Introduction to Dynamical Models in Biology
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Lecture 13
Concepts of Bifurcation

Hello, welcome to the third week of our course on introduction to dynamical models in biology, this is the first module of this week, here we will keep on discussing on the different dynamic aspects of system of ODE's. Remember till now we have focused more on how the dependent variable changed with or evolved with time and they are steady states. In a ODE or in a system of ODE you have a multiple components, one is obviously the dependent variables, it maybe one or more than one and then you have a independent variable for our case that is a time and we measure everything else changing with respect to time. Apart from that there is something else called parameters which remain constant which does not change with time. So in this video we will start discussing how this parameters can affect the dynamics of a system or the steady states of the system.

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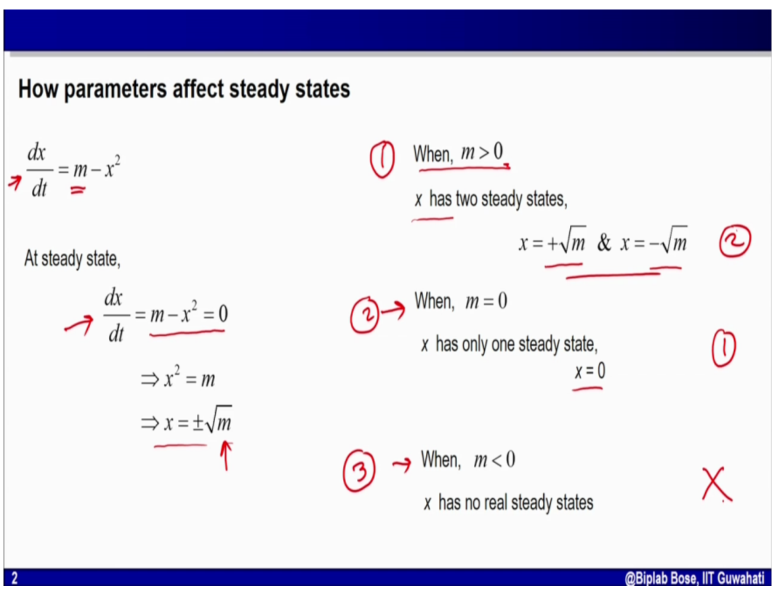

So let us look into this issue, to understand the issue of effect of a parameter on a dynamics of a system, let us take a particular example, this simple ODE I have taken $\frac{dx}{dt} = m - x^2$ so M is my parameter which remain constant, does not change with time, so I want to see how the dynamics of the system or the system property represented by this ODE is getting affected by the value, numerical value of M, so let us see. Let us start the steady state analysis for this ODE, we know for a state for steady state the derivate should be equal to 0 there is $\frac{dx}{dt}=0$ that means $m-x^2=0$.

So let me separate out x and m , so I take X on the left hand side, I get $x^2=m$ that means my steady state solution are $x=\pm\sqrt{m}$, so that means I have two steady value $x=\pm\sqrt{m}$. So let us take different values of M and see how the steady state changes, so when the first case when M >0, if M > 0 for example value 4, 16 or something like that, X will have two steady state, one is $+\sqrt{m}$, another one is obviously $-\sqrt{m}$, so if M = 16 then one steady state will be +4 the other will be $-¿$ 4.

What if m = 0, when m = 0 then I have only one steady state that is x = 0, what if m < 0 in that case, I get this one negative the something under the square root is negative that means I do not have any real solution here. Just look into this cases, case 1 where m > 0, I have two steady states where in the second case where m = 0 I have only one steady state, when the third case m < 0 I have no steady state, that means the number of possible steady state for this system represented by this particular ODE depends upon the parameter m when the m is positive number you have steady state, when the m is a negative number you have no steady state, when m = 0 you have just one steady state.

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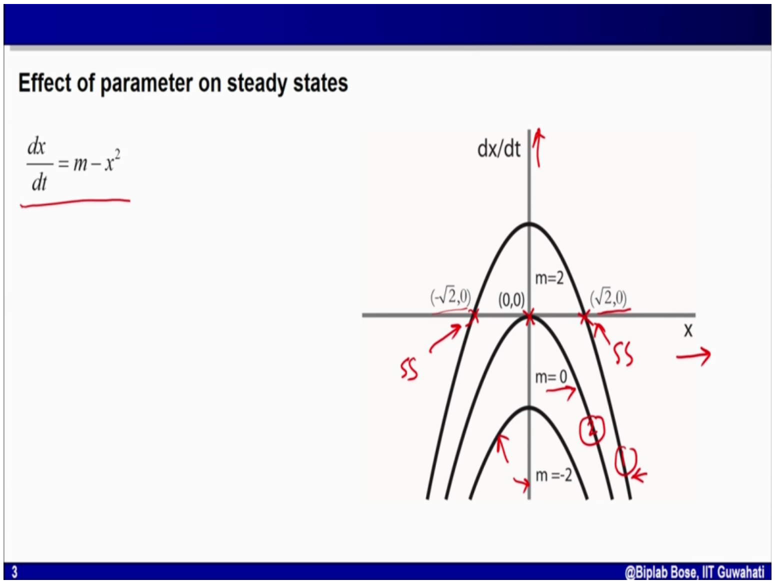

I can represent it graphically, so what I plotted here, x in the horizontal axis and $\frac{dx}{dt}$ in the vertical axis and then I am plotting these ODE in this plain, so essentially I get this parabolas. Now when m is positive value then I have this first parabola and as you can see this parabola is intersecting x at two position, so this curve is intersecting x at two position, so at these two position $x=0$ that means this is one steady state and this is also have $x=0$, so this is another steady state. It is very easy way to identify the steady state in $\frac{dx}{dt}$ versus x plain. So I have two steady state, I have consider m = 2 so that means this first steady state is $\sqrt{2},$ 0 and the other one is $-\sqrt{2},$ 0.

