Physics of Biological Systems

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Lecture – 22
Rotating flagellum

How will the, how will the force depend on the velocity, linearly or non-linearly? Linearly because this is the low Reynolds number regime, remember the governing equation is now the stokes equation which is that delta p the pressure gradient is eta Laplacian of v right.

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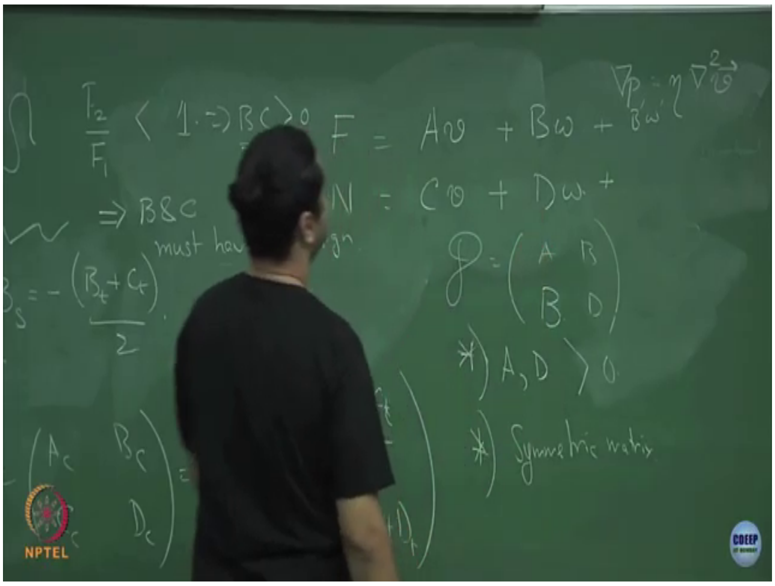

Which is a linear equation and you get a linear force velocity relationship in this regime.

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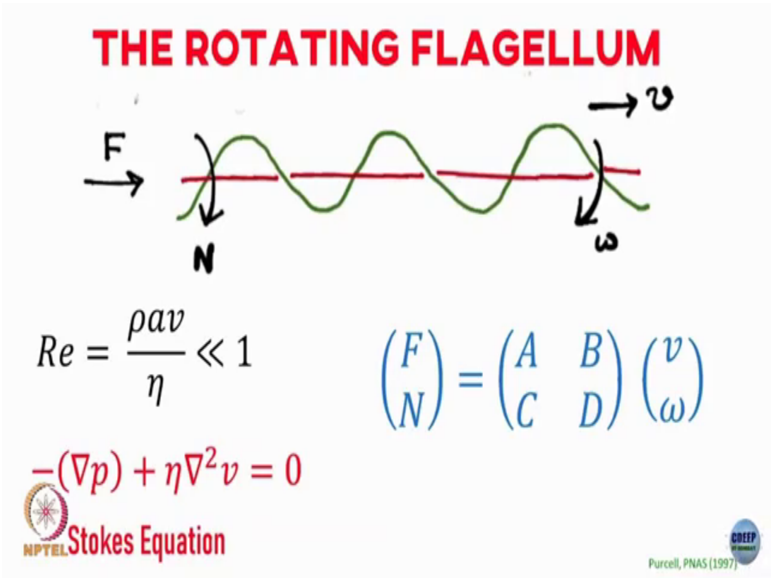

Once you take this low Reynolds number, Reynolds number much less than 1, then the governing equation is the stokes equation where the force is going to be linearly related to the velocity. So, what we can do is that we can write down a relation between this force and the velocity and the angular velocity. Let us say something I do not know how it will go what will be the coefficient, but I know it will depend linearly on the velocity.

Similarly and of course, any sort of linear velocity is also going to cause a rotation. So, it is going to depend it is going to be sum A v plus B omega I do not know what these a's and B's are we will try to sort of find them.

Similarly, if you put in a torque n that is going to go as C v plus let us say D omega ok. In this low Reynolds number regime, these will be linearly related the forces and the torques will be linearly related to the velocity and the angular velocity and I can construct this sort of an equation between them right. So, this is what perceived it. So, we said that, let me write my forces and torques in terms of this matrix ABCD and they relate my velocities and angular velocities to the forces and torques.

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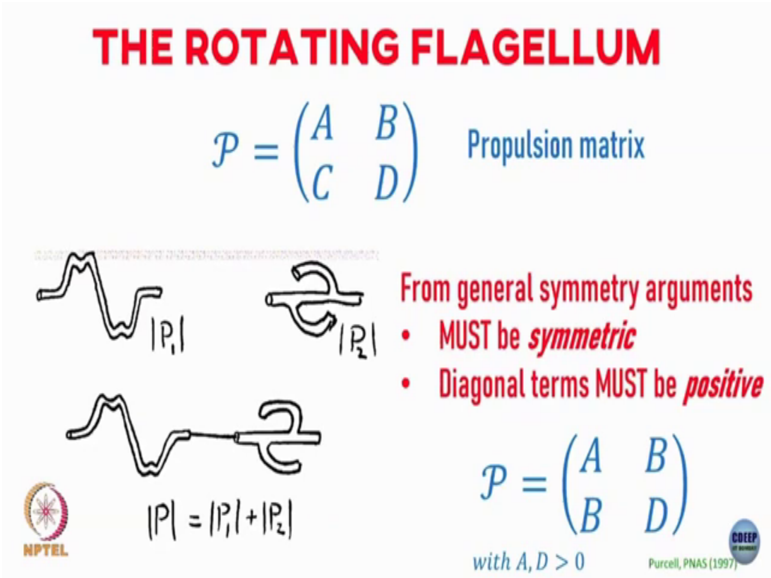

There is what is what Purcell called the propulsion matrix for a bacterium all right.

So, what properties would this matrix obey very generally? What this A B B C and D and soon will be will of course, depend on the body will depend on the shape of the body, will depend on the size of the body of this corkscrew or whatever swimmer that you have, but very generally can I say something about the structure of this matrix this propulsion matrix P which is ABCD ok. So, what Purcell asked let me first tell you the result and then I will just run through the proof quickly.

What Purcell said is the following that first he said that if I take; if I take two swimmers to do very different swimmers. Now I am not talking about this helical corkscrew or anything, it could be any arbitrary sort of swimmer that gives rise to net motion. Each of these swimmers are going to be characterized by their own propulsion matrix P 1 and P 2. So, we said that let me assume that, if I put these if I connected these two swimmers with this some very thin wire, then I can add up these propulsion matrices ok.

What does that mean it means; that means, a couple of things one is that these swimmers are well separated enough that the flow is generated by one of them do not affect the other ok. So, their wells the hydrodynamic flows of 1 do not impinge upon the flows of the other that is that is one of the assumptions that we are making and we assume that the disconnecting wire that I have that has no effect on the flow at all. So, its a very thin whatever wire that I have its an idealized case, but whatever, we can pursue this and see what it gives us ok.

So, for example, if it was if there was no torque, if it was just a velocity, then both of these if it was moving with some net velocity the velocity would be the same for both of these right.

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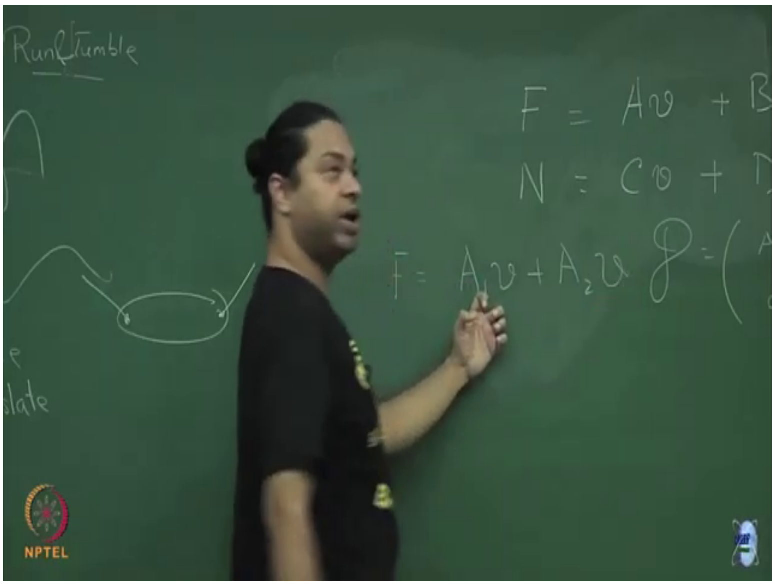

So, we would have a A 1 of v plus A 2 of v, but this came from one of the propellers this came from the other propeller. You will still have a linear relationship between the force and the velocities.

