And, we're going to make a major shift. You're going to feel like this is a whole different class compared to what we were talking about last time, because were jumping from the biogeochemical cycles, or looking at the biosphere as essentially a large biochemical machine, to studying individual populations of organisms, and the communities that they make up when they come together. So, before we were really talking about organisms as they function in the biosphere.

Mentally, we're grinding them all up and thinking of them as a collective biochemistry basically. And now we are going to stop grinding them up, mentally, and think of them as individual organisms. So, the next series of lectures, we're going to talk about population ecology.

If you remember the first lecture I gave we talked about the hierarchy of organization within ecological systems, and then we are going to talk about competition between organisms with a population, and between organisms of different species, and were going to talk about predation, and mutualism. These are all interactions between organisms that affect the fitness of organisms. And then we'll, at the end, talk about community structure. So this is sort of the outline for the rest of my lectures, not for this lecture.

So, today we are going to talk about properties of populations.

We're going to analyze how we measure growth rate, growth and death in populations, and this will include populations that have an age structure, and populations that don't.

And this is all in preparation for the next lecture where we will talk about human population growth. So, in this field of population ecology, which is as I told you in the first lecture, and some universities you could take three courses in population ecology, and you could get a Ph.D. in population ecology.

I mean, this is a whole field that we're going to cover in two lectures.

But what population ecologists worry about fundamentally, well, they don't worry about it. This is what they study, is what regulates the density of populations? Obviously, it's a function of how fast they're growing, the birth rate, and how fast they're dying, the death rate. But what are the factors that actually influence those rates? Is it competition with other organisms? Is it the entire structure of the community?

Is it the availability of food? Is it the various abiotic properties of the environment: temperature, etc.

So, they analyze these and basically try to model the population growth as a function of these various parameters.

The other questions they ask, is how are populations distributed in the environment? Are they clustered?

Are they evenly distributed? This has specific meanings about their ecology. And, the other thing that people are really fascinated by, which is a really tough question, is why are some species' populations extremely abundant, while others are rare? And one of the discussions we always have in my lab, we work on an organism that's extremely abundant, this prochlorococcus, which I told you briefly about, is the most abundant photosynthetic cell on the planet. So, my students tend to keep saying why is it so successful? And I keep saying, it's successful but there are thousands of other species who are also successful.

Abundance does not equal success. Endurance equals success.

If you're here in the next generation, you're successful.

If you're not, if your species is disappearing, then you're not successful. So, speaking of abundance, let's talk about how we measure abundance, population ecologists.

And this is just one example. Obviously, for microorganisms, or some microorganisms it's really easy because they're tiny relative to their habitats. So for the prochlorococcus that we work on, there are 10^5 cells per milliliter. So, we can go take a milliliter of water and measure how many cells there.

But for some organisms, larger ones, that are widely distributed, it's not that easy. So, one method is mark and recapture.

That's used a lot for things like birds and butterflies.

For a bird, the mark would be putting a band on the bird.

For a butterfly, they often take a magic marker and put a mark on the wing. Well, that's largely what they do. You try to mark individuals in some way that would not influence their survivorship rate. So, if N equals the population size, that is, that's our unknown, what we're going to do is capture, say, for butterflies or moths, you use a butterfly net, or moths you can use a light to track them; for birds, you put up these big mist nets. They fly into them; they get tangled up a little bit but they don't get hurt. Then you band them, and that we let them go. That's the way you mark them.

So, we're going to say n1 equals the total number of marked individuals released. So you capture them, you mark them, you release them.

n2 is equal to, and then you go out sometime later and you recapture as many individuals as you can find, and this would be the total number [SIREN] that doesn't sound like a fire drill, does it?

I assume we're good to go here. So, n2 is the total number of recaptured. And we're going to say m2 is equal to the numbers recaptured that are marked. OK, and then we assume that the fraction of the recaptured that are marked represent the fraction in the total population that was marked. So, we say m2 over n2 is equal to n1 over

N. And the number that we're looking for, population size, is equal to n1, n2 divided by m2.

So, of course, this assumes that there's no effect of the marking of the individuals. It assumes that there's no bias in the trapping for the marked or not marked individuals.

There's all kinds of assumptions that underlie this.

It's a start for assessing the population size.

OK, so how do we measure population growth? We're going to first start with looking at populations that have age structure.

Now, I hope you printed out the slides that were on the Web, because I'm depending on these overheads a lot for this lecture because we wouldn't get through any of it if I wrote all this stuff on the board. So, we're going to talk about populations that have an age structure. And the data I'm going to show you here is for human populations.

