# Marine Population Dynamics
## OCEA265

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Alexa would like to gratefully acknowledge the following sources:

- Alan Hastings' book, "Population Biology: Concepts and Models"
- 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:
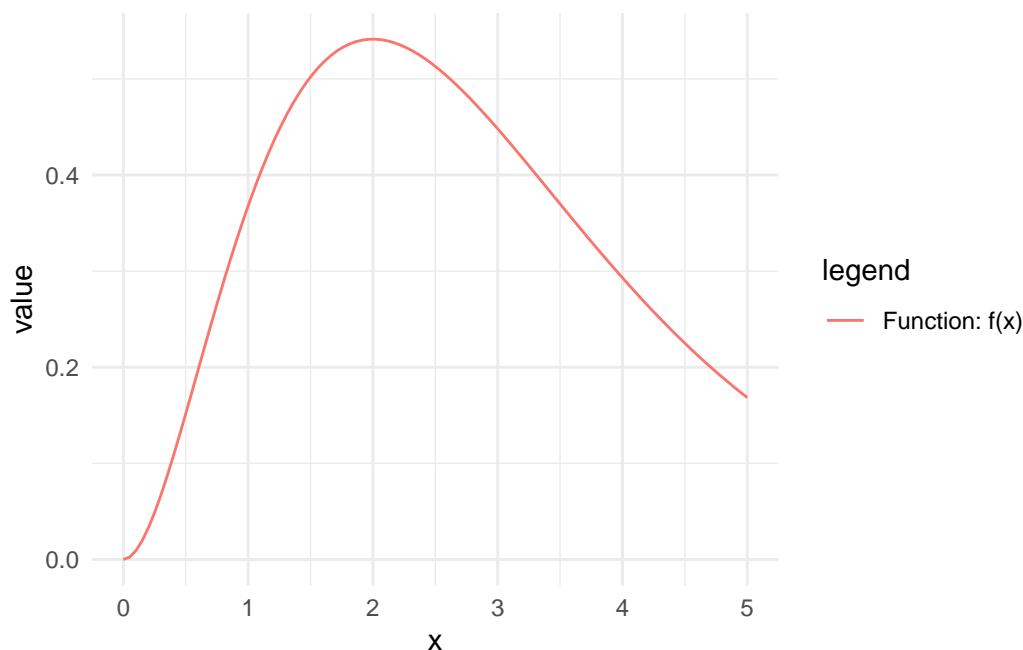


We don't need to do anything to know what the value of $f(x)$ is at any $x$ on this graph; we can already figure that out.

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 $\Delta x$ goes to 0.

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

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 $\Delta x$ 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
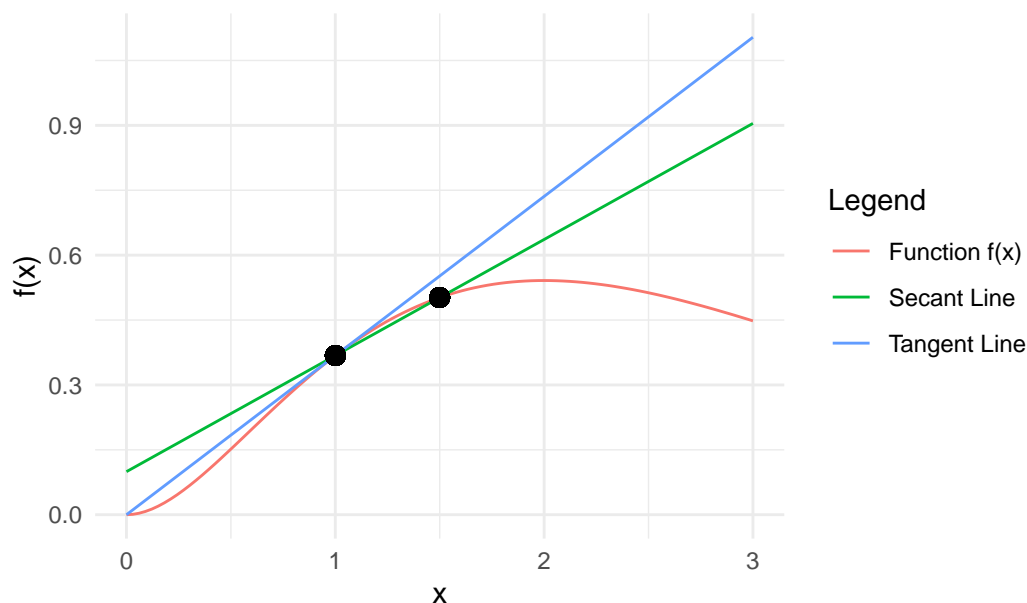


This is a good time to remind you that this course has zero memorization! Don't worry if these terms are unfamiliar or don't stick.