The coefficient you we are just going to decompose into this propulsion matrix for 1 plus the propulsion matrix for the other. Again this is an approximation, but. So, what he argued was that that from very general symmetry arguments. This propulsion matrix must necessarily be diagonal sorry, must necessarily be symmetric not diagonal forgive me which means that this B must be equal to C ok. And these diagonal terms A and B we must necessarily be positive.

So, very generally, what you argued was that this propulsion matrix for any sort of swimmer not necessarily a corkscrew or anything can be written in this form A B B D so, with the symmetric matrix with A and D greater than 0. So, I will try to show this. So, that is the result will try to show all right. So, let us say I have a propeller some propeller right of some arbitrary shape.

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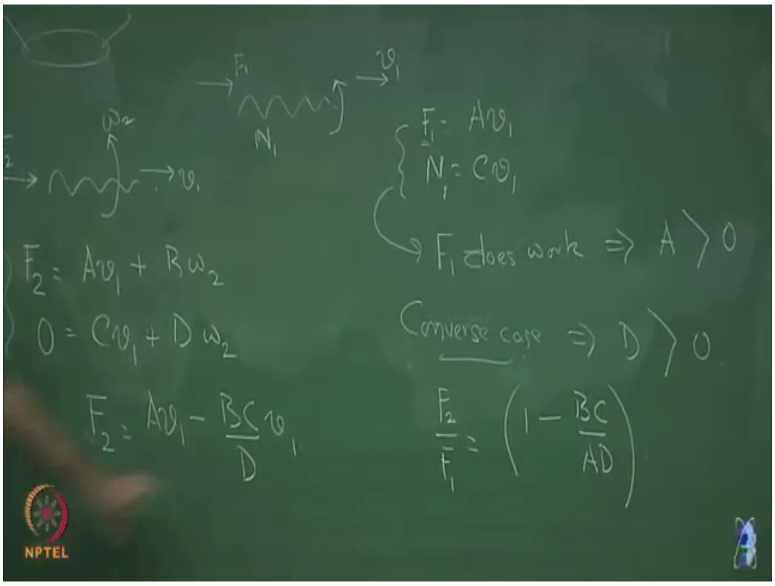

And I apply a force F 1 on it ok. This is going to cause it to move with some velocity right. And it's going to cause it to rotate with some angular velocity right that is what we saw.

So, then what if there is that let me imagine, I apply an external torque as well ok. What torque do I apply I apply precisely the amount of torque that is necessary to stop this rotation ok which means that after I have applied this force and this torque this propeller is only going to move with the velocity it is not going to rotate ok. In that case, what I have if I look at this angular velocity becomes 0 right.

So, let me say that I have this F 1 is equal to A v 1 and this N 1 the torque that I put is some C v 1 right. My propulsion matrix reduces to that. Now, because there is no net, because there is no net rotation this root this torque is not doing any work which means that the entire work is being done by this force that I am applying right and so, this external so, in this in a scenario like this.

This external force F 1 does this does whatever work is necessary in order to move this propeller through with this velocity v 1 Because it this is the only thing that is doing the work, it means that this; what this means is that this coefficient A this must necessarily be greater than 0 right. Because this is doing some network depending on what distance it is moving and so on. That is A v 1 times, how much it has moved and because that needs to be positive this A needs to be positive.

Similarly, you can imagine this converse scenario, where you allow this propeller to rotate, but you do not allow it to move by a suitable combination of forces and torques in which case the entire work is going to be by the torque that you apply which means. So, if I look at the converse case; converse case then the entire work is going to be done by the torque which means that this D is going to be 0 sorry, D is going to be greater than 0.

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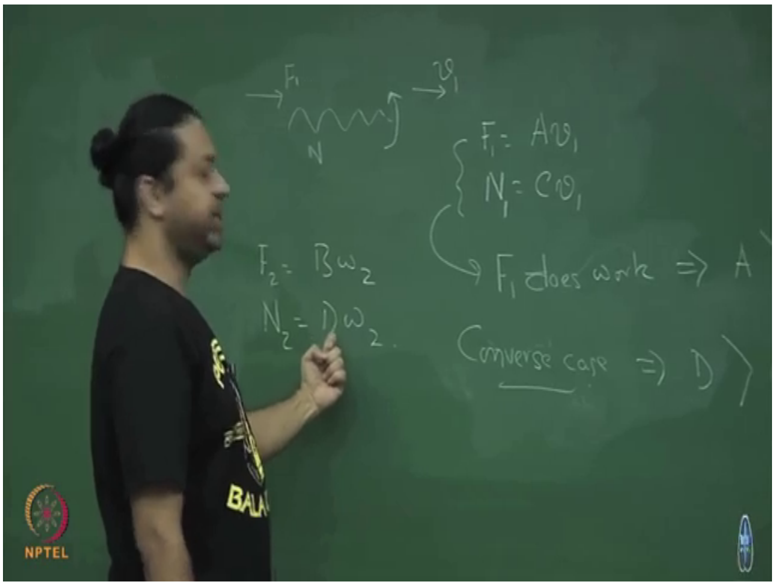

So, in the reverse case of course, you have this F 2 let us say which is going to be given by some B omega 2 and this N 2 which is going to be given by D omega 2 because I have now constrained it from moving with a velocity by the suitable combination of F 2 and N 2. Because it is not moving and only rotating, the entire work is going to be done by the torque which means that this D is necessarily greater than 0

So, very generally for this propulsion matrix what Purcell showed was that this A and D the diagonal elements these need to be greater than 0. Now, let me forget this. So, so I this case this first case that I considered, where I have applied the force and a torque such that I have canceled the rotation, these are my equations of motion all right. So, now, let me imagine that I is have this propeller.

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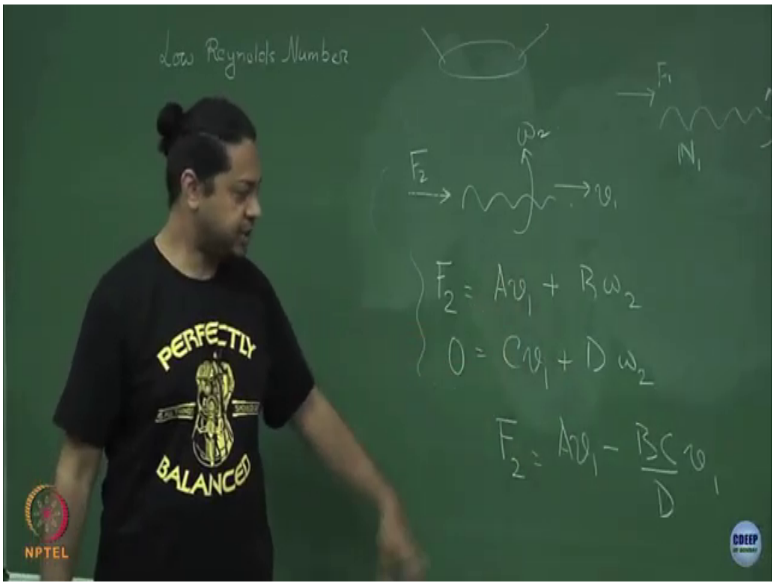

I apply a force no torque, I apply only a force, such that it leaves with the same velocity v 1 that it was moving in the earlier case.

In this case with this combination of forces and torques N 1 and F 1, it was moving with some velocity v 1. I now, apply a force F 2 let us see, such that this propeller is going to move with the same velocity, but it will also of course, move is also going to rotate right. Because I am not applying any torque. I am just applying a force which is exactly, what is required to make it move with a velocity v 1. So, what does this mean? So, let me call this omega 2.

What does this mean, if I write down the equations? It means that F 2 is equal to Av 1 plus B omega 2 right. And I am not applying any torque which means that N is 0 and this is going to be equal to Cv 1 plus B omega 2 right. Does make sense yes?

Student: (Refer Time: 10:12).

