Introduction to Evolutionary Dynamics

Prof. Supreet Saini
Department of Chemical Engineering
Indian Institute of Technology, Bombay

Lecture – 04
Logistic Growth Models – 1

Hi, and welcome to the next lecture. So, we had stopped last time where we had formulated two equations for growth of bacteria. The first one was called a difference equation and the second one was call was using was developed using differential calculus. And the two limitations that we had talked about which were not incorporated in any of the growth models that we had talked about was one that we had not incorporated death of bacteria and the second was there was no concept associated with resource limitation which would eventually halt the bacterial growth. So, let us before we incorporate these two features let us try and understand why is it important or how realistic are these two assumptions that we want to incorporate in our growth models.

The death assumption is very easy to understand there are no living beings which are which live eternally, hence that has to be something that has to be incorporated into any realistic model of growth. The second one resource limitation can be illustrated using a very simple calculation. So, let us go back to the two answers that we had received from our two models, and try to look at them in some more detail.

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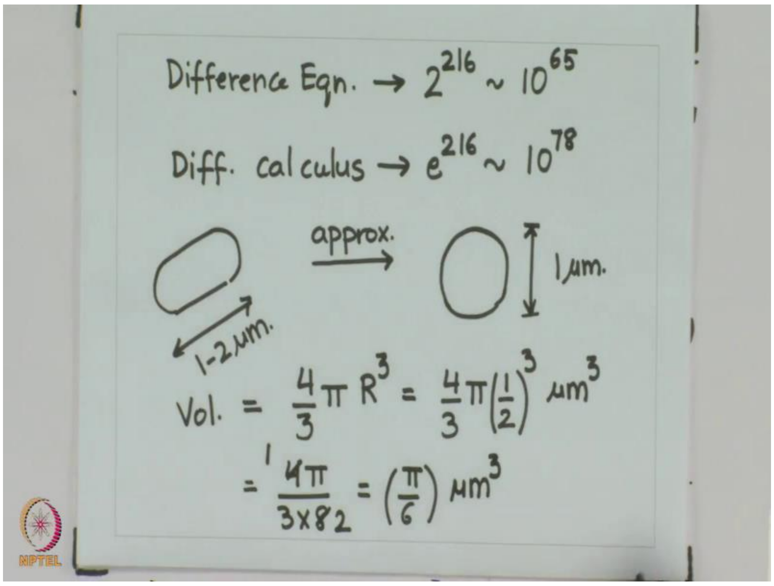

So, in the difference equation formulation our answer after three days of unconstrained growth of E. coli was two to the power 216, which is roughly equal to 10 to the power 65. And the answer that we got from differential calculus was e to the power 216 which is roughly equal to 10 to the power 78.

Now, we want to get a sense of how big or small are these numbers when looked at in an absolute sense. So, let us try and estimate how much do these bacteria way how much to 10 to the power 65 E. coli cells weigh. How do we estimate that; and for that we are going to use some very broad assumptions and very simple math sum engineering approximations to approximate the weight of one bacteria, and once we get that we multiply that with the total number of bacteria that we have here 10 to the power 65 or 100 to the power 78 depending on which answer we are talking about, to get the total number of mass of this many bacteria that we have got from the two approaches that we have been talking about. So, what we need here is an approximate answer to how much does one bacterium weigh.

So, typically E. colis dimensions E. coli is a rod shaped bacteria with typical dimensions of about 1 to 2 micrometres. Now to approximate this and this is important because very we have a really only interested in order of magnitude very crude approximations of weight of bacteria. So, we are going to approximate this E. coli cell as a sphere and we are going to take the diameter of that sphere as 1 micrometre. So, that is the assumption that we are starting with. And since we are only interested in order of magnitude estimates of weight of a single E. coli cell this is not too bad in approximation. Even if we are off by our answer by a factor of 2 4 5 it really does not matter because what we are interested in is an order is an order of magnitude estimate of weight of one bacteria.