Now consider $m=0$ then this curve goes down and I get this one, the second plot, so this is for $m=0$ and obviously this intersects the X axis only at one point and that is (0,0). When m is negative this curve goes down further, so this is the one for $m=-2$, as you can see this curve is not intersecting x anywhere, that means I do not have any real solution, any real steady state for this system, so I can represent the effect of m a parameter on the possible steady state using this type of plot.

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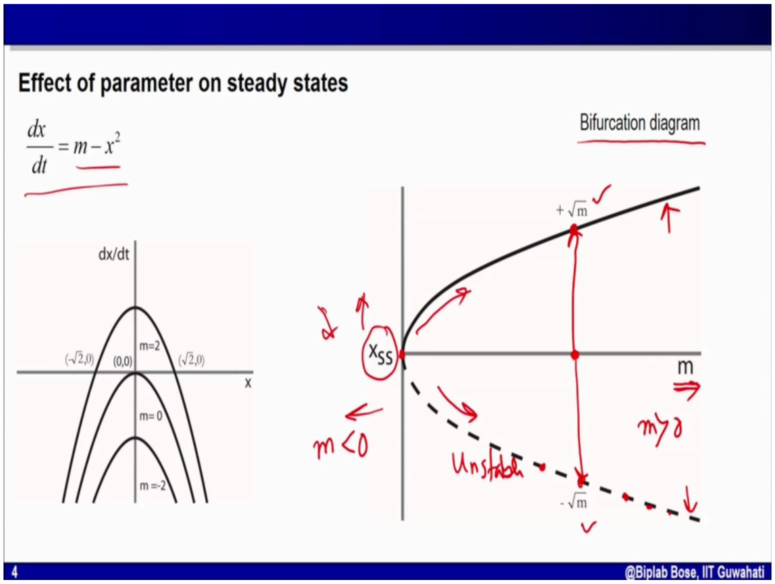

There is a better way of representing the same thing that is what I have drawn here and this type of plot is called bifurcation diagram. What you do in bifurcation diagram, you take the parameter which is showing this type of effect for example in this case M on the horizontal axis and the steady state values of x the dependent variable on a vertical axis and you try to plot, so obviously when m is negative, m <0 I have no real steady state, so nothing is shown in this region. When m =0 which is this position, I have only one steady state so I have one point and for $m>0$ for all positive values I have this quadratic form, so I have two solution $+\sqrt{m}$, $-\sqrt{m}$, so I get two curves like this, so I can easily identify suppose I have a positive value of m then I will have two steady state one here the other one is here.

This type of diagram where you take the parameter which is effecting the number of steady state in the horizontal axis and the steady state value, remember it is the steady state value of the dependent variable the vertical axis and then you plot the curves and the curves represent the number of possible steady state, this type of curves are called or plots are called bifurcation diagram and here I have the bifurcation diagram for the equation $\frac{dx}{dt}=m-x^2$. Notice one thing, these line the upper line is bold and filled the lower line is dotted, I have used these dotted line to represent that these particular steady state, the steady state on all these along this line, anything, anywhere if you take any steady state, these are all unstable steady state. I will show

how to calculate the stability of a steady state on a bifurcation diagram, for the time being let us move into different system.

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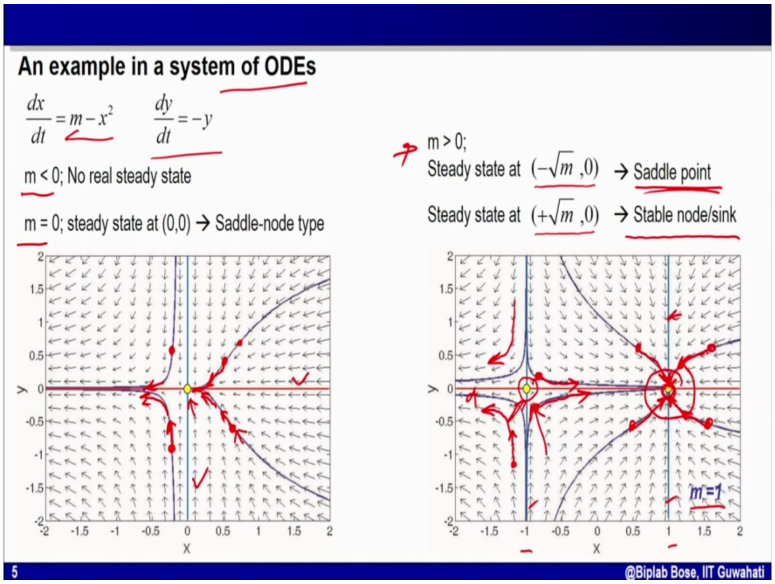

The example that I have given just now is for a single ODE, what will happen if I have more than one ODE, so let us take a system of ODE to understand the effect of a parameter on the behaviour of the system, so I have a simple system of ODE, $\frac{dx}{dt} = m - x^2$ the same equation that you have earlier and then $\frac{dy}{dt} = -y$, so I have a system of ODE, so I want to see how the systems stay to steady state get affected by by m the parameter, so effect of m will be seen on the steady state behaviour of this system, so let us look into it.

If m < 0 as we have discussed in the earlier case as the equation is same, $m - x^2$ so obviously your do not have any possible real steady state for this system. Remember to get a steady state for a system of ODE like this both $\frac{dx}{dt}$ has to be equal to 0 and $\frac{dy}{dt}$ also has to be equal to 0, so both this has to be equal to 0 at the steady state, so when m < 0 I have no real steady state, when M is 0, if I draw the phase portrait I can see this type of graph which is shown here, these two are the nullclines and the intersection point is (0,0) and that is my steady state.