So, it could be like a corkscrew. It could be any object. So, for example, it could be that Purcell simple swimmer that I showed. It could be any object which manages to swim in the low Reynolds number environment ok. I do not care, what that object is? What that object is? Is going to be encoded in the values of this A B C and D ok. For example, if you were to think of a sphere, if you give it a force it is going to move with a velocity which is 6 pi eta R v it is not going to rotate right. Which means that this a is going to be 6 pi eta R B is going to be 0 and so ,on right.

Similarly, if you give it a torque, it would just rotate it would not move. So, which means C would be 0 and B would be whatever is the appropriate drag because of a torque ok. So, what these elements of the matrix are depends on the exact propeller that you are looking at, but the propeller can be generically anything ok. So, I am drawing a squiggle which is like a corkscrew, but it need not be a corkscrew yes.

Student: What is that (Refer Time: 11:35).

Ok you got this part right this F 1 part. So, remember I am applying a force and a torque on this propeller ok.

Student: (Refer Time: 11:51).

You just apply a force on it and you apply a torque on it ok. Generically that will cause it to move with the velocity and it will cause it to rotate ok, but you balance these forces and torques such that, you cancel out the rotation. So, let us see you were just applying a force it would move. So, let us say I think of a corkscrew. It would move while moving it would rotate ok. So, then I apply an opposing torque such that it would stop the rotation ok. So, now, once I have applied both of these, it only moves forward with the velocity there is no there is no rotation. So, that is this set up

So, then once I plug back in that there is no rotation which means omega is, 0 I get these 2 equations F 1 is a v 1 and N 1 is Cv 1 yes ok. So, generally, I had in mind something which is a simple propeller which has one axis of rotation. If it has multiple that is what you are seeing right, if it can if it has multiple axis of rotation ok. So, if it has multiple axis of rotation, you would have actually additional terms over here which would be B prime omega prime and so on.

So, about each axis of rotation, you would have a corresponding drag coefficient and so on. So, that, you would need to include. So, let us say this is for a swimmer which has one a single axis of rotation.

Student: (Refer Time: 13:22) like what kind of (Refer Time: 13:28).

Well you can, if I think of a corkscrew for example that is easy right so that I push it like this, it is going to rotate about its long axis. In general if you know the symmetry of the body, you can say that around what direction it is going to rotate (Refer Time: 13:52)

Student: (Refer Time: 13:54).

This video that you are saying so, what is happening?

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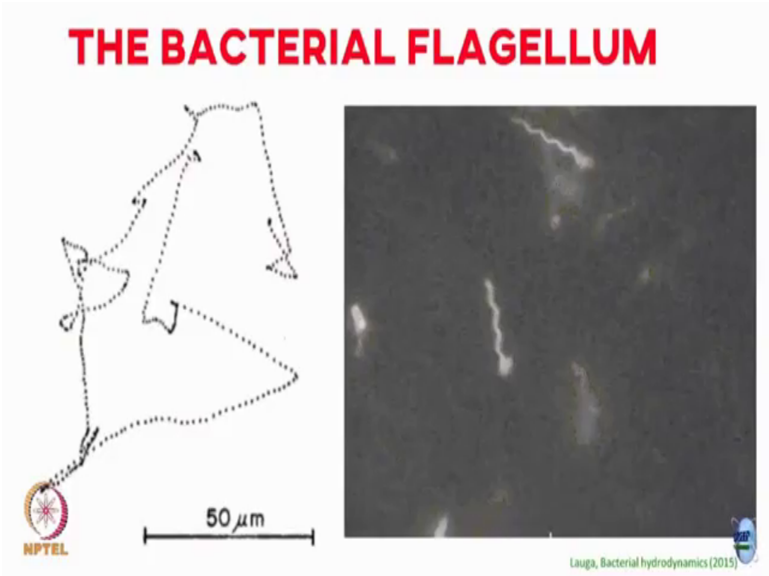


The flagella is rotating yes.

Student: But in bacteria (Refer Time: 14:09).

This is a particular case, it need not you can have some value of F and in fact, any value most values of F N N will give you a rotation and a translation. I am choosing a particular value such that you switch off the rotation, you only have translation that is always possible. So, in general of course, you will have a velocity and you will have an omega given an arbitrary force and an arbitrary torque. So, this is a thought experiment.

Because I want to argue something generally about what is going to be the structure of this matrix ok. What is going to be ABC and D. So, I choose a value; I choose this very special value of F 1 and N 1 such that I switch off the rotation ok. Then the second step, the second thought experiment is that I apply only a force no torque such that I get the same velocity as I had in this earlier case the same v 1.

But its of course, will to have a rotation as well because I have not applied this torque which canceled it out, in general its I am going to have rotation as well. So, then these are my equations of motion F 2 is A v one plus B omega 2 and because I am applying no torque 0 is equal to Cv 1 plus D omega 2 right ok. So, now, given this second solve for F 2 in terms of v 1.

So, F 2 is going to be a v 1 omega 2 is minus C. So, minus BC by D v 1 right. I just solved these two equations, I put it in express the force that I need in terms of this velocity v 1 ok. So, now, I can write down the ratios of these two forces F 2 and F 1. So, if I have my F 1 over here. So, let me write F 2 by F 1. So, that is going to be 1 minus BC by AD right.

I just divide throughout by AD 1 ok. Now, genetically can you just think and say which of these forces is going to be greater F 1 or F 2. Remember in this case I apply a force then I apply an opposing torque such that I cancel out the petition and I get some velocity. In this case, I do not have that opposing torque, I just have this force and I need to achieve that same velocity that I achieved in the first case.

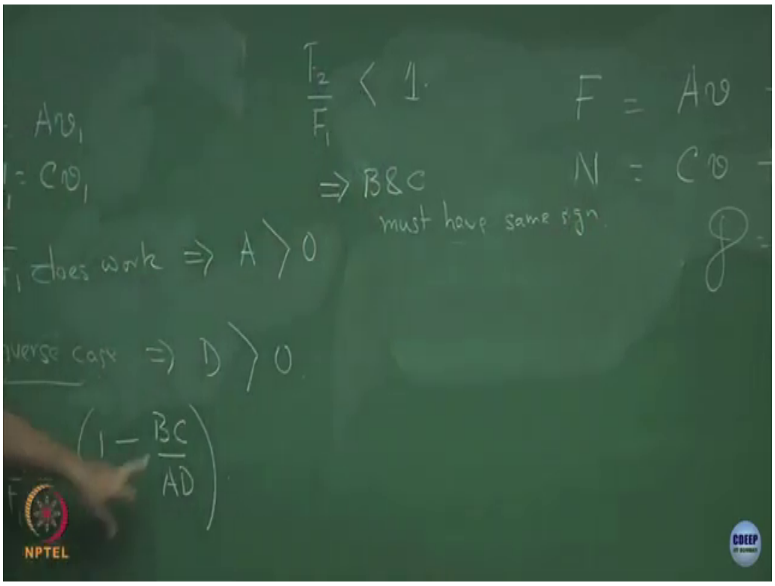
So, in which case would I require less force this one F 1 everybody agrees.

Student: F 2.

F 2 I will require less force. So, why?

Student: (Refer Time: 17:09).

Exactly right. It Is the opposite way, here you are applying an opposing torque. So, in order to reach the same velocity, you must you must apply a little bit more force right (Refer Slide Time: 17:23)



So, given this setup very generically F 2 must be less than F 1 which means that F 2 by F 1 must be less than 1 sorry, not same right. Which means, now that I know that A and D are both positive, what it means is that B and C. So, what this implies is that B and C must have the same sign all right; must have same sign.

If one of them was positive the other was negative, then this would become 1 plus something which would not work right. So, B and C necessarily has the same sign. So, basically this implies that BC must be greater than equal to 0 which means that B and C must have the same set.

Now, for the final part of the proof remember what are we trying to prove, we are trying to prove that this matrix needs to be symmetric which means that B must be equal to C right. So, that is what Purcell said that one property is this that, the diagonal elements are greater than or positive, the second property is that this is a symmetric matrix ok. So, that the second thing is what we are trying to show right now this is matrix. What we have shown is that till now, that B and C must have the same sign.

So, what Purcell what we do is that we say that, we create a propeller by hand which has approached this propulsion matrix which is non symmetric ok.