So, now if we approximate our E. coli cell as a sphere of diameter 1 micrometre what is the volume of this sphere? The volume of a sphere we know from its formula is 4 by 3 pi R cube, where R is the radius of the sphere. We pluck the numbers in and we get 4 by 3 pi 1 by 2 micrometre cube as the volume of an E. coli cell. We can work out the numbers, but essentially this is just equal to 4 pi by 3 into 8 which is pi by 6 micro metre cube and the next thing we need to approximate mass of an E. coli cell its density, and again we are going to make up make a very generalized broad assumption and assume density of an E. coli cell to be equal to that of water it is not technically going to be an equal to a water, but since we are only interested in order of magnitude estimate of weight of an E. coli cell this estimate is not a bad estimate.

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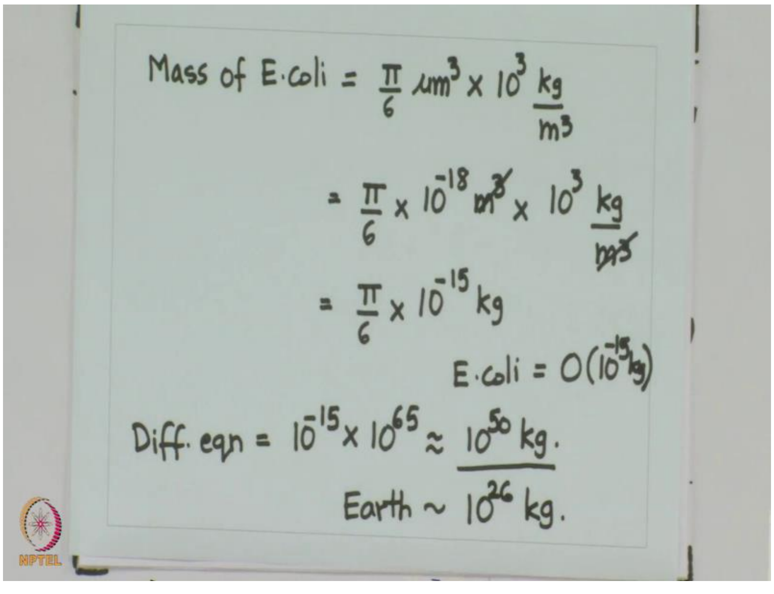

So, when we multiply this volume by the density of water we get mass of an E. coli cell as equal to pi by 6 micrometre cube times density of water which is 10 power 3 kg per metre cube. Now we want to make that unit identical here, so we can cancel them and we can do that by doing pi by 6 into 10 power minus 18 meter cube times 10 power 3 kg per metre cube, and we get our answer as pi by 6 into 10 power minus 15 kg. So, we can roughly approximate that an E. coli cell mass is of the order of 10 power minus 15 kg. Now let us revisit the two answers that we have got from our two different approaches which using the difference equation we had gotten approximately 10 power 65 bacteria and from the differential calculus approach we had gotten about 10 to the power 78 bacteria. So, how much do these actually weigh.

So, now it is trivial the difference equation answer is going to be 10 power minus 15 times 10 power 65 which is equal to 10 power 50 kilograms of bacteria, if E. coli were to grow unconstrained for three days without any resource limitation altering its growth. And now of course, the answer from the differential calculus approach is going to be higher than this because there the answer number of bacteria was not 10 to the power 65, but 10 to the power 78. So, the answer in that approach is going to be even higher than 10 to the power 50. Now is this what sort of how big is this mass compare that with mass of earth and the best estimates that we have for mass of earth is about 10 to the power 26 kg, which really means that unconstrained bacterial growth for three days is not likely to happen because if it that would have happened E. coli would have taken over the earth many many times over and their combined mass would have exceeded that of the planet by several orders of magnitude hence the requirement that incorporate resource limitation in our model.

So, we are going start and do that first by incorporating death and then incorporating resource limitation and from now onwards we are going to not work with the difference equation approach, but we are going to work with the differential calculus approach, because as we saw in the last lecture that approach is more representative of biology of growth of E. coli cells.