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
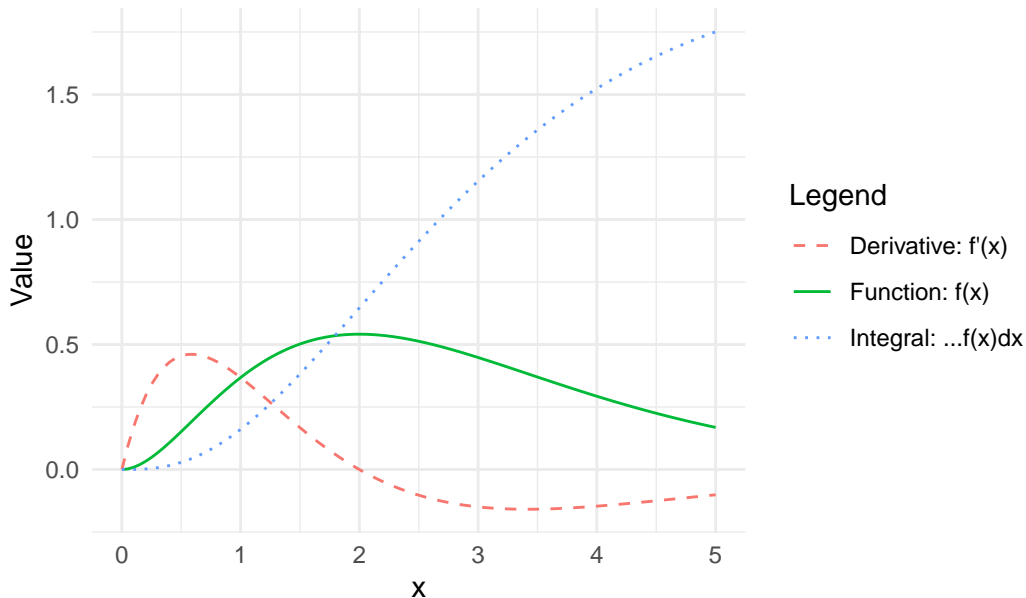