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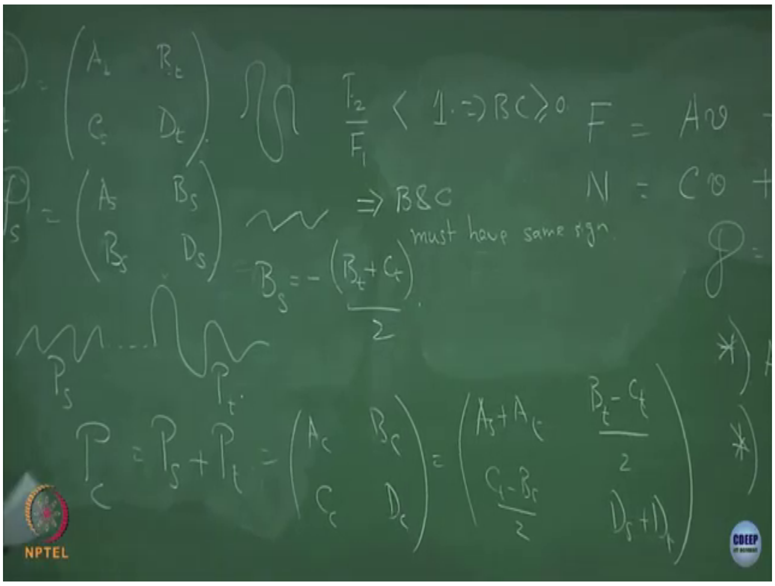

So, I create a something a propeller which is characterized by this propulsion matrix P, let us say Pt which has elements At Bt Ct Dt some propeller (Refer Time: 19:24) very generic I do not care what the precise shape is. All I care about is that this is not symmetric which means that Bt is not equal to Ct

So, then Purcell says is that let me construct the symmetric given this that is one propeller something, I do not know. Given let me construct a symmetric propeller, let us say let us call this P of s which has elements As Bs Cs Ds with a particular. So, this is symmetric. So, I should not write C s, I should just write As Bs Ds. So, I take a propeller which has the symmetric matrix with this off diagonal term given by B s is equal to minus Bt plus Ct ok. These are all thought experiments remember.

So, given me a propellant which is not symmetric. I conjure up a propeller which is symmetric and where the strength of these off diagonal terms is related to the strength of these off diagonal terms of this non symmetric propeller according to this Bs is minus Bt plus Ct by 2. And this is some; this is a again a some propeller kind of thing ok. So, this is what you have given me once you have given me that I construct another propeller like this.

Now, I put them in sequence so, it connect these two propellers like I talk with a thin wire ok. So, this is my symmetric propeller, this is my non symmetric propeller that you had given. So, together this will have the propulsion matrix, let us call it something the P combine which is going to be the sum of these two the symmetric plus the non symmetric that you are going to get ok. And let me say this is elements A c Bc c Cc and Dc right.

So, these I can just write. So, Ac is just At plus As ok. As plus At Bc is this plus this which means Bt minus Ct by 2 C t by 2 here it Is going to be Ct minus Bt by 2. And here it Is going to be D s plus Dt ok. Again this is an idealized popular in that I assumed, its connecting wire fields no forces and torques and so on. These propellers are well separated such the hydrodynamic flows of this do not affect that. In that sort of a limit I combine this I come get this combined propeller which has these elements right ok.

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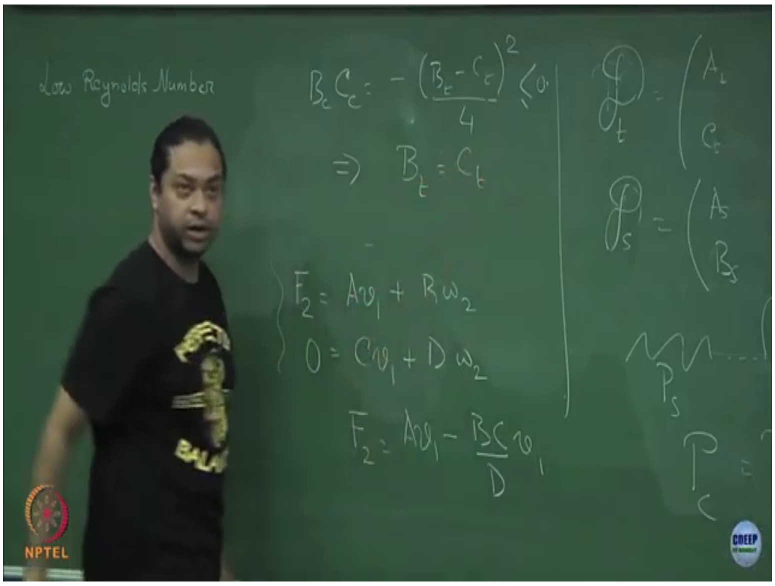

So, now, if I take the product of these off diagonal elements B c times C c What do I get? So, if I take the product of these off diagonal elements B c times C c, I get what minus B t minus Ct whole square by 4 right. It is this term into this term. So, minus of something whole square divided by 4 right. Which is necessarily less than or equal to 0 right

Because this is a positive definite quantity, I have a minus sign in front. However, I have proved that again very generically with the product of these off diagonal elements must be greater than or equal to 0 for a general propeller right. Which means, what is the only option for this Bc times Cc, the only option for this is to that Bt is equal to Ct is right Which is consistent. So, this will give you a 0 which is fine with over there ok. Which means that very generically, you cannot construct a propeller which has Bt not equal to Ct we are going to run into problems ok.

So, very generously from symmetry arguments without caring about what is the actual shape of the propeller, you can show that this off diagonal elements must always be equal to one another which means that this propulsion matrix must very generically to be a symmetric matrix ok. This is clear, you can think about its a little convoluted argument, but it Is very powerful argument in that the other alternative is to solve these equations for every shape write down the boundary conditions and soon And then trying to get the equation trying to get out the properties from there.

This is true for any arbitrary shape, it its yeah I like it yes. The magnitudes are equal ok. So, let me think about that this is R cross F right the torque because C is the same as B this is fine right. If I take an omega cross R over here then I get an R cross F which is the torque. So, this will have if I see let me think. So, this is A which is like dimensions of length right 6 pi r, this will have dimensions of R square, this will also have R square and this will have an R cubed.

For example, for a sphere it is 6 eight pi eta R cubed yes. So, this will have R cube B and C will have R it will have R square right. It dimensions do and. In fact, come out to be the same right yeah I do not have it worked out, but it seems.

Student: Same.

Same dimension yes, ok. So, that is this part of that all right. So, we have constructed this general propulsion matrix which has this A B D form for any generic propeller. Now, let me come back to my come back to my case of E coli right what do I have for E coli?

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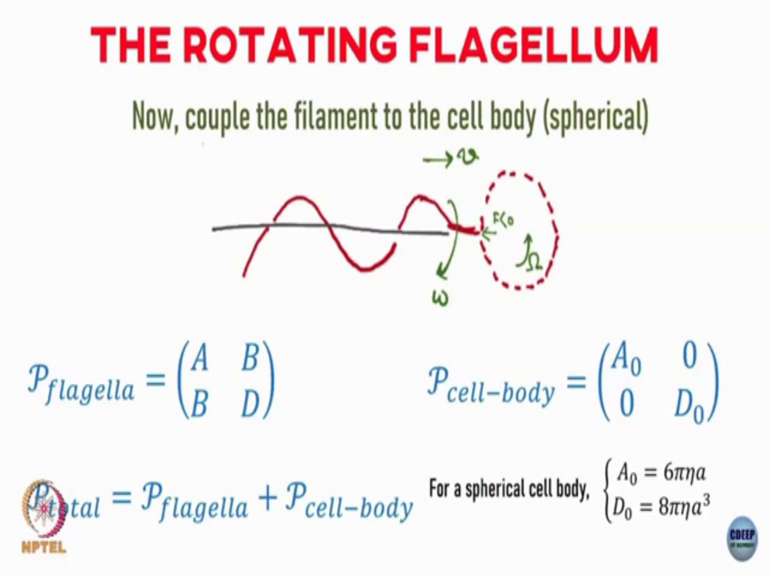

So, what do I have for E coli I have this cell body which is connected to a flagellum right. Which and this flagellum is this corkscrew flagellum which is my propeller in this case. For which I have said that this matrix is symmetric, I do not still know what is A B and D.