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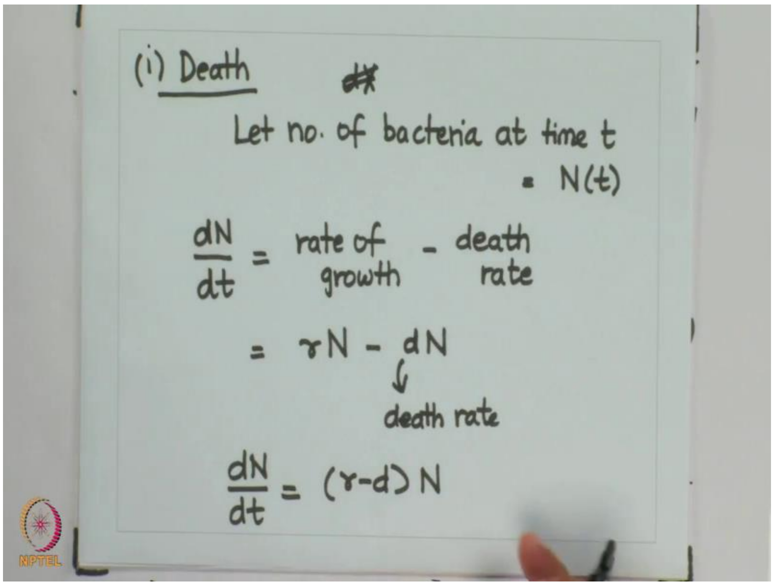

So, now we are incorporating the first limitation which is death, and again we have d x by dt let me rewrite that let number of bacteria at time t be equal to N t, and now dN by dt which we saw from the last lecture is the rate at which number of bacteria change with time is equal to rate of growth minus death rate, and this we saw can be written as r times N where r is the rate of growth and death rate can be approximated as d times N where d is the death rate and N in both these cases is the number of bacteria at that particular time t which is N t here. So, again dN by dt can be written as r minus d times N.

This equation looks very similar to the one that we had gotten from the differential calculus approach, which was just dN by dt equals r and hence the solution to this equation also looks very similar to the solution we had received in that approach.

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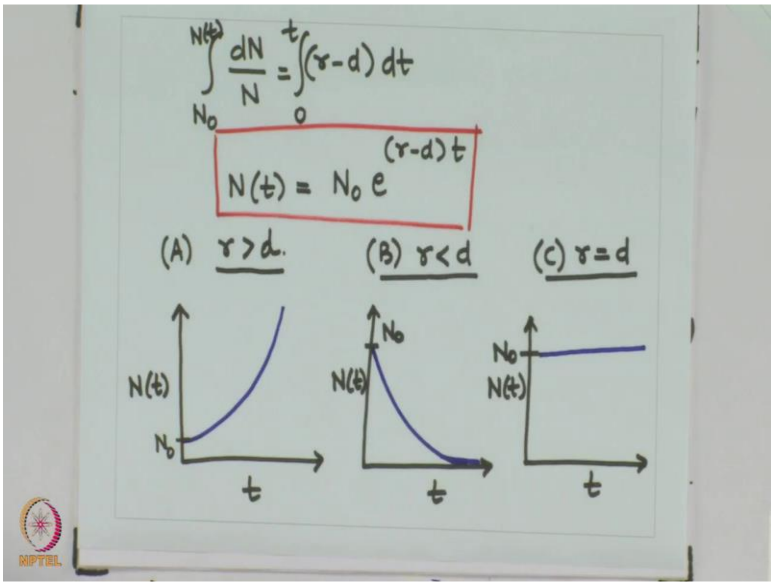

And when we integrate this by separation of variables dN by N equals r minus d, dt integrating from N not to N t and integrating from time t equal to 0 to time equal to t, we get our solution as I am skipping the steps now and writing the solution as N t equals N not e to the power r minus d into t. So, that is the growth model that we have after we have incorporated death in to our analysis; r remember is the rate of growth d is the rate at which death is taking place in our system.