**BREAK**

## 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.)

$$N_3 = RN_2 =$$
$$RRRN_0 = R^3N_0$$

$$N_2 = RN_1 = RRN_0$$

$$N_1 = RN_0 = 200$$

$$100 = N_0$$

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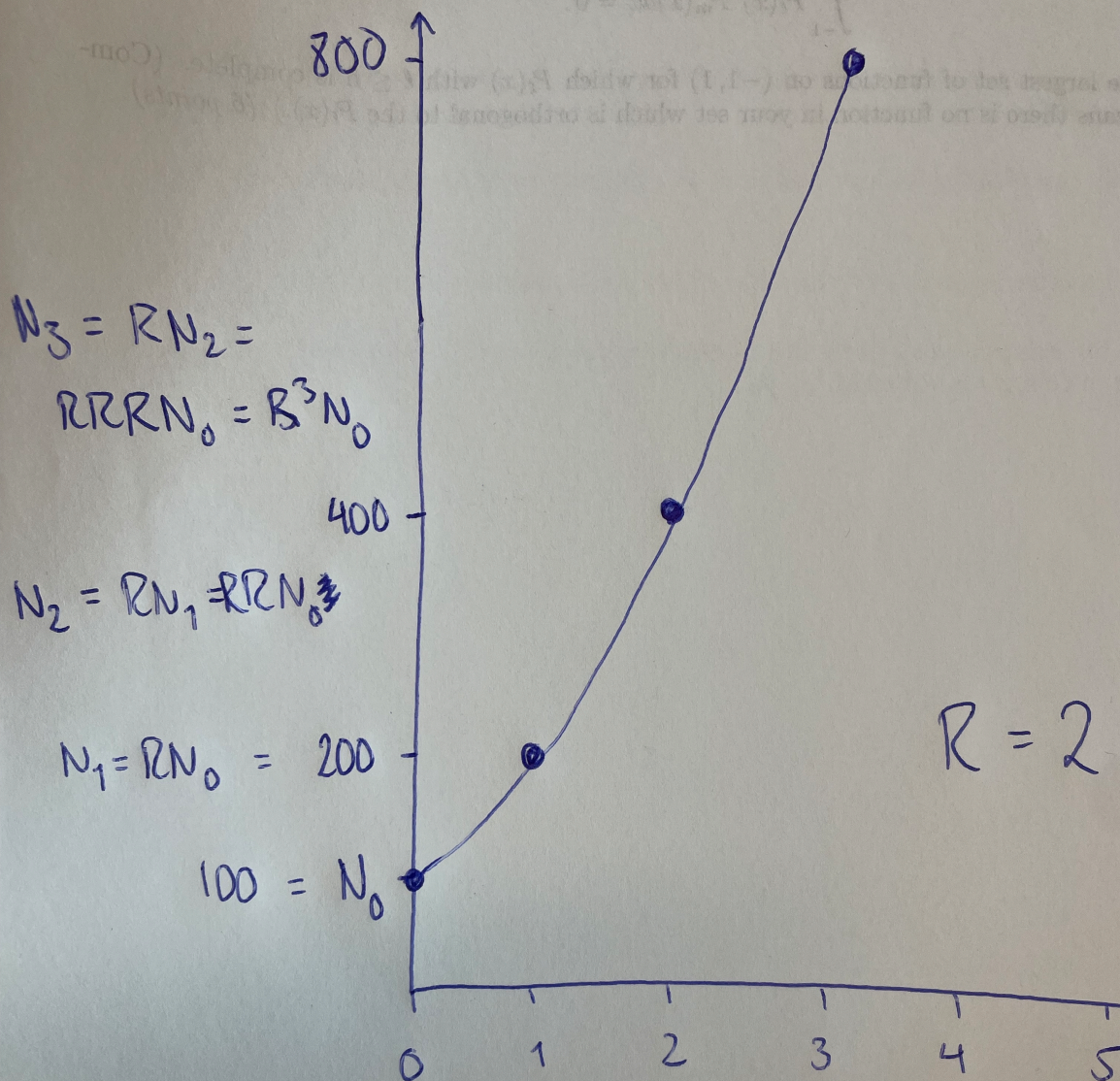
$$N_1 = 2 \cdot 100 = 200$$

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 $1/time$. 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,

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

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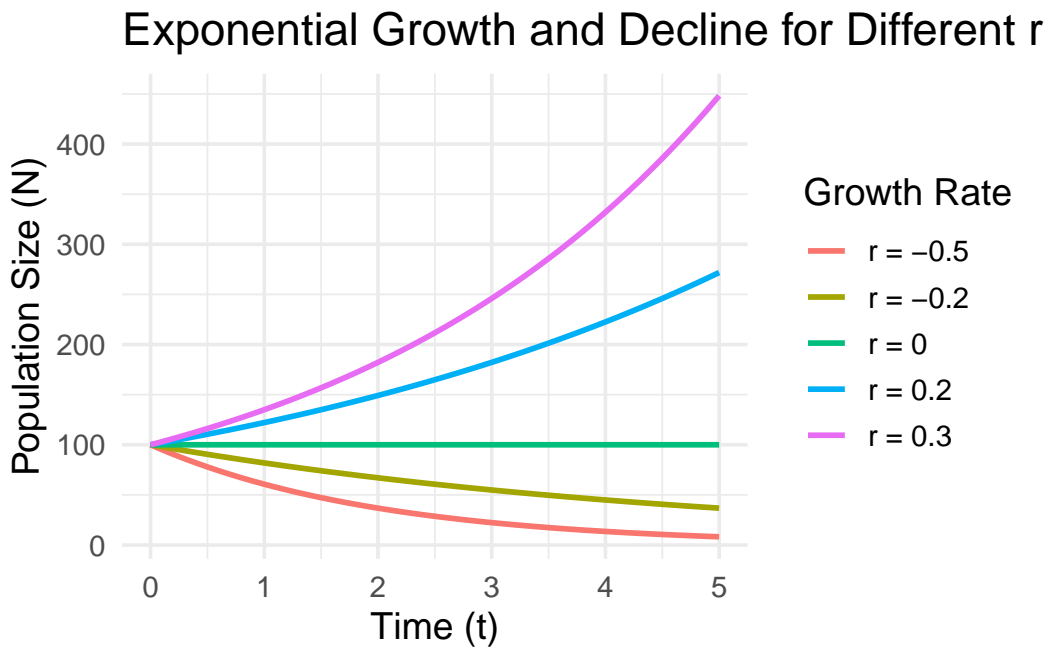
Let's think back to how this model connects to the discrete-time case. To recap, we started thinking about rates of population change in discrete time:

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

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.
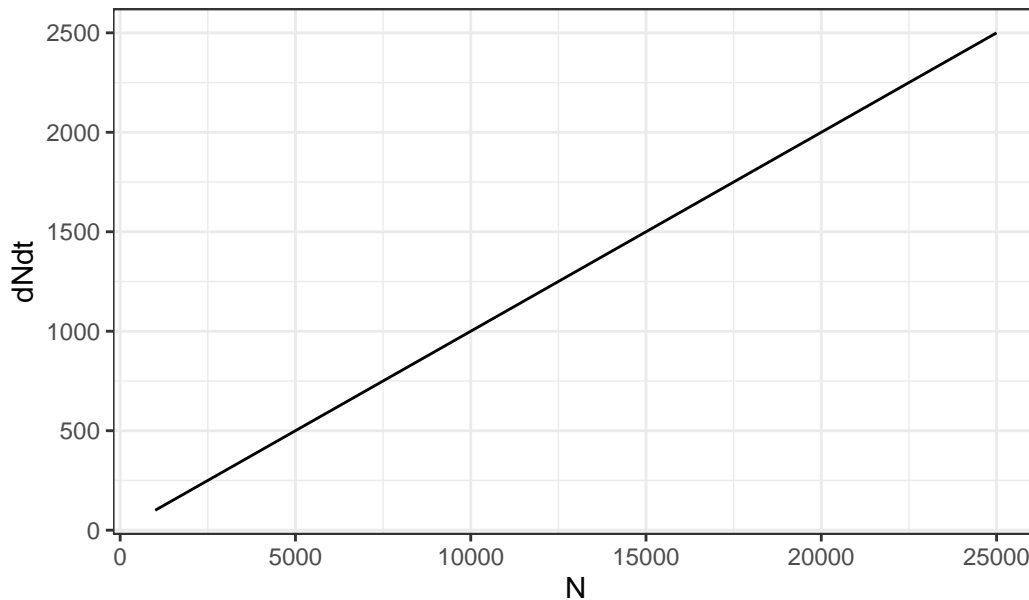
Here's a graph of $N$ vs $t$:

# Exponential growth in continuous time, r = 0.1
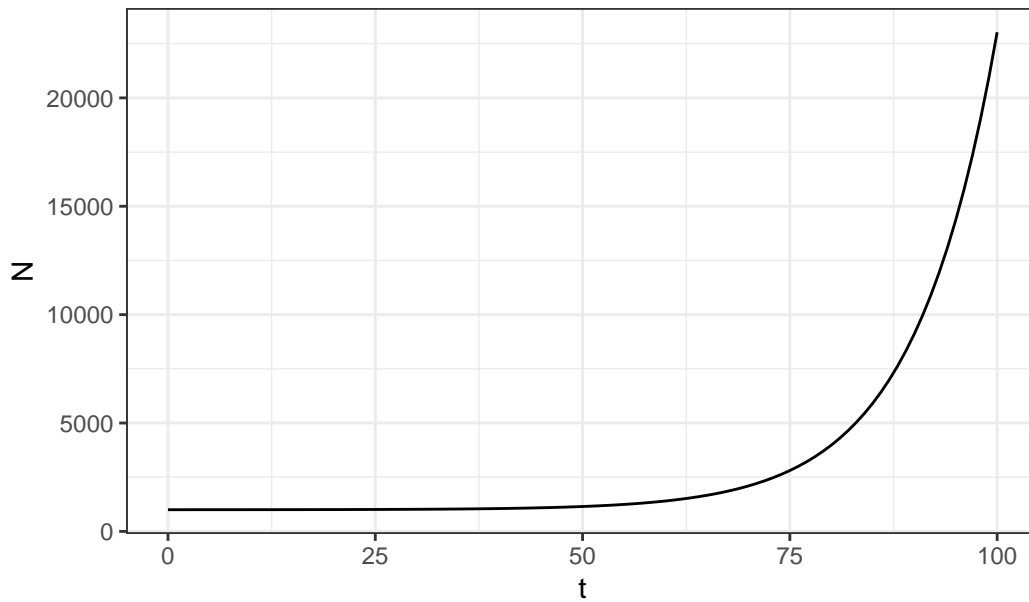


Now, let's plot the derivative of this curve:

# 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?

## Per−capita population growth rate vs. population size, r = 0.1
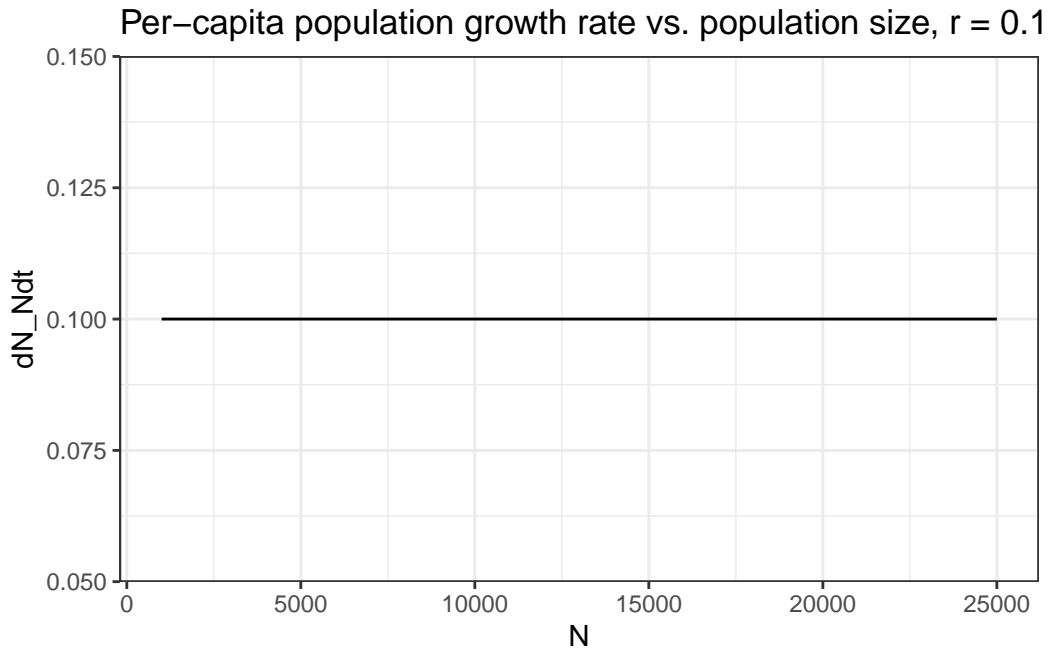


The simplest possible extension to this is that the *per capita population growth rate*, $g(N)$ or $dN/Ndt$, goes down with $N$. This suggests that when the population size is higher, the average number of offspring per individual goes down.