I will need to work out the mathematics for that for a helical corkscrew or whatever shape you give me, but at least its symmetric with and D greater than 0 ok. So, that is the propulsion matrix for this. Correspondingly I will have a propulsion matrix for this cell body, for simplicity let me assume that the cell body is a sphere right. So, what is going to be this propulsion matrix for the cell body?

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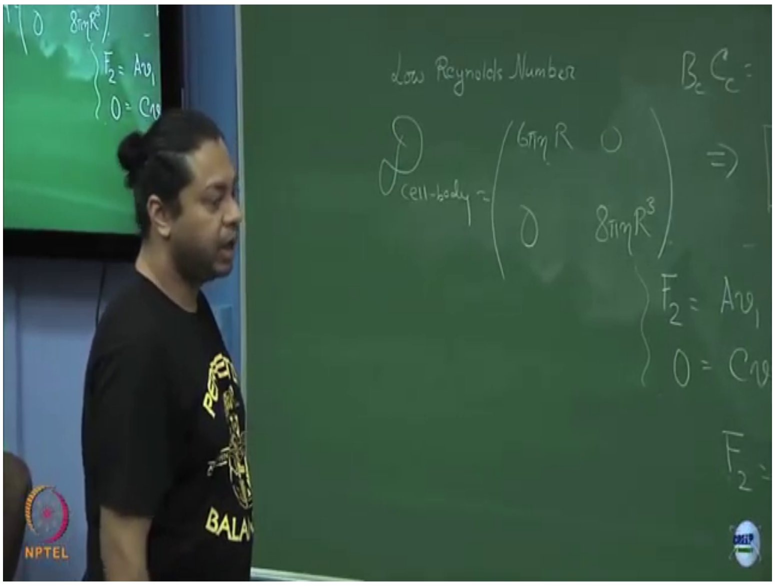

What is going to be A 6 pi eta R, what is going to be B and C 0, what is D that you may not remember, but. So, D is 8 pi eta a cubed ok. So, if you work out for its sphere, just like you work out 6 pi eta a this is 8 pi eta a. So, here are my two propulsion matrices, this is this part is for my flagellum, this part is for my cell body ok. So, this is the cell body exerts a force on the flagellum right. It exerts a torque on the flagellum through this motor which causes this to rotate and the flagella to translate ok.

Similarly, by the action and reaction, the cell body is also going to rotate right in the different direction with some different angular velocity omega, but its going to move together because these are connected to each other, they are going to move together which means of the velocity v is the velocity of the flagella as well as the velocity of the cell body right. This whole unit is going to get translated that is my aim right.

So, if the cell body the flagellar motor is applying a torque on this N let us say on this flagella. The flagella is going to act exert a reverse torque minus N on the cell body which is going to cause it to rotate, but it Is going to cause it to rotate in the opposite direction, because as long as you are not putting any net dot from outside the total torque must be 0 right. The total force must also be unless you are pushing the bacterium. This whole thing is going to move on its own right. There is a motor inside which consumes energy and so on.

But you are not going and pushing, the cell body is exerting a torque on these flagella. The torque the flagella has to exert a reverse torque on the cell body right. Similarly the forces must be equal and opposite, if you are applying no external force.

Student: Sir VB (Refer Time: 29:10).

If you take a?

Student: (Refer Time: 29:13).

Right so, this is not a deformable corkscrew remember. So, this is a helical corkscrew which cannot change its shape ok. It can rotate, it can move, but it cannot deform, if its if it can deformed, then you will have to take into account additional factors. So, this is a rigid corkscrew which can only rotate and translate ok. So, once I have that this propulsion matrix for this whole object this E coli is a whole of this bacterium as a whole is this propulsion matrix for the flagella plus the propulsion matrix for the cell body ok.

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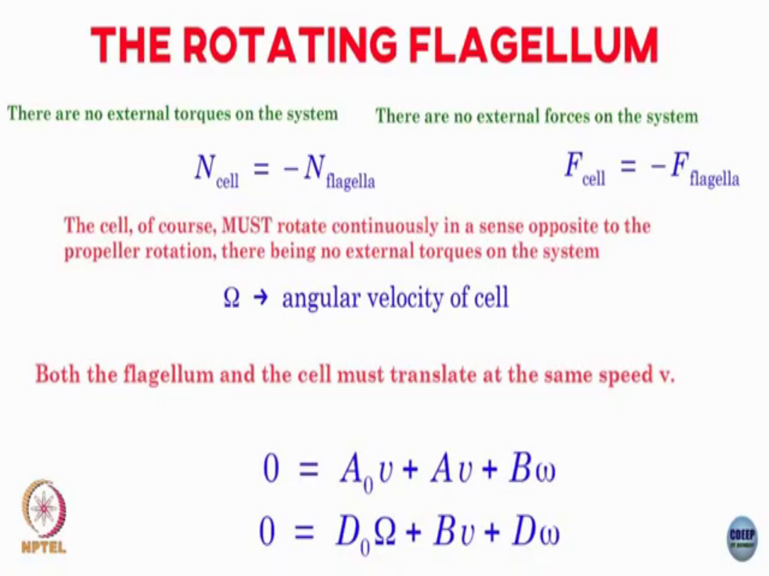

Now, like I was telling within that,if you have no external torques on the system, then the torque on the cell must be equal and opposite to the torque on the flagellum right. Similarly the force on the cell must be equal and opposite to the force on the flagella right. You are applying an external force you are applying an external torque on this system. Because you have a torque on the cell, the cell body itself is going to rotate like in the picture and it must rotate in a sense which is opposite to the propeller rotation.

Because there are no external torques and it rotates with some angular velocity which I call as capital omega ok. And of course, v is the same. So, I have these three quantities. So, I have this propeller attached to a cell body, this is rotating with some small omega this one is rotating in the reverse direction with some capital omega and they are both moving with some velocity v together clear.

. So, now, I can write down the force and the torque equations. My propulsion matrix is the sum of these two cell body plus flagella and therefore, I can write down what is the force and torque equations for this whole for this whole objects right.

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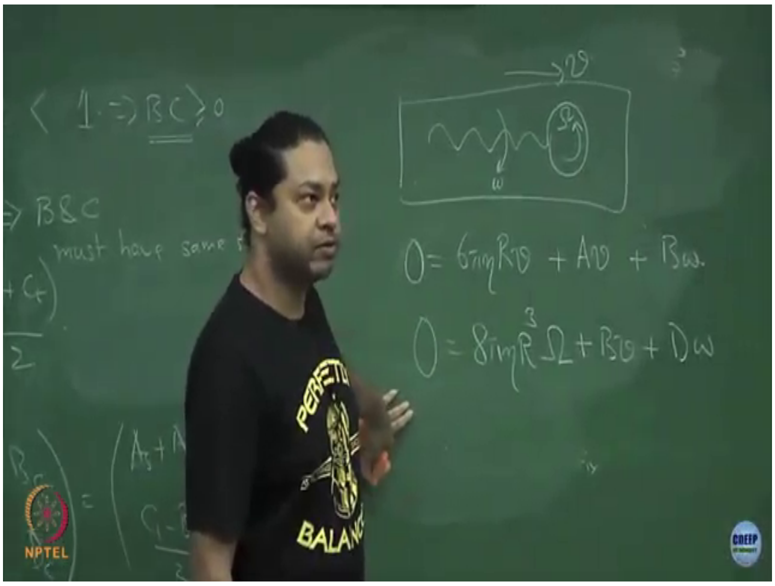

So, I put no external force which means that my F is 0 and that is going to be A naught times v. So, 6 pi eta R v plus A v. So, plus A v plus B omega right this is the force equation.

Similarly, I have no external torque which is 0 which means that I have 8 pi eta R cube capital omega plus B v plus D omega right. Once I put everything together both the flagellum and the cell body, these are my equations for the force balance and the torque balance. So, that is this these are my equations A naught and D naught you know let us see if it is for a sphere. If it was not a sphere, if it is a cylinder or something again you can work out what is the corresponding A naught and the corresponding ok.

Now, let us say I have this small omega and a capital omega which means so, remember here is my picture of this flagella this bacterial flagella.

