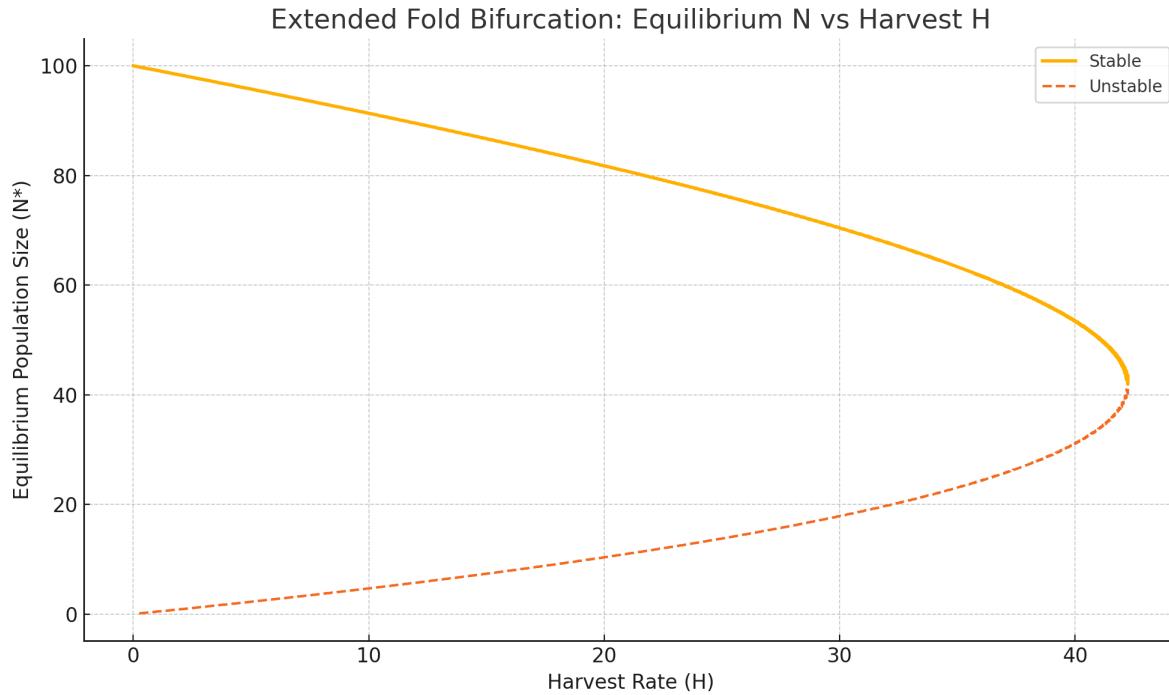


Even smaller?