Let us look into trajectories, if I start somewhere here at t= 0 I follow this curve and collapse at the steady state, if I start somewhere here, I follow the arrow and collapse at the steady state. The phase portraits are telling me if I start form this right hand quadrants, I move and collapse at the steady state, what happened on the left hand quadrates, if I start somewhere here, the phase portrait arrows are telling me that I will move along this path and I will divert away from the steady state, the same thing is here, if you guys start from here I will move along this and move away.

So you can see from one side the left hand quadrants the system, the steady state is unstable, if you slightly get perturbed then you move away from the steady state on the other hand on the other side you are converging, so it is like combination of two things, from this side that the right hand side it is like a source note on the other hand this side you have on the left hand side you have the saddle type behaviour. So I have saddle not type here.

Now let us take the third case where m >0, when m >0, I have two solutions for steady states, I have two steady state, one is $-\sqrt{m},0$ and the other one is $+\sqrt{m},0$. I have drawn the phase portrait for this situation where m >0 and I have taken value m =1 for this system and drawn the phase portrait, these colored lines are nullclines. You can see the nullclines have intersects at two position, one here at this yellow dot another one is this yellow dot and as $m=1$ you can see one intersection point is add equal to one the other one is add equal to minus one. So look at the behaviour of the steady state or the trajectories behaviour of the trajectories around the steady state.

If I start somewhere here at t=0 I will follow this trajectories and eventually collapse at this steady state, if I start from this point at t=0 I will follow this path and collapse at the steady state. If I start form this direction again I will with time I will collapse at the steady state, the same is if I start from this direction also. So if I have this particular steady state one 0 I stay there but if I slightly perturb the system from there I will again collapse, the system will again collapse back to the same steady state but that is not true for the other steady state this (-1,0). So here if I am there at the (-1,0) and stay at that steady state but if I disturb slightly for example, if I bring at t=0 the system is at this dot and then with time system will move away from the steady state.

If I have the system here at t=0 with time it will move away, if I start from somewhere here at t=0 I will move towards the steady state and then divert so the same thing here also. So you can easily recognise this particular steady state is nothing but saddle point whereas the other one this one is a stable note and synced. So in this example are observing two phenomena, when m is changed in different domains when m is negative we don't have any real steady state but $m=0$ you have only one steady state. When m >0 you have two steady state, so the number of steady state is changing with the value of the parameter, not only that in this case the type of stability of the system is also changed.

So here when m =0 I have a saddle note type which is unstable whereas in case of m >0 I have two steady state, one is saddle point which is obviously unstable and the other one in a stable note type. So here the parameter M is not only affecting the number of possible steady state but also affecting the trajectories or the phase portrait of the system and the stability of this steady states.

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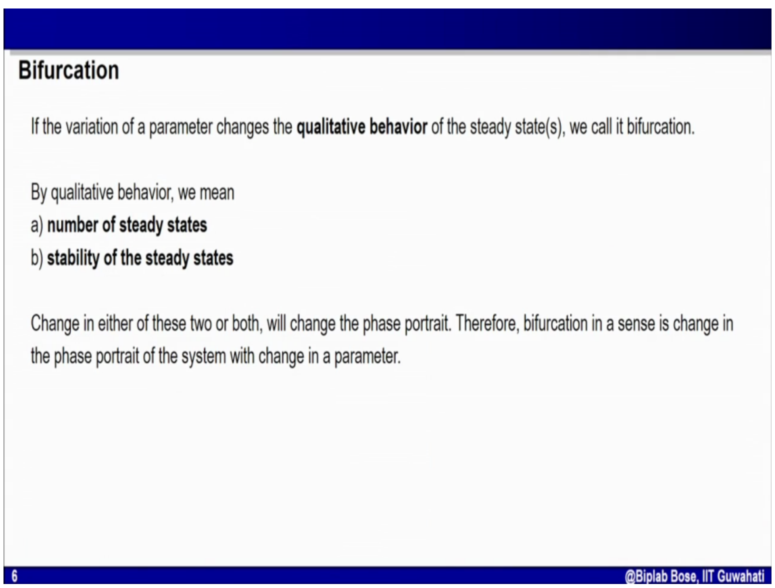

So let us now define this type of behaviour. This type of behaviour where the quality behaviour of the steady state are changing or getting affected by the a particular parameter is called bifurcation and by qualitative behaviour what do I mean, by qualitative I mean that the number of possible steady state and the stability of the phase portraits around the steady states. So there can be a parameter which controls either the number of steady state possible steady state or it may control the stability of the steady state without changing the number of it may affect both of them together simultaneously.

So in all these cases I will say these parameter causes bifurcation in the system and the system as a bifurcation and the parameter that is causing is this bifurcation will be called bifurcation parameter. So I can have a generalised broad definition, if the variation of a parameter changes the qualitative behaviour of the steady state I will call the system as bifurcation.

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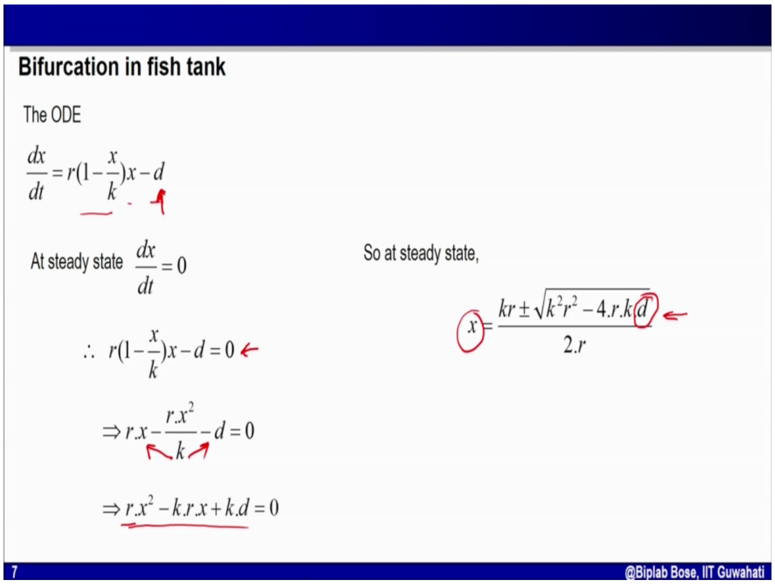

Now let us look into another example and analyse in detail to understand this concept of bifurcation, so let us take the old problem of fish tank where we are growing fish in a tank and at equal interval we take out some fish to sell in the market, so as the tank has limited space and resources I will use a logistic growth model with removal as a negative one. So X is the number of fish in the tank at any time, so the rate of change of number of fish is $\frac{dx}{dt} = ¿$

$$r\left(1-\frac{x}{k}\right)-d$$

where k is the carrying capacity, r is the constant for growth and d is constant rate by which we are removing the fish.