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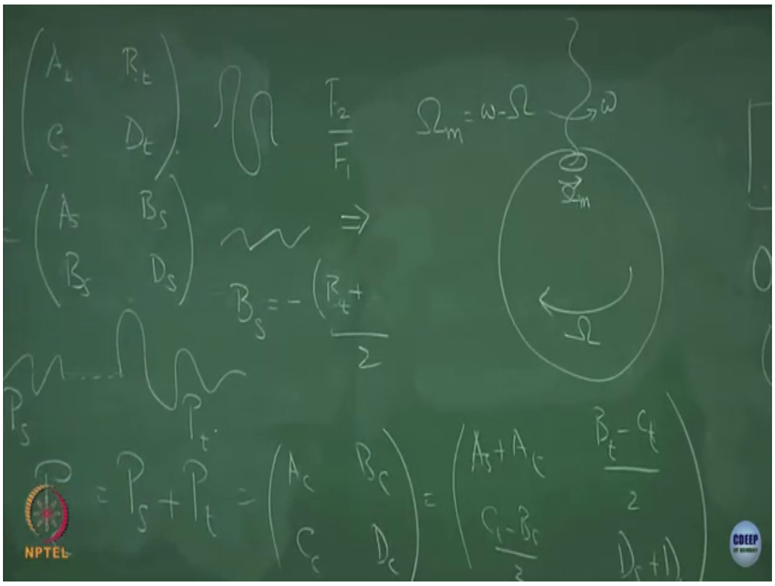

So, here is my bacterium cell body, in here sits my rotary motor to which is attached the flagella right. This motor rotates with some angular velocity let us call it omega motor which causes this flagella to rotate with some angular velocity omega that exerts a torque on this which causes this to rotate with capital omega.

So, what does that mean for the motor; for this motor angular velocity? The motor angular velocity is nothing, but the small omega minus this capital omega right. This omega m is nothing, but this small omega minus this capital omega right because the motor is fixed to the cell body right. So, if the cell body is rotating which means the motor is also rotating, then the motor is actually turning at this speed at this relative angular velocity omega minus capital omega.

So, now I will try to express well, I will just write down the answers, but you can so given these two equations. Now I can solve for this velocity and so on. The efficiency in terms of this motor angular velocity, motor and motor rotation speed omega N ok.

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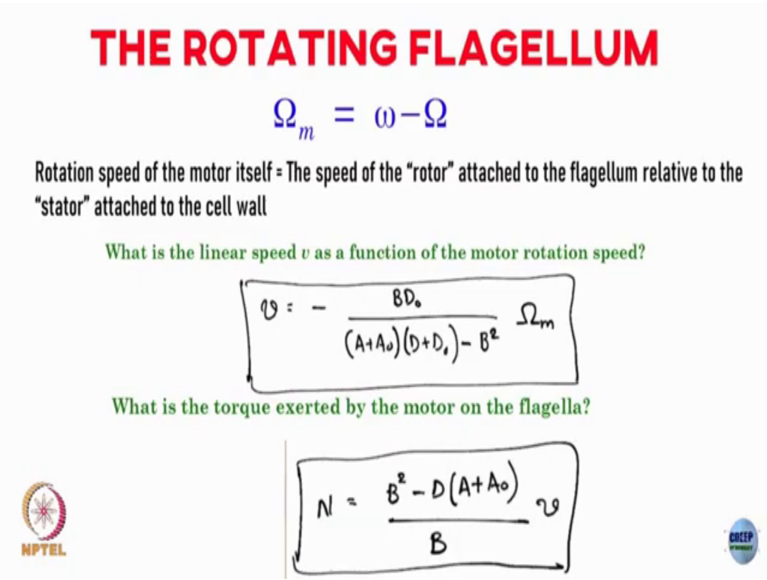

So, I will express everything in terms of this omega m. So, this is the rotation speed of the motor itself all right.

So, first thing what we could ask is that, what is the linear speed of this bacterium as a function of the rotation speed ok. So, of course, this will involve all this A B A naught D naught A naught D naught and soon. But you can solve these equations, this is just algebra, you can solve this and you can express the linear speed in terms of the motor rotation speed ok. So, you can solve these equations, I will not do it explicitly, but you can check the notes I will upload the notes. So, you can solve for this velocity in terms of what is the angular speed omega m

Again this is true for a generic propeller still not substituted BD and soon. This you can do for whatever propeller you design or whatever flagellum you design ok. You could also ask that what is the torque exerted by the motor on the flagellum and again you can solve for N which is going to be some function of v and therefore, some function of omega m again by solving these equations.

But what I want to focus on is this question that, you might think that the bacterium has designed this marvelous system, it has designed this marvelous motor which is a very complicated motor to rotate this helical flagella in order for it to propel itself. So, what is the efficiency of this motor ok.

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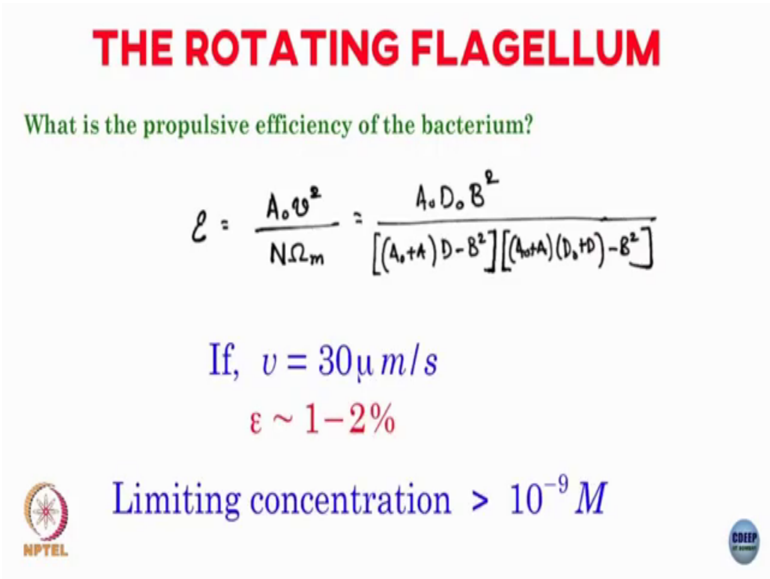

So, we can ask what is the propulsive efficiency of this flagella and that is. So, that we define as the ratio of this N times omega the torque times the angular velocity and on the numerator is simply the work done if you were to drag this whole thing along.

If you were to drag this whole body along with a velocity v that is just A naught times that is just the forces A naught V. And therefore, the work done is A naught power is A naught v into V. So, A naught v squared ok. So, this is and this is the N times omega ok. So, this I will call as the efficiency of the flagella and again I get some expression in terms of this elements of this propulsion matrix.

So, now we can go ahead and put numbers ok. So, how do you how do you calculate this A naught and v naught. So, one way is to actually take this helical body and try to solve for these drag just like you solve for the drag coefficient in its sphere, drag force on a sphere or the due to the torque, you can solve for this helical body, but Purcell said is that let me not bother.

So, let me do a semi phenomenological thing which is that, I need to know three things A B and D right. So, what I will do is that, I will take this propeller, let me rub his out again let me imagine our corkscrew helical propellant.

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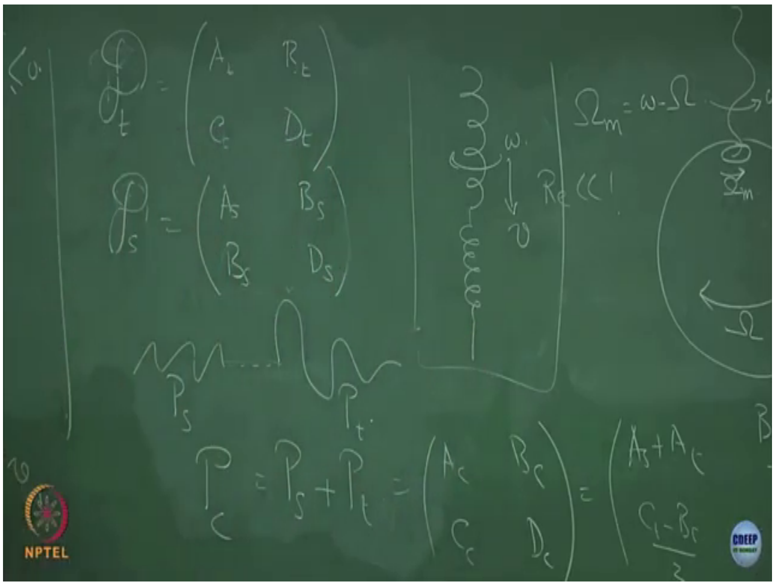

They said that this is my propeller I will just drop it into a liquid which has this low Reynolds number that I am interested in ok. And I will observe what is the velocity with which it falls and what is the angular velocity with which it rotates ok. So, this I can measure experimentally.