But this applies to any population that has differential birth and death rates as a function of the age of the organism, OK? So, in these populations if birth rate and death rate are high, the population is dominated by young people.

And, we'll look at this in a minute. And, if B and D are low, dominated by old people, or older I should say, since I now fit into the old category. OK, so here's a typical population age distribution for developed countries, where each slice here, these are females on the right, males on the left, and each slice is an age category: zero to 10 years, 10 to 20.

And you can see that in these kinds of populations, you have a fairly even age distribution. Long periods of no net growth in a population lead to this. In these developed countries, and we're going to examine why this is, there's basically an even replacement rate of children for adults. And one of the things we worry about when you see this kind of age distribution, although it's good in terms of population growth, is when you have few young people and a lot of older people, who's going to take care of them, which is what's behind the Social Security crisis. But we won't get into that.

Since you're the young people and I'm the old people, I don't want to dwell on that. OK, so what demographers do for human populations is project what the population will look like in the future based on the reproductive rates of the present.

And you can see for the US here, it's reasonably stable if you look at these three snapshots. We're going to go backwards starting with 1950, and show you what the population has been doing since 1950. And I'm just going to walk through this. You only have one in your handouts, but I'll show you how it's moving along. Moving along, you can think of this as generations moving through the population. And this is the date up here. So, this is 1950, 1955, you can see this red cohort.

A cohort is a group of individuals that were born at roughly the same time. So, you can see that red cohort there. And we are going along, 1965. This lip here, that we can now see, is the postwar baby boom. That's what I'm a member of.

If you can see it in this bulge in this population.

And now were marching along. Here's my cohort, and I just put these lines on to keep you oriented. And here comes you guys. I think those are you guys, 1985. That's roughly right, because I never know when I've last updated these slides.

So, and here you go. See, here's the big bulge of all of these baby boomers that you guys are going to have to take care of.

And now, we can actually see an echo. This is what's called the baby boom echo. These are the kids of the baby boomers, which is you guys. But you can only see that as we march through it. So, here we are at 2020.

But you get the impression that it's a fairly stable, now, even age distribution in the US and these developed countries.

Oops, here we go a little but more. Sorry. 2035, 2045, OK.

Now, in less developed countries, the birth rate's high and the death rate's low. We see a much different age distribution.

And here's Uganda, with a very high reproductive rate showing the projections to 2050. And here, we can march through from 1970. You can see that this huge expansion, do you know what that noise is? OK. Does anybody have a hypothesis for what that noise is that we could test?

Oh, OK, I guess we can't do anything about that. OK, so here's Uganda. And you can see the dramatic difference in a population where there is large birthrates, and reducing death rates. And we're going to get into analyzing that in the next lecture. I just want to show you this here so you have a feeling for what we are talking about in age structured populations. So, let's now look at how are going to analyze these populations to try to quantify growth rates or replacement rates. And to do this, we set up life tables. And this is basically what insurance agencies do for human populations. But we do the same thing for populations of ecological interests. We use the same techniques.

In this lecture, going to use a unicorn is my example, because I can make up the numbers because they don't exist.

But in a textbook there are examples for real organisms like lizards and things like that. OK, so we need to define an age interval, X, and then this is the number of intervals in the original cohort. Again, a cohort is a group of individuals that are born within a defined age interval.

I mean, I think of you guys as a cohort. DX is the number dying during that interval. All of this is on the Web.

These slides are on the Web. So, you don't need to write it down, but you can. And, NX is that number of individuals surviving to age X. LX is the portion of individuals surviving to age X. So, that's just equal to NX divided by N0. And, we're going to look at a table that shows this in a minute.

And MX is something that's measured. It's the per capita births during age interval X to X plus one. And this is also called age-specific fecundity. And you can think of it as the number of female offspring produced per female in a particular age category. OK, is everybody comfortable with that? So, with these definitions, we're going to build a life table that will allow us to actually calculate some things of interest.

And, what do we want to calculate? We want to calculate the survivorship probability, LX. We want to calculate the net replacement rate.

No it's not really a rate, net replacement of population per generation, which we are calling R0. It's basically the number of children people have to replace who's there per generation.

And then, for now, this is what we are going to look at.

And to do that, we are going to generate what's called a cohort life table. And to do this, we follow a cohort of individuals throughout lifetime. Or, we can also generate a static life table because it's not that easy sometimes to have a group of organisms that are born at the same time to follow them throughout their entire lifetime. So there is a static life table of taking a snapshot at one time of the population, and calculating the age structure. So, you take a snapshot, and we look at the age structure. And, we are going to do this in a second so it will make more sense. OK, so we've defined our terms.