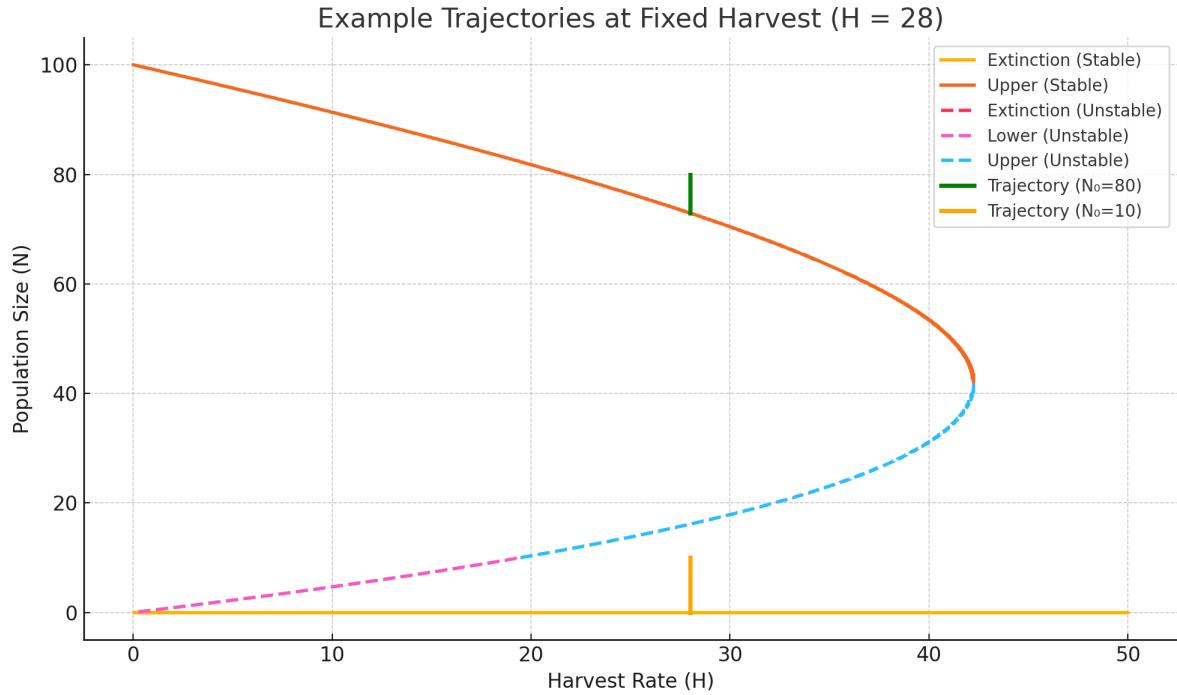
We will see this pattern both as a function of different initial population sizes, and different values of H (recall that when H was just below H_{max} there was a stable and an unstable equilibrium value). Think back to the curve above with different values of H. The values of H below H_{max} generated two equilibria, one stable or unstable. Now in this resilience framework, let's focus more on the outcome for population size (asking—does the system still look the same, ie have a bunch of fish?) and on varying H.

Hysteresis

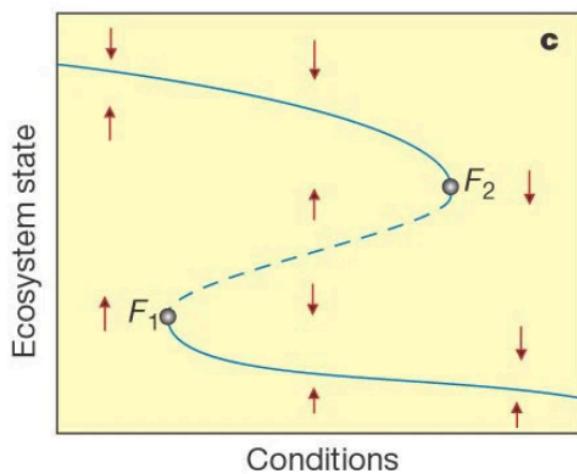
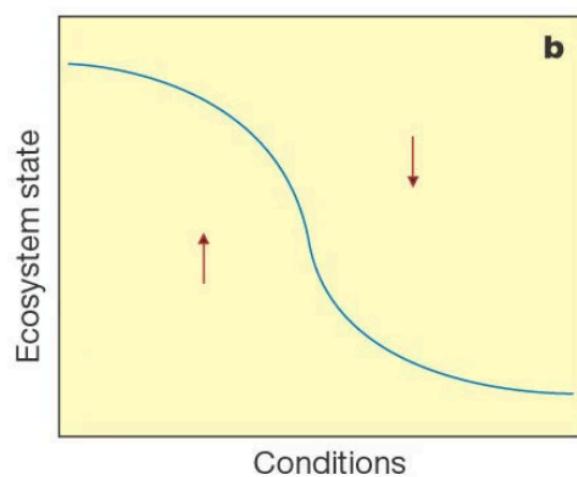
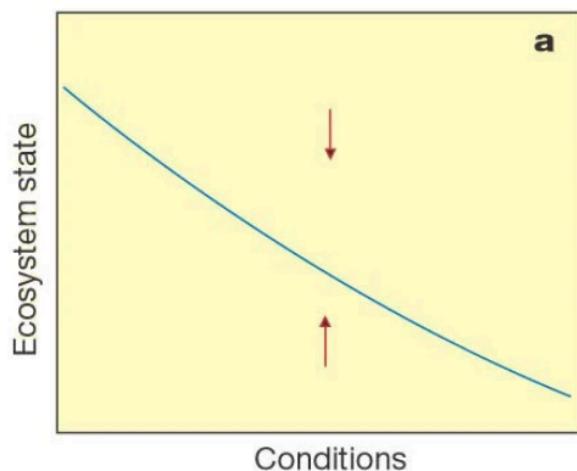