So I want to see whether this system has bifurcation with respect to this parameter d or not, so to do that I have to first check identify the steady state of the system and then I have to analyse how this parameter d affects these steady state either in terms of number of possible steady state or in terms of the stability of the steady state. So to get a steady state I have to put $\frac{dx}{dt}=0$ as a simple one, so I can put $\frac{dx}{dt}=0$ that means $r\left(1-\frac{x}{k}\right)-d$ is equal to also 0, so I will take x and everything else on the other side so I can multiply this and I get a quadratic form like this $r.x-\frac{r.x2}{k}-d=0$. So if I rewrite it multiply k with d multiply k with $r.x$ and then I get $r.x^2-k.r.x+k.d=0$. Note that I have multiplied both side with minus sign so that now I have got positive sign here $r.x^2-k.r.x+k.d=0$ is a simple algebraic rearrangement. So I have a quadratic equation for x that means x will have at least two solutions, so $x=\frac{kr\pm\sqrt{k^2r^2-4rkd}}{2r}$, is simple following the rules of quadratic solutions. So now I want to see how d will affect the value of x and the steady state obviously and the stability of the steady state obviously.

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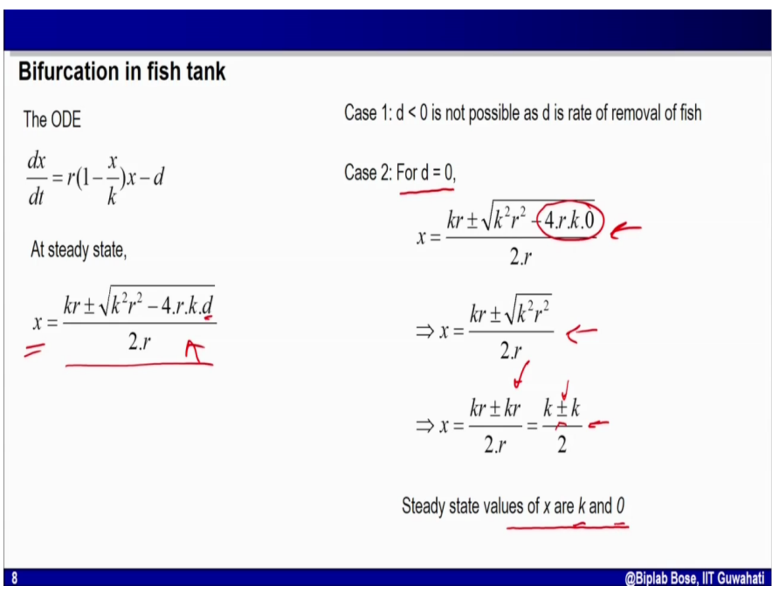

So let us look into it, so at steady state I have calculated value of x is this time and I want to change the value of d here to see how this exchanges. Let us take at d case one where d<0, now is that possible. Actually in our case d is representing the rate by which we are removing the fish from the tank, so d cannot be negative it will be always positive or equal to 0. So let us take the case two, d=0 that means fishes are growing but we are not removing anything from the tank. So in that case I can put d=0 in this equation and I get this term $x=\frac{k.r\pm\sqrt{k^2r^2-4.r.k.0}}{2.r}$ I can simplify it, so this whole thing becomes 0, I get $\frac{k.r\pm\sqrt{k^2r^2}}{2.r}$, so $\sqrt{k^2r^2}$ is nothing but k.r. So I get this one here and if I cancel r because r is not equal to 0, so I get $\frac{k\pm k}{2}$. So that means I have two steady state value, when I take the plus sign here in this equation here, I get $x=k$, if I take the minus sign then $x=0$, so that means when d= 0 I have two steady state for x , one is k and another one is 0.

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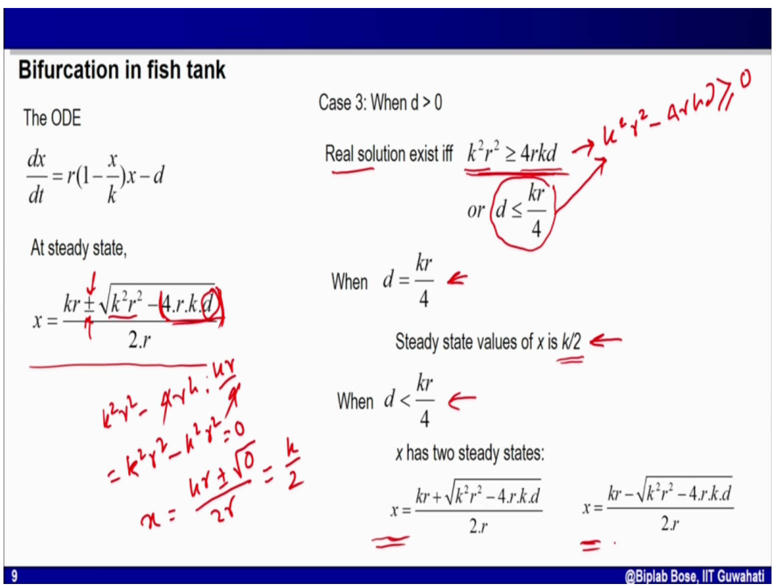

So let us look into the third case, we have already discussed two cases one d is negative which is not possible, one is d = 0 where I have two steady state k=0 I take the third case where d>0. So here d>0, look into the solution for x is this quadratic solution that you have got. If d>0 then we may have a trouble. I have $\sqrt{k^2r^2-4.r.k}$, I have to keep this whole term under square root as a positive thing because otherwise I will not have any real solution, so if I have to keep $\sqrt{k^2r^2-4.r.k.d}$ which is under this square root as a positive value thing that means this whole thing, $4.r.k$ has to be smaller than $\sqrt{k^2r^2}$ otherwise I will get a negative value here.