So, now let us consider three particular scenarios, and see what does what do these three particular scenarios represent for growth when we try and plot them graphically and understand variation of N with time. So, in case A we are going to take a case where r is bigger than d, which means the rate at which growth is taking place is more than the rate at which death is taking place. If that is the case the exponent of this equation r minus d is a positive number, because our is bigger than d and hence when we plot the dynamics of number of bacteria with time N t with time.

Remember this is a case when r is bigger than d then if our starting number of bacteria is N naught, r bigger than d means that this exponent is positive and this is just going to exponentially grow, this is not to dissimilar from what we saw in the previous approach, just the only difference being that r is now the exponent associated with the solution is not just r, but r minus d where d is the death rate associated with the bacteria. The second case is that we want to plot and understand is r less than d. Now this is the exact opposite because when we plug r and d values here and if is less than d as in this case it means that the exponent associated with this solution is negative, which means that the solution is going to be of the decaying nature and thus and the bacterial numbers approach 0 and approach extinction.

So, this is N t, this is N naught and if r is less than d the actual number of bacteria with time are going to approach 0 in an exponential passion. So, these bacteria because they are dying at a rate faster than the rate at which they are growing, it is only natural that because death is taking place faster than growth the number of bacteria actually start to come down and approach 0. The third case that we want to talk about briefly is when r is equal to d, which is a case where growth rate in exactly matched by the death rate associated with the bacteria; what happens to the numbers then and we do the same plot again t verses N t we start with N not number of bacteria, and if you mathematically look at this if r is equal to d we get exponent e to the power 0 here 0 times t is again 0, e to the power 0 is 1 N t remains at N not into one at all times which means the number of bacteria stays constant.

So, you can have these three scenarios associated with growth when you incorporate death into account. And what I would like you to do here is take a look at these three solutions and try and plug these solutions graphically in Microsoft excel or any software of your choice by plugging in numbers of r and d which represents these three particular cases. So, choose a number of r which is more than d again then and try and draw this plot. Then choose another r which is less than d, try and see if you get this plot with time and then choose r exactly equal to d and then try and see if you get this plot. So, the point being one it should make mathematical sense to you these three plots, and it is all it should also make biological sense to you in the sense that when r is more than d; that means, it is dividing faster than it is dying. Hence, the numbers of bacteria are producing more progenies, but the number of deaths happening is actually less than the number of progenies being produced, and hence the numbers keep adding up over time and increase exponentially as shown in plot a here.

In the other case when r is less than t growth is happening slower, but the bacteria are actually dying 0 faster than they are producing progenies and hence numbers are going to diminish with time and approach 0, and in the third case when r is exactly equal to d you have the same number of progenies being produced as the number of deaths been taking place in the system which exit birth and death exactly match each other and the number of bacteria stays constant with time. These three have implications which we will get to so, but for now let us move to incorporate second limitation of our previous models that we had talked about incorporating which was resource limitation.

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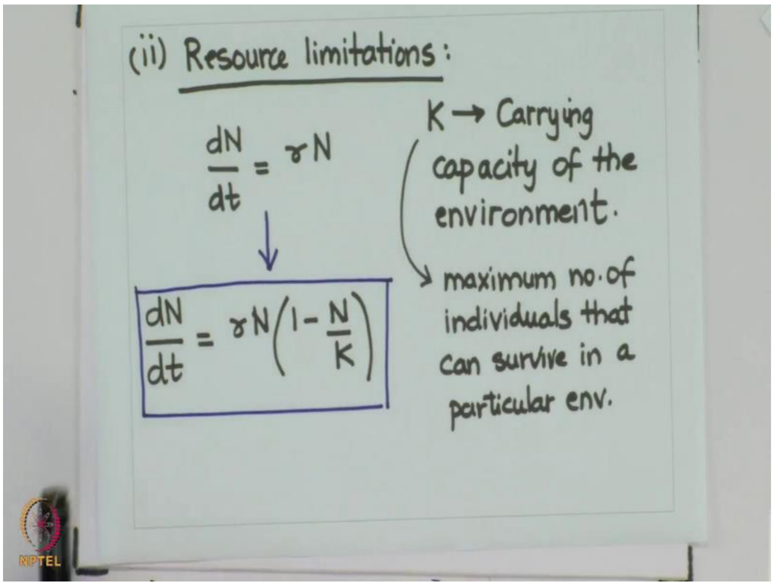