The solid line delineates the basin of attraction; think of it like a valley. The dashed line can be thought of as a ridge. On that ridge, the system can roll toward the state it may have started in—the relatively high-abundance state shown by the solid line. But what if the system rolls in the other direction—below or to the right of the lines? In those domains, *no amount of harvest reduction will avoid collapse*. The possibility of resilience evaporates and—because of the memory of the system—it cannot be recovered by changing any parameters. This is the definition of *hysteresis in ecology*.

In the interior area defined by these lines, **alternative stable states** exist: the system could have the same level of harvest and very different population sizes, depending in part on its history. Don't be fooled by the use of "stable" in this name. Recall that when we solved this model, some equilibria were stable and others were not. Equilibria that aren't stable don't count as alternative stable states. What we're talking about here as the two "alternative stable states" are the two stable equilibria: moderate harvest and relatively high N, or moderate harvest and extinction. Let's try to draw this second stable state.



This figure now is a quantitative representation of the core property of hysteresis: the S-shaped plot. Where the curve folds back on itself and the middle equilibrium is unstable, we get a situation like two valleys separated by a hill. There are two domains of attraction, both of which have some degree of resilience and stability, so systems are likely to stay within them. But when conditions push the system from one into the other, it's very difficult to reverse—and, crucially, cannot be reversed just by reverting to the initial conditions pre-transition (see Scheffer *et al.* 2001 *Nature*).



Regime shifts

There's a couple of phrases that are often thrown around in ecology and conservation that are intimately related to the concepts of resilience, stability, and hysteresis. Have you ever heard of **regime shifts** or **ecological tipping points**?

Regime shifts are usually defined as the ecological changes observed when systems transition between states. Different criteria have been proposed for what counts as a regime shift, but they are usually:

- Abrupt
- High-amplitude (big changes)
- Across multiple functional groups or trophic levels (community-wide)
- Resulting in a change in the structure or function of an ecosystem

Frequently, although not always, regime shifts look like ecological collapses to us. It's important to realize that the concept of an ecological collapse is a human-created one. When a rocky reef transitions to a mangrove forest, or a desert transitions to a grassland, we can describe those as regime shifts—but whether they are “collapses” is not really an ecological property.

The dashed line in the hysteresis figure above is often what people mean when they say tipping point. This term is really poorly defined, and it is also used to mean *the abiotic or environmental conditions that caused a regime shift* (describe the planetary boundaries project). Try drawing and labeling the hysteresis diagram for an estuary or a coral reef.

We learned earlier about another nonlinear ecological feedback process whereby removing a predator causes huge changes across trophic levels—a *trophic cascade*. Not all regime shifts are trophic cascades, and not all trophic cascades are regime shifts. For example, I'm not sure the *Pisaster* rocky reef example is a regime shift; it still was a rocky reef afterward. By contrast, the removal of sea otters causing a transition from kelp forests to urchin barrens is definitely a trophic cascade *and* a regime shift.

This discussion is hopefully illustrating the ways in which these definitions are a bit slippery. There is not clear consensus about exactly which state variables at exactly which values should define resilience or regime shifts. Yet understandably, conservationists would like to avoid regime shifts, and protecting resilience is seen as the best path forward for conserving many ecosystems. You are probably aware that UCSC has a huge focus on “coastal resilience”. I didn't introduce this yet, but there is also a vast literature on *social-ecological resilience*—building resilience into the societies that interact with nature as well as the ecosystems themselves.

A large and controversial meta-analysis study recently found that across the published literature measuring some state variable in response to some environmental driver, “Thresholds for ecological responses to global change do not emerge from empirical data” (that's the actual title of Hillebrand *et al.* 2020 *Nature Ecology and Evolution*). They found that instead, responses scale gradually with changing conditions (this could be nonlinear or linear but the key

insight is there is not much support for the S-shaped curve). So the degree to which resilience theory and regime shifts actually characterize many ecosystems in which we work is a huge open question.