So that means to get a real solution I have to Keep $\sqrt{k^2 r^2}$ this is here $¿4.r.k$, so that $k^2 r^2 - 4.r.k$ is a positive thing, so this will give me that $k^2 r^2 - 4.r.k.d \geq 0$. I cannot have a negative value there otherwise I will not get a real solution, so if I rearrange this inequality then what we get is that d ≤ $\frac{k.r}{4}$, I have cancelled one r because r is not equal to 0, I have cancelled one k because k is not equal to 0, so d ≤ $\frac{k.r}{4}$ these inequality has to be satisfied so that I get this relation and then I will have a real solution for this system.

So let us consider the case first where d= $\frac{k.r}{4}$, so I am taking the value of D here $\frac{k.r}{4}$ then I have only one steady state value, I can easily calculate $k^2 r^2 - 4.r.k.d$ so $k.d$ is replaced by $\frac{k.r}{4}$, 4 and 4 get cancelled, so I get $k^2 r^2 - k^2 r^2$ which is equal to 0 that means $x = \frac{k.r \pm \sqrt{.0}}{2.r}$ which is equal to nothing but $\frac{k}{2}$. So when d= $\frac{k.r}{4}$, I have one steady state and that is equal to $\frac{k}{2}$ What if d ≤ $\frac{k.r}{4}$, so in that case, in that case what will happen?

This whole thing, this whole thing as I replace the value of d with a value which is less then K square or KR by 4, this whole thing in this bracket will be less than K square R square, so that means I will have this two solutions, $x = \frac{k.r + \sqrt{k^2 r^2 - 4.r.k.d}}{2.r}$ and then another solution with this negative sign $\frac{k.r - \sqrt{k^2 r^2 - 4.r.k.d}}{2.r}$. So when I have d= $\frac{k.r}{4}$, I have only one steady state at $\frac{k}{2}$ when d ≤ $\frac{k.r}{4}$, I have two solution one is this one, the other one is this one, so I have two steady state.

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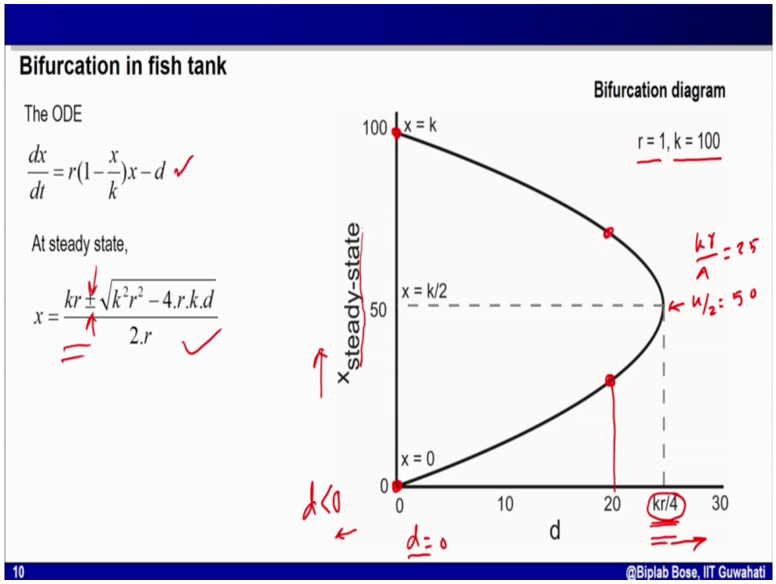

So let us pull all this together and represent it graphically. So what I have, this is my ODE, my generalised solution for the steady state is from the quadratic equation is this quadratic solution, so I have plotted a bifurcation diagram here, d is the parameter with respect to which I am studying the bifurcation, so d is in the horizontal axis and the x is a dependent variable and the steady state value of x is here, remember this is a steady state value of x. So when d is negative that means in this direction d ≤ 0 that is not possible because d has to be positive or 0 in our system, so I have nothing on this side.

When d = 0 I have two steady state, x =0 other one is $x=k$ that we have discussed just now. When d = $\frac{k.r}{4}$ and what I have done here, I have taken r = 1 and I have taken K = 100, so $\frac{k.r}{4}$ is nothing but 25, so when d = 25 or $\frac{k.r}{4}$, I have only one solution, if you remember just in the previous slide we have derived that, so that solution is K by two that is $\frac{k}{2}=50$ in this case but in between this d = 0 and d= $\frac{k.r}{4}$, D is positive but ≤ $\frac{k.r}{4}$.

So in that case I have two solution if you remember from the this quadratic relation, one with this plus sign another one with this negative sign. So if I take for example 20, so I have one solution here, the other solution is here, so let us explore this bifurcation diagram further.