So, when we want to incorporate resource limitation this is the incorporating second limitation which is resource limitations in the environment; because as we saw with the E. coli environment E. coli example of growth with three days the entire planet is not sufficient to support E. coli growth unconstrained for three days. So, this is a very important aspect associated with growth models and we want to understand how can we do that. So, when we have unconstrained growth we have dN by dt equals r times N.

Now N here is the number of bacteria at time t, dN by dt represents the rate at which that number is changing with time and if it was unconstrained growth this is the equation that we would get, but limitations happen the environment in which this experiment is taking place is not going to be able to support growth for a very long time. So, how do we incorporate that limitation? The standard way to do that is a by introducing the variable called K which is called the carrying capacity of the environment.

What does this variable mean? What K means is; what is the maximum number of individuals that can survive in that environment that the environment can actually support. So, this represents K represents which is K, which is called the carrying capacity of the environment represents the maximum number of individuals that can survive in a particular environment. So, if you have E. coli growth taking place in one millilitre of media culture, typically if you have rich media E. coli grows to the density of above 10 power 9 bacteria in one millilitre. So, if you are if your environment is a test tube with one millilitre of culture; that means, the carrying capacity of that environment is 10 power 9 bacteria. However, if you were to take another test tube and add two millilitres of living media to that, the carrying capacity of that environment is going to be two times 10 power 9 bacteria. So, depending on the exact environment in which the experiment is being done on the carrying capacity changes.

Now, how that is incorporated in this equation is that we are going to be going to change our unconstrained equation and add another factor which presents K, and on incorporation our equation looks something like this dN by dt equals r N times 1 minus N by K, and this equation faithfully captures the resource limitation that is happening as bacterial numbers are increasing with time how does that do that let us take a look at that.

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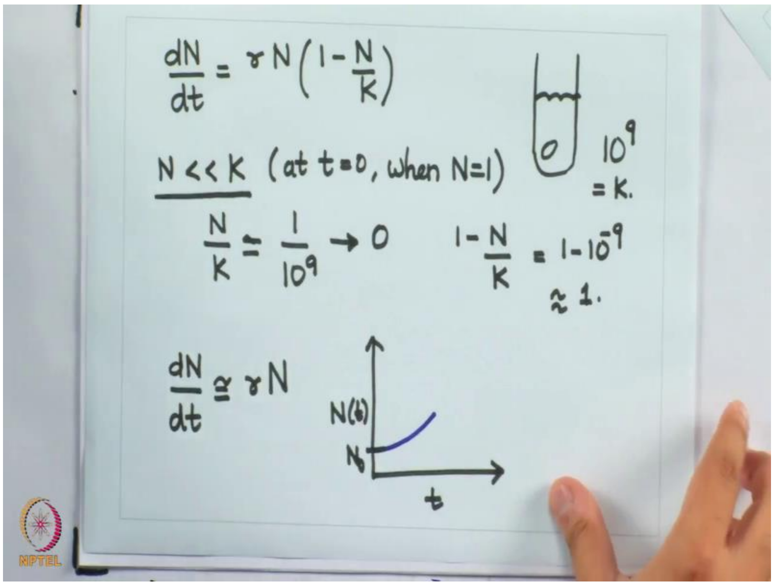

So, again let me just write down the equation again we have dN by dt equals r N times 1 minus N by K where K is the carrying capacity of the environment and N both these places is the number of bacteria at that time t, r is our growth rates that we were discussing so far. So, what does this represent?