And now, we are going to start by calculating LX.

So, this is a cohort life table for unicorns. We're going to start out with a hundred baby unicorns that we have in our imaginary unicorn pen.

So, this is a cohort size of 100. And, we find that after a year there are 50 of them left. 50 of them die in the first year.

So, the probability here, the proportion surviving is 0.

, NX over N0, and then a year later, .4, .3, and then by four years older, no unicorns left. They don't live very long.

All right, so this is what's called the survivorship probability, and what we can do is look at there. Different types of organisms have different, what we call, survivorship curves. And this is discussed in your textbook. We'll just describe the extremes.

These are just theoretical survivorship curves.

But some organisms have a very high probability of survival as a function of age until they reach an old age.

And then, they have a very low probability of survival.

There are other organisms whose survivorship probability drops very fast, right after they're born. But if they make it through that interval, they're pretty good to go. And then there are some that have a steady probability of dying. So, where are humans, do you think, on this? Two? No, but that's OK.

Let me ask you the other way; where our frogs, do you think?

Yeah, OK, so you got that image. Tons of frogs' eggs: everybody eats them. Or for that matter, the video I showed towards the end of the last class where there were all those eggs of, what was that? Remember all those eggs that everybody was eating?

Herring, thank you. So, any organism that puts out just tons of fertilized eggs, and knowing that most of them will be eaten, but some of them will survive, falls here.

And, humans actually fall here. Any organism that has a high investment in the care of offspring, they have few offspring but they invest a lot into the care of those offspring, would fall here.

And then this, actually birds and things fall here.

So, here's some real but idealized survivorship curves.

These are humans. And males and females are different.

I'm not sure whether we understand that completely yet.

Does anybody know whether that's socially constructed?

Now that there's more women experiencing equal stress in the workplace as there are men that will probably even out.

But, I think there are more women born, or girl babies.

Anyway, there's some interesting biology behind this, but I don't know. I don't remember.

And, here's grass, of course grass spew out all these seeds everywhere, and very few of them survive, also these frogs, etc. and birds are commonly like this, where they're somewhere in between. Why do we care so much about survivorship curves? Who cares? Well, I mean they're inherently interesting to population ecologists, but there are also uses for them. For example, if you want to conserve a species, if you're worried about a species going extinct, you want to figure out whether it's better to conserve the young ones or the old ones. For example, turtle species, you would pick a certain age group where the probability of survival is high, and decide to target the conservation of that age group.

So, let's continue with, we are building our life table here.

So, we have the survivorship probability, but what we really want to get at is understanding whether or not the population that we are describing is replacing itself with each generation.

So, maybe we should define, when R0 is equal to one, that meets the population is exactly replacing itself.

So, this is replacing, so the actual growth rate of the population would be steady. If R0 is less than one, the number of individuals is declining. And R0 of greater than one, it's increasing. So, we want to know for our unicorns what that is.

And to get to that, we have to know something about the birth rates.

So, MX is the average offspring per female of age X.

So, this is called the age-specific fecundity. And that's something that's a known property of the population.

Whoops, oh, my, my, my, my, I'm missing a slide.

Oh, there we go. They're out of order. OK, so we have MX.

So, how do we calculate R0? Well, R0 is the sum of LX MX.

With the sum of the survivorship times the age-specific fecundity, and in this case, it sums up to three. So, what's happening to our unicorn population? It's growing.

Yeah, we are getting three unicorns in each generation for every one that existed before. So, in our imaginary unit of our population, we're going to be knee deep in unicorns pretty fast.

OK, so I forgot my watch, so I have to look at my computer.

What if we can't follow cohort? Oh, thank you.

How do we create the same kind of analysis for a population that we can't follow through time, but can only look at as a snapshot?

OK, this is where we go to the slide. If you don't have it in your handout, it doesn't matter. I just got off the web this morning.

I couldn't find a skeleton of the unicorn because, of course, that's totally imaginary, but I found a mastodon. So, just imagine that this is a unicorn, and I couldn't find a unicorn horn, so this is a sheep's. But, all these principles apply. I just discovered Images in Google, which is really exciting. So, you're going to get subjected to this for awhile. So, OK, so what you can do, and this has actually been done with mountain sheep, is you go out you find dead sheep, you find skeletons of sheep that have died for whatever causes. And you go out, and you sample until you have, say, 100 skeletons.