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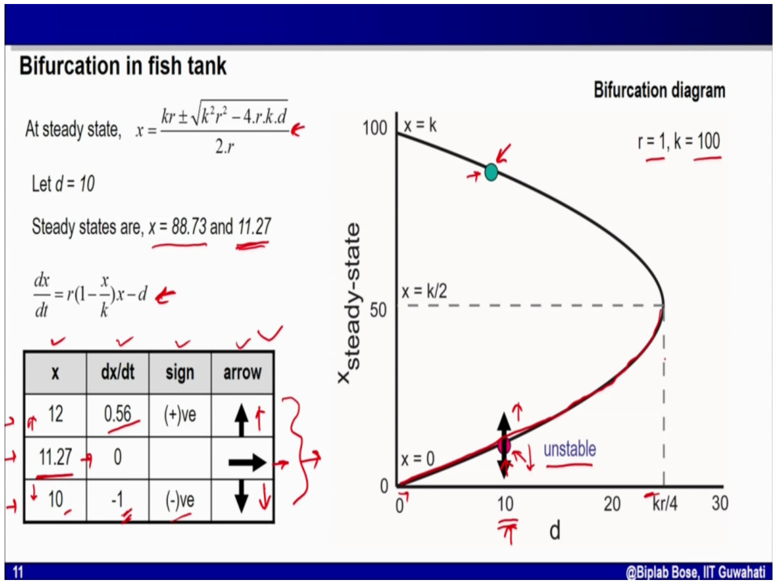

If you remember in the first bifurcation diagram that I have drawn for $\frac{dx}{dt} = m - x^2$. I have one solid line and the other line was dotted and I said that that dotted line represent unstable steady state. Now the question is how do I calculate steady state, stability of steady state in a bifurcation plot. So the same thing we will do here, we will try to understand the stability of the steady state shown in this bifurcation diagram. I have a curve here which is parabolic curve which represent the steady state possible steady state when d is varied from smoothly from 0 to $\frac{k.r}{4}$, remember when d is negative I don't have anything real because d cannot be negative in this case.

When it is bigger than $\frac{k.r}{4}$. I have no solutions real solution, in between 0 and $\frac{k.r}{4}$. I have this parabolic curve representing that I have two possible steady state. And I want to see the stability or I want to calculate the stability of this possible steady state, so let us take d= 10, if d= 10 then I have one steady state here by this red dot and I have another steady state here by this green dots and if you do the calculation using this relationship, you will get I have already done that, x = 88.76 this is this one is 88.7 and the other solution is 11.27 this one. So now question is these red dot and green dot which are representing the steady states when d= 10 are the stable or unstable, so let us do the calculation for that.

Let us take first the case where the steady state is at 11.27 and if you remember for one dimensional system when we were discussing about direction field we have used a tabular method to calculate the steady states, so we will use the same thing here because I have just one ODE. So let us make a table, I have drawn a table, if you remember the table should have 4 columns, X, the derivative, the sign of the derivative and the arrow and I have three columns, three rows, in the middle row I have put the steady state value that is the 11.27 here and I take a slightly bigger value on the upper row that is 12 I have taken and slightly lower value than the steady state 10 in the lower row.

For 12 for 11.27 obviously $\frac{dx}{dt}=0$, you can calculate it, so the arrow is here horizontal whereas if I take x slightly lesser 10, then $\frac{dx}{dt}=-1$, you can put the value of x = 10 in this ODE with value of r = 1, k = 100 and d = 10, you will get $\frac{dx}{dt}=-1$. So the sign of the $\frac{dx}{dt}$ is derivative is negative, that means my arrow will be pointing down I have taken slightly higher value 12 again using a same ODE I put the value of x there as 12 and take r = 1, k = 100 and d = 10, I get point 56 and the sign is positive, that means the arrow will be pointing towards this.

So what I can do, I can put the arrows on this red dot based on these result that I have got in a tabular fashion, so that is what I have done. So as you can notice, these red dots is steady state that is 11.27 when d=10, so x will stay there if you don't perturb it but if you perturb this slightly it will move away, one arrow is pointing up, one arrow is pointing down, so that means this point is unstable, you can do this calculation for any point value greater than D from starting from this value of D up to value less then $\frac{k.r}{4}$ so that along this whole curve you will see this whole cure all points on this whole curve will give steady state which are unstable.

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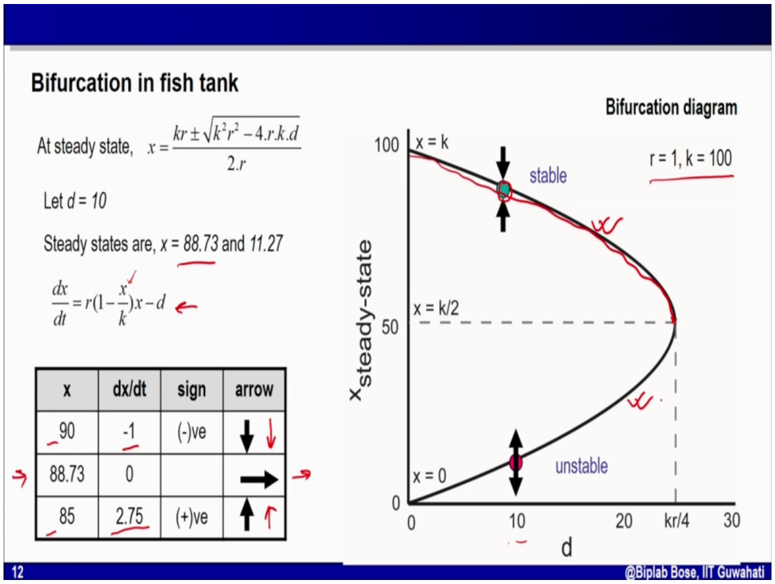

Let us look into green part that is 88.73, again I will use the tabular calculation, so I will table it in 4 columns and three rows, the middle row is representing steady state 88,73, obviously the $\frac{dx}{dt}$ will be 0 so I have a horizontal arrow, I took a slightly higher value 90 here and I put the value of 90 in this text, in this ODE and k = 100, r = 1 as I have mentioned here and d as we have decided is 10. So if you put those values, club together and calculate the $\frac{dx}{dt}$ you will get -1, so have a negative sign that means the arrow is pointing towards the steady state the horizontal one. If I take a smaller value of x say 85 then if I calculate $\frac{dx}{dt}$ using the same relationship we get 2.75 is positive, that means arrow will be pointing up.