Imagine that you have a test tube, this is my environment and this environment and support 10 power 9 bacteria. So, that is my K and I start of by adding just one bacteria to this test tube. At this point in time N which is the number of bacteria at time t is much smaller than K, this is at t equal to 0 when N is equal to 1, at this time N is much smaller than K what that means, is N by K is which is equal to 1 upon 10 power 9 is very close is a number very close 0 because this is 10 power minus 9 which is very close to 0, and what that means, is 1 minus N by K which is equal to 1 minus 10 power minus 9 is approximately equal to 1. So, at this point in the growth phase when N is much less than K, this factor 1 minus N by K which is the additional factor that we have introduced in our equation is actually approximately equal to 1 and hence can be removed from our equation. So, when N is much less than K, dN by dt can be approximated by just writing it as r times N, because 1 minus N by K is approximately equal to 1.

Now, if we plot this, we have already plotted this in the previous lecture where we plot t by N and we start with a N not number of bacteria we know that this equation solution is an exponential increase in numbers like this, but the trick here is to realise that this solution that we have just represented is actually only valid when the condition that we have developed the this where the condition where we have developed this solution is actually valid, and that condition where this solution is valid is when N is much less than K and as we see here our solution develops with time the number of N increases with time, and as N increases with time N by K this assumption is no longer going to be valid and we will no longer be able to ignore this factor which we have assumed to be one here. As N increases N by K becomes a very substantial fraction of 1 and 1 minus N by K will therefore, can no longer be treated as approximately equal to 1. So, this solution is only valid under the specific condition that N is much less than K.

What happens as N approaches K? Let us take a look at the other extreme of the solution.

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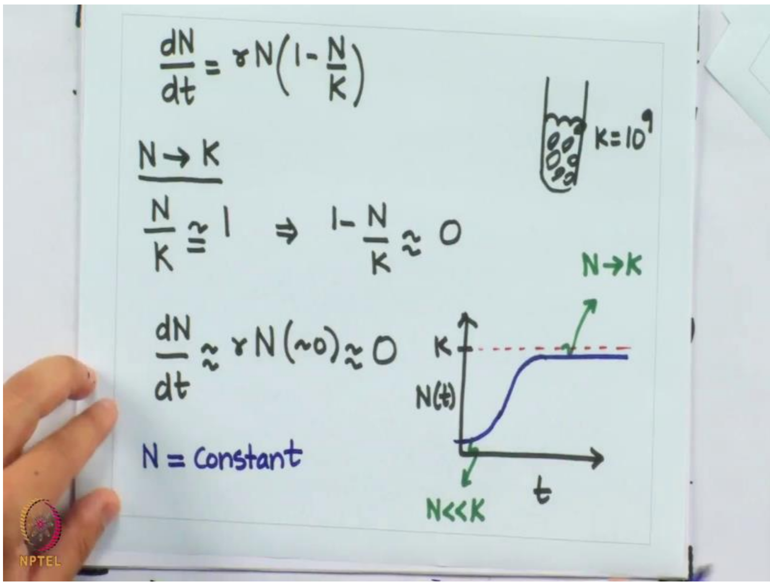

So, let me just write our equation again we have dN by dt equals r N, 1 minus N by K; now when N approaches K that means, the number of bacteria in my test tube is approaching N power 9 so there is not much room for bacterial growth anymore. K is equal to 10 power 9 which is the maximum number of individuals that may can be supported in this environment, and now my number of bacteria is also approaching K.

So, what how do we understand this? When we plug N approaching K in this factor, we have N by K because N is very close to K, N by K is approximately equal to one which implies that 1 minus N by K is approximately equal to 1 minus approximately 1 which is 0, which means dN by dt in this regime can be approximated as r times N times this factor which is now approaching 0, dN by dt is actually approaching 0 as N approaches K.

Which means if I were to graphically plot this when N is very close to K we just draw dotted line here, when N approaches K dN by dt approaches 0 and remembered the definition of dN by dt is what is the rate at which number of bacteria are changing with time. If we say dN by dt is equal to 0 that means, the rate of change of number of bacteria is 0 with time; that means, the number of bacteria are constant they are not changing with time. And that solution is approached when N approaches K; that means, when N is approaching K, dN by dt is 0 which means N t is not changing with time and hence the profile looks something like this.