## Per Capita Growth Rate in Logistic Model
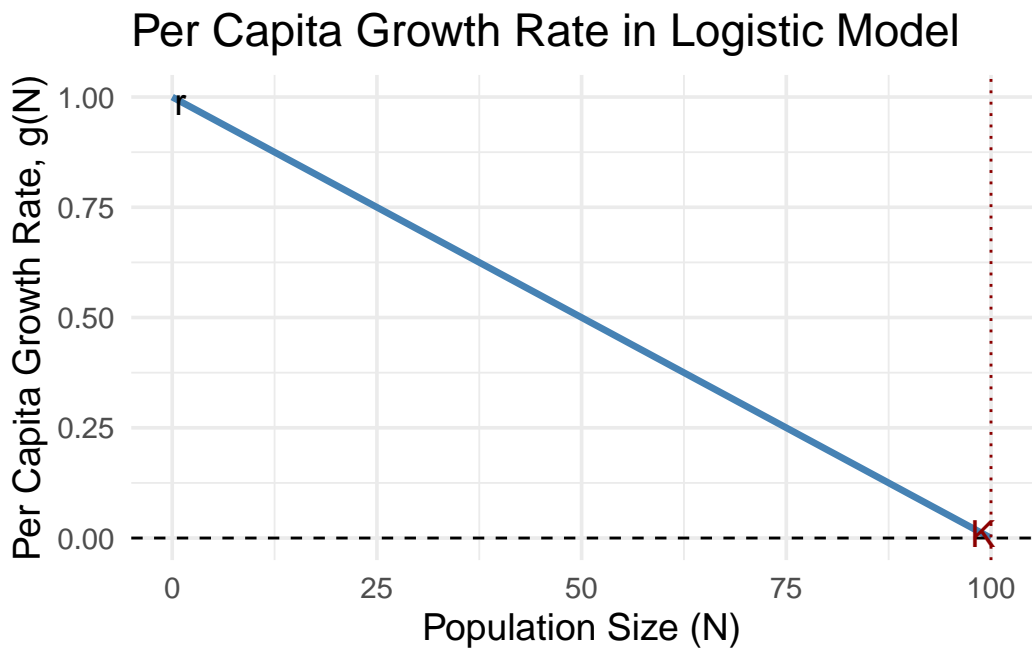
The equation describing this line is,

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

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?
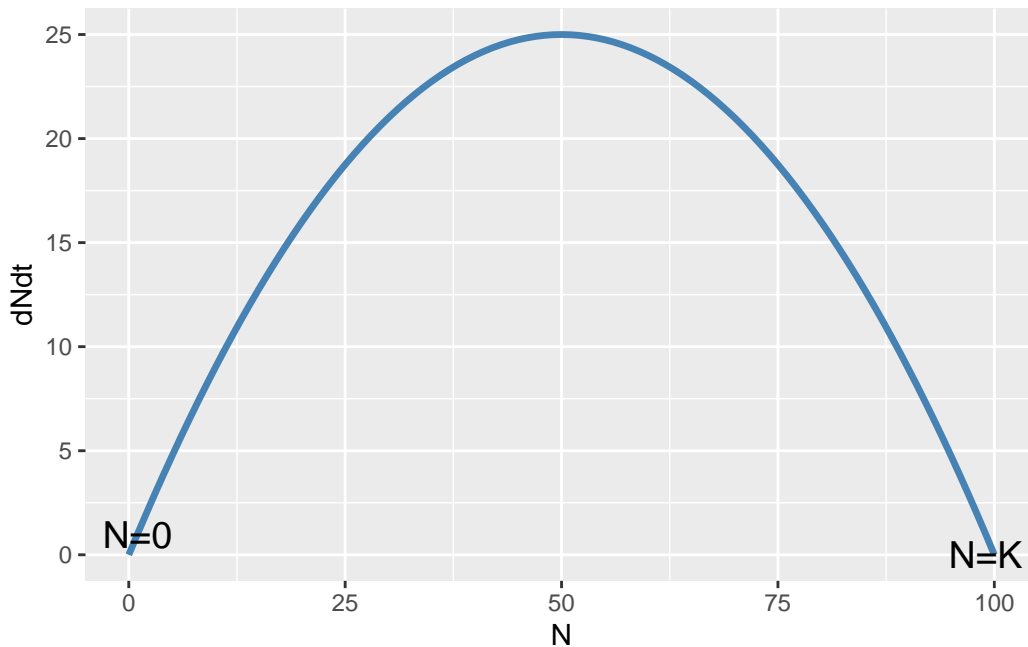


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Because $g(N) = dN/Ndt$, if $g(N) = r(1 - \frac{N}{K})$, then the equation for the curve above simply multiplies both sides by $N$:

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

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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.

**Stability analysis and intuition**

# Extensions to harvested populations

# Age and stage structure in discrete time models

# Stochasticity

# Dispersal and spatial population dynamic models

# Interacting populations

# Coexistence

# Applications of population modeling to management and research

# Other topics to add:

- R*
- Stability analysis