So if I put the arrows I get like this, so the both the arrows are pointing towards the steady state at 88.73 that means if x is at 88.73 it will stay there but if you perturb x slightly then from higher value it will again collapse at that 88.73, from lower value of that again it will time, it will collapse there, so this point is stable one. You can try any other point along this curve up to this, you will see all points are stable steady state. So this upper curve is a stable steady state, where as this lower one are unstable steady state. So let us compile all these in one single bifurcation plot.

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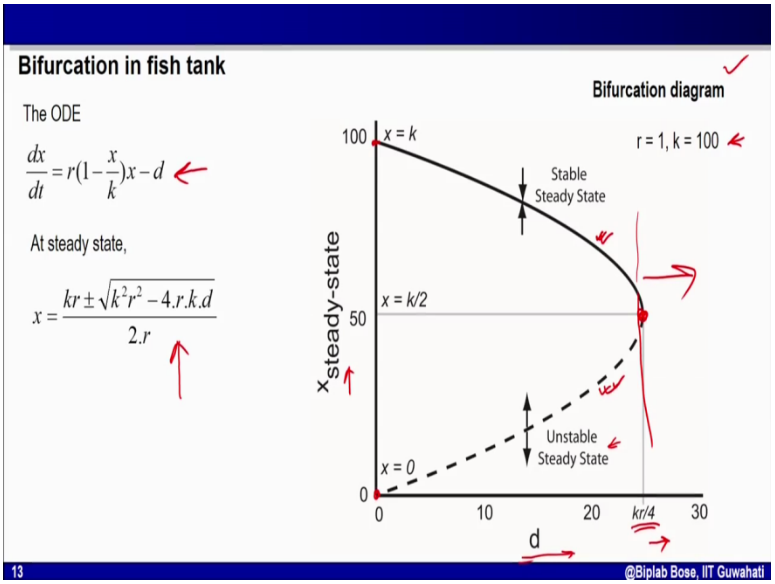

The ODE is given this one for my fish tank problem the solution, generalised solution for steady state is given by this relation and I have drawn the bifurcation diagram here for specific value of RK and I have taken d which is callusing the bifurcation in the horizontal axis and the steady state value of X in the vertical axis. And when d is negative that is not possible because d has to be positive in our case because there is a state of removal of the fishes it cannot be negative. If d = 0 I have two steady sate one here, one here the curve is intersection only at two point.

If D is bigger than $\frac{k.r}{4}$ then I do not have any real solution so you don't see anything on this side. If d= $\frac{k.r}{4}$ then I have only one possible steady state here which is $\frac{k}{2}$, in between from 0 to $\frac{k.r}{4}$ I have two possible steady state for each value of d as shown by this smooth curves and this upper curve, upper steady states are all stable steady state and the lower steady state this in the steady state in the lower curve are all unstable steady state and that is why the lower curve is shown as a dotted line.

So what I have discussed till now, I have taken a ODE and I have identified the steady state and then I have picked one parameter and I have taken different cases of that parameter and again calculated number of possible steady state. So that told me whether the number of possible steady state in this system is affected by the parameter, in this case parameter is d and that is true based on d value of d number of possible steady states are changing. At the same time I have also shown you how to calculate the stability of each of the steady state.

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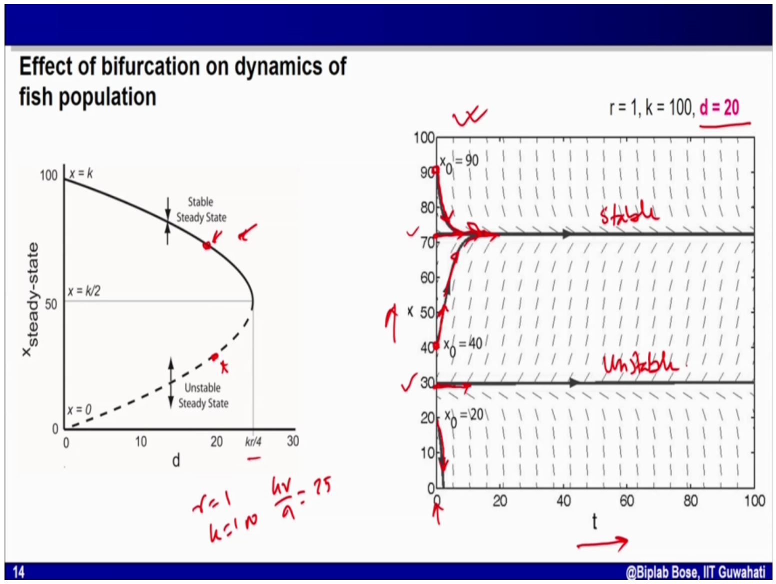

Now we have seen bifurcation but let us now look into for this particular example how this bifurcation will actually affect the dynamics of a system. So you know I can have two interesting region when d is in between suppose 0 and $\frac{k.r}{4}$, if I take r = 1, k = 100 then $\frac{k.r}{4}$ is 25. So let us first take a value of d when $d<\frac{k.r}{4}>0$. I have taken d equal to 20 and I have drawn a direction field plot here with t in the horizontal axis, x in the particle axis. So if you see the bifurcation plot here d is here at 20, so that means, that means I will have one steady state here another steady state here.

So bifurcation plot is telling me that I should have two steady state and one is unstable, this one is unstable other one is stable. So in a direction field also I have one steady state here near at 30 and another steady state near 70. So if I stay start at this steady state, if I start somewhere here at t = 0 I will remain in this steady state if I start at this steady state I will stay at this. So if you start with 70 fish then you will always remain at 70 fish in that tank, if you start at that 35 at the steady state there is a number of fishes at the very beginning then you will stay at the steady state.