Now, what I can do is that I can take two such propellers and connect them such that they are mirror images of each other ok. And then I drop that composite thing into this liquid then this thing is not going to rotate anymore ok, but it is still going to fall with the velocity. So, I can measure that new velocity v prime. So, I have these three measurements of this angular speed and the velocity in the first case and this velocity in the second case, I can use them to solve for these three coefficients A B and D ok.

This is a semi phenomenological approach, but you can imagine doing it for any shaped object because the mathematics or any sort of realistic propeller shape is going to get extremely complicated. You can do it for a helix for example, using resistive coil theory, but whatever. So, you can just measure it what are these A BS and Ds let us say for a helical propeller.

So, this experiment has been done so let me see. So, let me see you have put in a speed of swimming for this bacterium. So, if you put in the speed of swimming and you put in these numbers A B and D. What you get is a propulsive efficiency of this motor which is extremely low. You get this motor functions at an efficiency of 1 to 2 percent roughly ok. So, although you have if evolution has come up with this beautiful motor, it is not optimized it for efficiency, it is actually extremely inefficient.

But what Purcell argued is that does the back should the bacterial care. And the bacteria does not care because ordinarily it is swimming in a environment which is extremely nutrient rich. So, even if the efficiency is pretty low, it is getting the amount of nutrient that it requires to survive and that is that it is going to continue to be the case until you reach a limiting concentration of some nano molars ok. Then it is going to feel the effects of this small efficiency.

But as long as you are at concentrations above this efficiency does not really play a role ok.

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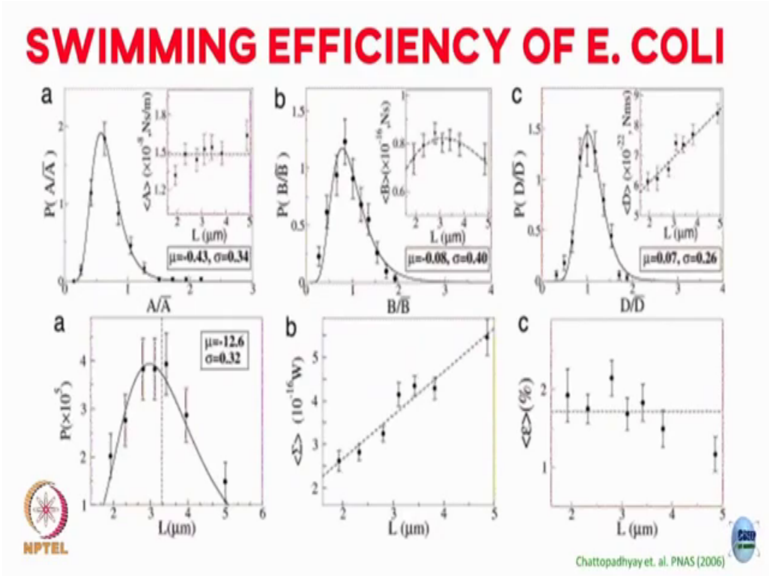

So, I will just show you these experiments oops ok. So, these are experiments with where they do this sort of experiment by dropping the propeller into a liquid. So, they find a these are distributions these are actually full distributions of this propulsion matrix elements A B and D ok. They can calculate, what are the mean values of these elements ok. For a given helical propeller let us say. And from there you can then plug in these numbers these mean values of A and soon. Into these expressions for the efficiency and here you will see.

So, this is as a function of the length of the bacteria. So, there is a range of lengths for the bacterium. So, for the propeller and as a function of length you can plot the efficiency and you will see that the efficiency over's around between 1 to 2. So, the mean efficiency is roughly around 1.7 ok.

I forget what, I think this was the power, but I forgot what this was. So, this was the mean efficiency that they calculated in this mean efficiency is extremely low. it is 1 between 1 and 2 percent. So, what we have done is that we have done, we have developed a sort of generic theory for writing down propulsion matrices which do not depend on the exact shape of the propeller that you are talking about. Then you can take that particular propeller that you are interested in do an experiment like this in order to find out what are these elements A B and D.

You can then plug them back in these expressions, these algebraic expressions which you get by solving these equations, these two equations and you can find out what is efficiency what is the speed and so on and so forth. So, we come next to a end with a related sort of aspect. So, what Purcell said is that, this low efficiency does not really matter the fact that this epsilon is just 1 to 2 percent.

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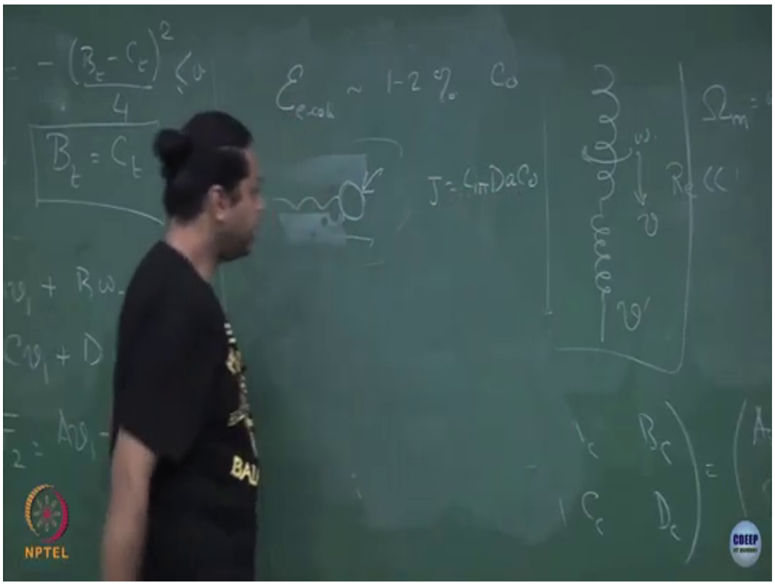

So, what we get for this E coli roughly is efficiencies of 1 to 2 percent. So, Purcell in argued is that this low efficiency does not matter because the problem for the E coli is not the fact that it is sitting in a nutrient rich environment is not the fact that is sitting in a nutrient poor environment. So, it does not really care about the efficiency, the problem for the E coli is the environment itself. What does that mean; that means that because it is in this low Reynolds number world right.

As this E coli moves, it drags along the surrounding fluid with it right because this is an extremely viscous medium. It drags along the surrounding fluid with it this fluid falls away only very slowly right. As opposed to if v was swimming, we would actually propel ourselves the water that we started off over there would remain over there we would see a new water environment, when I have swim some distance. That is not true for an E coli.

As an E coli swims, this environment is going to fall back only very slowly. So, it does not and E coli depending on how much it has swamp does not really see a new environment by swimming ok. It is going to see the same environment because this environment is getting carried along with it. Because of this very low Reynolds numbers. So, what Purcell asked is this related question.

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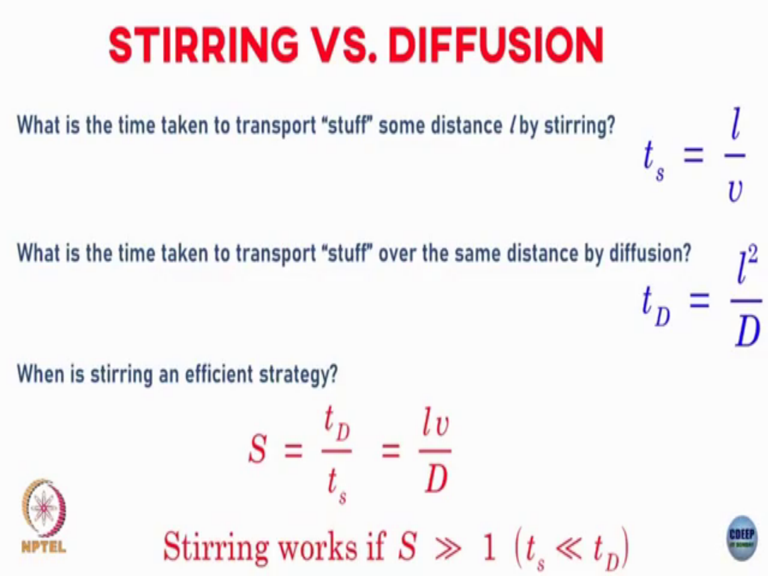

Let me say that so, what is the so, what is generally the advantage of swimming or as he calls it stirring. The advantage is that you sort of mix up this the medium that you are in.