And that's your cohort that you're looking at, at one point in time.

And from their horn, you can actually tell how old they were when they died. You can count the number of rings, so that's what's here, annual horn rings. This is for a dall mountain sheep. So, you can say well now it died when it was two.

That one died when it was 10. That one died when it was whatever age. And then you can create the same kind of life table, a static life table, where you have a hundred skeletons.

That is your cohort. You look at the number dying of age zero to one, the number of one year olds, the number that died when they were one year old, the number that died when they were a two-year-old etc. And so, from these data, these are the data that you collected, you can calculate this column, NX, so NX is DX, or NX minus DX equals NX plus one.

Does that make sense? I can never tell whether.

I know if I write this on the board it might be easier, but it's so obvious isn't it? We are just saying that this is the number that died at the age. This is the number you started with, so that's how many are going to have that age, that age, and that age. And then, once you have this column, your proportion surviving LX, you can calculate LX. LX equals NX divided by N0, OK? So, we are doing exactly the same thing as we did before. It's just that we're getting the NX column instead of getting it by following the cohort.

We're getting it by calculating it based on how old dead organisms were when they died. And in my ecology class that I teach, some years we actually go out to the Mount Auburn Cemetery.

And you can do this from human gravestones. You can go to the cemetery, and pick out a number of gravestones, and see the age at which humans died. You create yourself a cohort, and you can create a life table. And you can do that for different eras, and see how replacements have changed.

OK, now so that's the analysis for populations that have an age structure. Now we are going to go more into simpler type of population, and that is a population with a stable age distribution.

And to do this, you're going to help me, and we're going to use your calculus that you've all been studying. So, instead of the unicorn now, have your imaginary population be a population of microbes that divide in half. They multiplied by dividing in half.

So, each one of these is a microbe that's dividing in half.

This is your mental image. This is what's called exponential growth. It's obvious how that happens. And we're going to model this population, we're going to first assume unlimited resources. OK, so we're going to say that the rate of population increase is equal to the average birth rate minus the average death rate times the number of cells.

OK, so we are going to now turn this into math, and that is to say the dN/dt, the increase in population where N is the population number is equal to the birth rate minus the death rate times N which is the number of cells, OK? And then, we're going to let B minus D, the birth rate minus the death rate, be what we call r.

And, this is what's called the intrinsic rate of increase of a population. OK, what are the units of r?

One over time, exactly, time to the minus one.

So, let's look at that more carefully. And also, it's a little misleading to say it's the rate of increase because r can be positive or negative, however it turns out. It can be positive or negative, but that's what it's called.

So, we have the dN/dt equals rN. We're substituting r in this equation for one over N times dN/dt equals r.

OK, so ours has the unit time to the minus one. And so, let's ask a question. Given N0 I give you the population density at some time which we're going to call T equals zero.

Given a population growing according to this, which is exponential growth, what if we want to know the population, what N is at any time T?

We want an equation that will give us, given N0 what would the population density be at some time, T? What do you have to do to this to get that? Yeah, so who wants to do that for me?

Come on. You guys did this freshman year. It's the easiest thing there is, right? Every class I've had has had somebody who was willing to come up and do this. OK, so we'll just add a T there.

So, N at sometime T is equally to N0 e to the rT.

And so, We could say, then, r equals natural log of NT minus natural log of N0 divided by T. And I like to write it that way because then, we know what this looks like, right?

Let's plot that. This is N and this is T. What does that look like? I know this is really rudimentary but remember we're modeling population growth.

So here, if we plot the log of N, and this is what we do with cultures of microorganisms. That's a flask. Those are a lot of microbes in there. And what we do is we sample it at various points in time, and if you take the log we get a nice straight line that we can draw a regression through.

And what's the slope of that line equal to? r. Exactly.

The growth rate in the units: N to the minus one.

OK, what's the Y intercept? N0. OK, now suppose we want to calculate the doubling time of the population, the time it takes to double. How would we do that?

Let's first define it. It's the time, T, that it takes for NT to equal to N0, right? If we start with N0 the population doubles. Then, that's the time at NT.

So, we want to solve for that T for the time it takes for the population to double. Since natural log of NT over N0 equals rT, then the natural log of, sorry, 2N0 over N0 equals rT, and T equals the natural log of two divided by r equals our doubling time. Does that make sense?

I'll put this out there so you can see it better.

What's the natural log of two? 0.69, thank you, always a handy thing to have in our repertoire. So, that's just the way, it's easier to think about the time it takes for a population to double often, then the instantaneous growth rate.