But if you start growing your fishes with a value in between this two steady state, say $x=40$ here, so you starting with your fish tank with 40 fishes when r = 1, k = 100 and d = 20 that means you take out 20 fish per unit time then the direction field is telling that I will follow this arrows and eventually collapse at this steady state which is near 70. If I start at t = 0 with 90 fish my direction field is telling me I will follow this trajectory and collapse at this steady state. So this is a stable steady state whereas if I start with a number of fish below this unstable steady state, this is 30 then what will happen, for example if I start with 20 fishes then I will move in this direction away from the steady state and as my fishes get used up by picking up I will eventually go towards 0 fishes, so this one is unstable.

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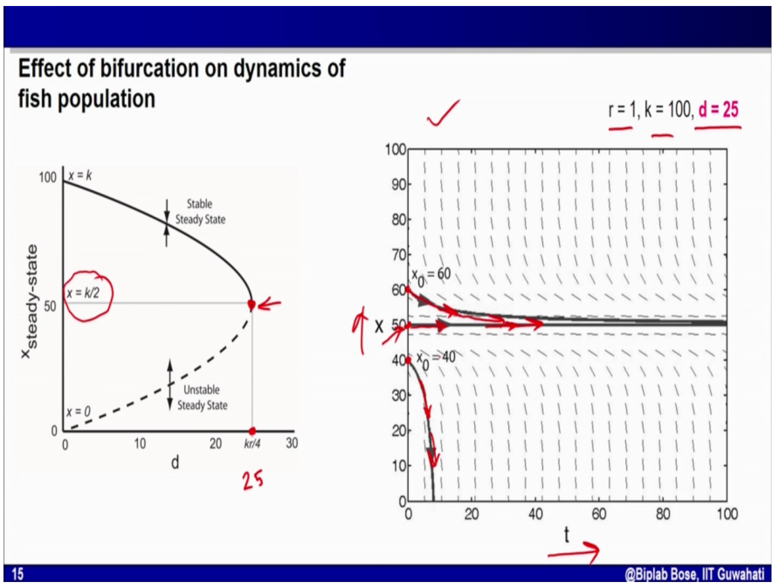

What if, if I take a different value of d now I have taken a value of d as this $\frac{k.r}{4}$ that is 25, remember r = 1, k = 100 so $\frac{k.r}{4}$ is 25, I have taken d having value equal to 25 that means I am removing 25 fish per unit time from the tank, so my bifurcation diagram is saying that I will have only one steady state here, so if I start the direction field here with t in the horizontal axis, x in the vertical axis, so here I have the steady state, the direction if you telling, this is the steady state and obviously bifurcation plot also tells me the steady state will be at $\frac{k}{2}$ so that is 50.

So if I start with 50 fishes at the beginning at t = 0 I will stay at that steady state, I will always have 50 fishes in my tank. If I start with slightly higher value that means I am starting with a number of fish bigger than 50 the steady state value say 60 then my trajectories in the direction field is saying that with time that will decrease and eventually I will reach 50 the steady state and then with time it will be stable there.

But what if I start with a number of fish slightly lesser than 50 say 40, so t = 0, I have only 40 fish in the tank and I am revealing they are growing by logistic growth and I am revealing 25 fish per unit time so then my direction field tells me that this will be the path followed, followed by x so number of fish will eventually decrease, it will move away from the stable steady state, at 50. So as you can see from one direction it is stable, from the other direction this is unstable, so this is same state. So these example explain how the bifurcation plot in combination with the direction field tells me how a particular parameter affects the steady states, possible steady state and a dynamics around the steady state for a particular system.

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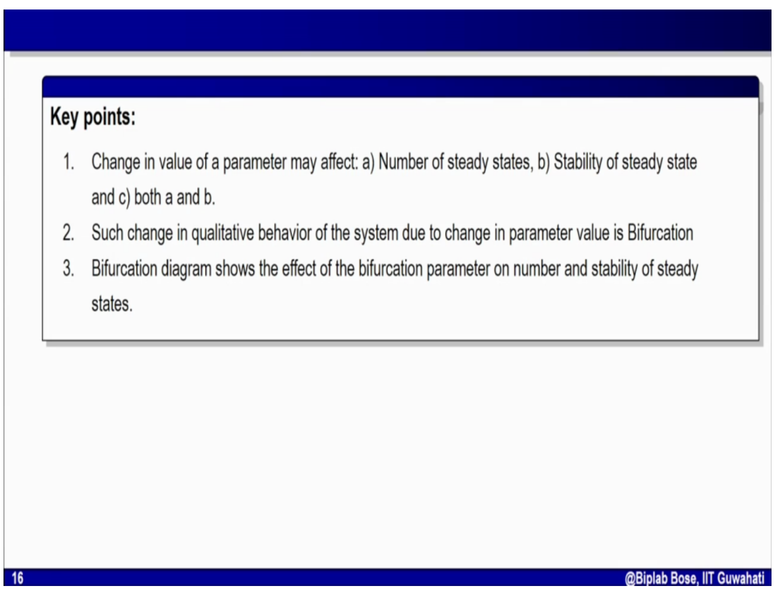

So let us jot down what we have learned in this video, the key points are change in value of a parameter may affect number of possible steady state in the system, it can affect the stability of the steady state or it can affect both number and stability and such changes are actually changes in the qualitative behaviour of the system. So when such changes occur, when such qualitative behaviour change occur due to the change in the parameter value we call, we have bifurcation in the system and the parameter which is causing this such changes is called bifurcation parameter.

We have discussed how to draw bifurcation diagram, so bifurcation diagram shows that the effect of bifurcation parameter on number of possible steady state and the stability of those steady state. Thank you for watching, we will discuss further on this topic in the next video.