So, this is my profile for the case when N approaches K; from the previous slide we saw that this is my profile when N is much less than K, I am going to plot at here this is the profile that we derived when N is much less than K from the previous slide. So, we have these two approximate solutions for the two regimes when N is much less than K, and when N is approaching K. And what you want to do is solve this equation and if were to solve that the analytical solution approaches something like this.

So, my exact solution of bacterial growth with time, when I have incorporated resource limitation would look something like this, in the initial phase when there are only a handful of bacteria in the environment that I am talking about resource limitation is not really an issue, and if resource limitation is not really an issue there is no competition happening and every bacteria is dividing very rapidly, 20 minutes being our generation time in which 20 minutes being the generation time when E. coli being grown in rich environments.

So, in this phase there is no competition because there are too few bacteria to compute growth is exponential, but as the population approaches the carrying capacity associated with the environment, growth automatically slows down and eventually resulting in halting of growth when N is equal to K, because when we plug N is equal K here this factor becomes 1 minus 1 which is equal to 0, which means dN by dt approaches 0 which means N becomes a constant. The last thing that we want to talk about here is that there are there is a curious aspect associated with the equation that we have just talked about, and will continue that in the next lecture let me just introduce that subject here.

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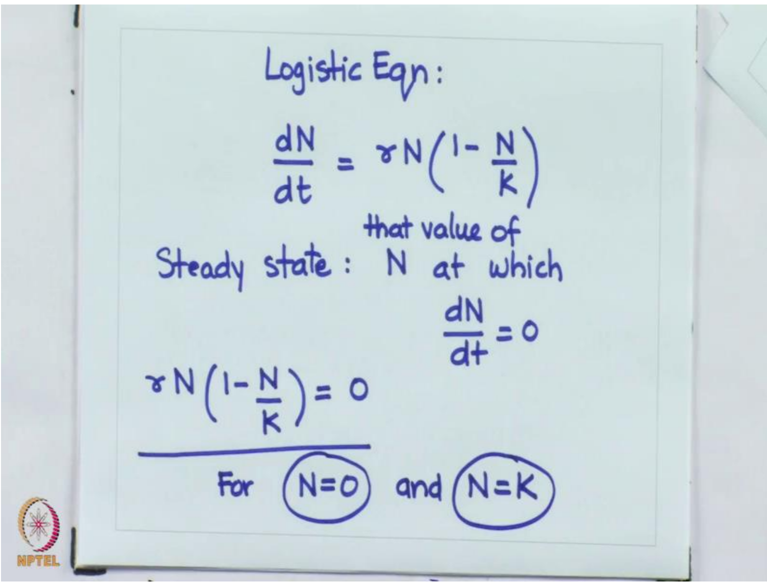

The equation that we have just talked about is called logistic equation, let me rewrite that again dN by dt is equal to r, 1 minus N upon K this is the equation that we have just arrived. Now we are whenever we have dynamical equations like this we are we are measuring rate of change of any quantity in this case N with time, what we are interested in is what is the steady state of the solution.

The steady state of the solution is that value, steady state of the system is that value of N at which dN by dt is equal to 0, which means we are interested in those values of N for which dN by dt is equal to 0 which means N does not change with time the rate of change of N with time is equal to 0. For our equation what are the values for which dN by dt is equal to 0? We know dN by dt is just equal to r N times 1 minus N by K is equal to 0 and this whole expression is equal to 0 for N equal to 0 because when I plug N equal to 0 here this becomes r times 0 times this quantity in bracket which is 0 times is quantity which is 0 and N equals K. Because when I plug N equal to K here this becomes 1 minus 1 which is 0, 0 times r N is equal to 0.

So, we have two values of N for which dN by dt is equal to 0, in the next lecture what we will start with is looking at what do these two values of N represent and what does this say about the dynamics of the system and what biologically and mathematically is this equation telling us about two values of N for which the quantity dN by dt which represents the rate of change of number of bacteria with time is equal to 0.

Thank you.