So, you get access to new nutrients maybe ok. He says that well, if we are in this way if we are an E coli bacterium, you can sort of estimate how advantageous the stirring is or swimming is going to be as opposed to diffusion. What does it mean what does he mean by diffusion. What it means is that this E coli could just sit here right. And we have solved and we have solved you know this cell signaling problem.

So, if I had some nutrient concentration. I know at what rate this nutrients are going to reach the cell surface which is simply my diffusive flux which is 4 pi what is it 4 pi D a C naught right. So, it could just not say swim at all and stays simply by diffusion it would get a source of nutrients ok. So, when is this swimming going to be advantageous to the E coli as opposed to just sitting there and waiting for nutrients to come to it.

So, he asked that well, what is the time taken to transport stuff; stuff doing nutrients, chemicals whatever you are interested in. Some distance l by stirring and by stirring again. So, what he means is there will be swim with a velocity V. What is the time taken to move a distance l ok. And what is that that is just l by v right you have a distance you have a velocity.

So, the time taken to move some distance l is the swimming time or the stirring time which is l by V. Conversely you could ask that what is the time taken to transport stuff, the same stuff, chemicals whatever over the same distance, but now by diffusion ok. So, what is that typically what is the time scale to cover a distance l.

Student: l square by D.

l square by D right. So, that is the diffusion time I do not know ok. So, here is the time that you achieved by swimming, here is the time that you achieved by diffusion ok. So, then he asked that when is swimming or stirring going to be an efficient strategy for the bacteria. It is going to be an efficient strategy, if the swimming time to cover a distance l is much smaller than the time, it would take by diffusion for nutrients to come in right.

So, what you define is the stirring number which is this diffusion diffusive time tD divided by this swimming time ts for the stirring time ts. And that if you just do it is just lv by D right. So, what he says. So, the idea is that if the swimming time is much smaller than this diffusive time which means that if the stirring number is much greater than 1 then swimming is an efficient strategy.

Then you can access new nutrient regions by swimming so, ok. So, now, we can put in put in the numbers for E coli again, a typical E coli if you looked at those tracks it swims with a velocity of around 30 microns per second.

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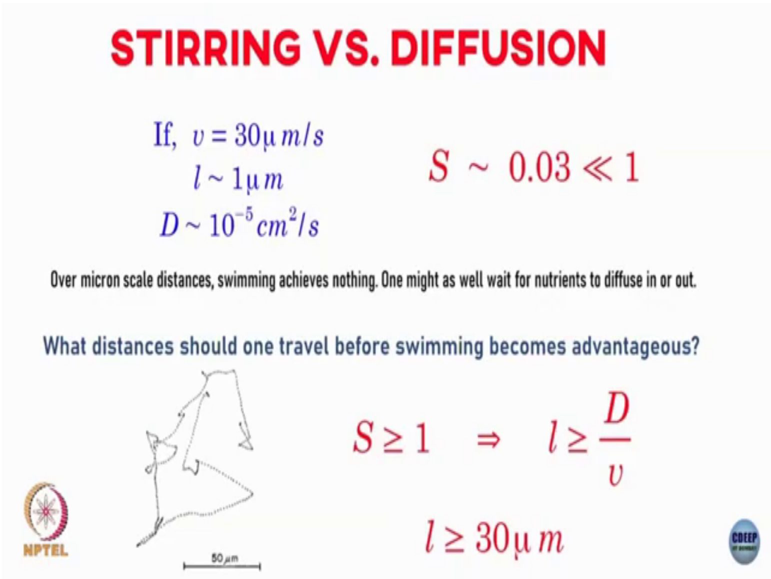

So, let us say I put in thirty microns per second, let us say I am going to swim a distance of a micron that is typically the size of an E coli right. And a typical diffusion coefficient of small molecules is going to be of the order of 10 to the power of minus 5 centimeter square per second.

So, if I now put this, if I now put this in this stirring number which is l into v into D what is that stirring number going to be of the order of? So, you can just put it to convert everything to microns or whatever you convert everything to a consistent unit. And what you will see is that given these numbers E coli an E coli swimming with 30 microns per second.

And if it wants to swim distance which is around a micron which is the length of its own body and this is the diffusion coefficient. The stirring number comes out to be 0.3 ok. Which is much less than 1 which means that over length scales of microns 1 microns, 2 microns, 5 microns swimming is not an efficient strategy.

If it wants to get new nutrients which are five microns away, it might as well not swim it might just sit there and wait for things to get there by diffusion ok. Provided its swimming with that 30 microns per second. On the other hand, you could ask that well given this 30 microns and this B what is the l that I need to swim in order for it to access a new environment. In order for this S to be greater than 1 ok. So, you can now solve for l given that S is of the order of 1 or greater than 1 and asked that what is the distance then E coli needs to swim in order to act c a new environment. So, ok.

So, this is the same thing that over micron scales a couple of microns swimming achieves nothing you might as well just sit there, but you can ask that what distance should one travel before swimming becomes advantageous. And. so, you solve for this S greater than equal to 1 and what that comes out to be the distance that you need to swim before you see a new environment comes out to around 30 microns ok. Given again the swimming speed and these Ds ok.

So, now if you go back and look at these trajectories that we see in these experiments, you feel typically that these so, this scale bar is fifty microns. So, you will see typically that this runs in this run and tumble motion of bacteria, these runs are typically of that order there are 10s of microns 30 microns 50 microns and so on.

So, what then Ecoli is doing is that when it is tumbling, it is just sitting in one place, its waiting for things to diffuse to it. Once the nutrient sort of get over, it swims a distance and enough distance that it sees a new nutrient region. And then again it sits there. So, it again it tumbles and again then once the nutrients over there is over, it again swims to a new region. Make sense good that is all I have to say to it.

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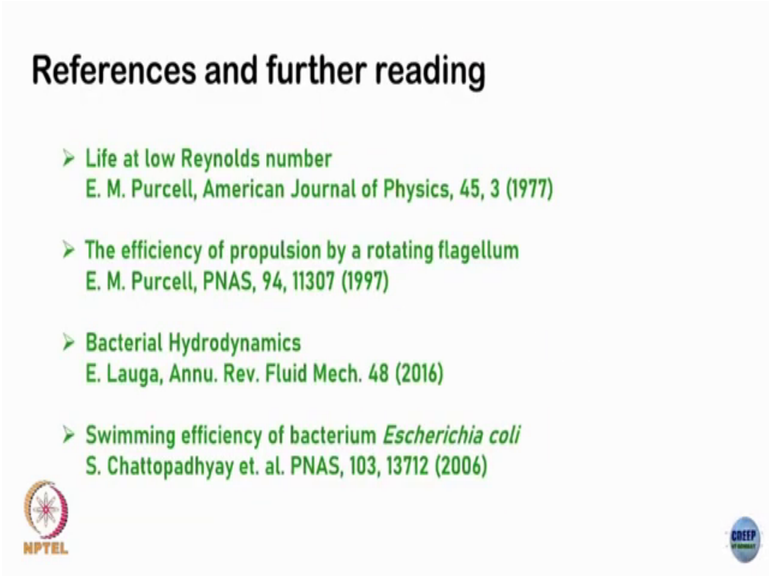

So, this is actually a very nice intuitive approach. I urge you so, these are from these papers this life has low Reynolds number has this idea. This is the paper that I flashed in the beginning of the class. The mathematics is worked out in this paper this Purcells 97 paper, the efficiency of propulsion by a rotating flagellum. So, all these epsilons and soon the algebra that I did not do well actually Purcell also does not do you need to do that yourself, but at least it is listed out nicely whatever I did in this 97 people. This is a nice review on bacterial hydrodynamics through the recent papers as well .

So, you might want to read that if you're interested this 2006 paper, this is the experiment which finds out this A B D and so on for this bacterium E coli for this E coli flagellum ok. So, you can it does it does not do it by dropping it through a liquid it does it using of laser optical trap and holding the sort of bacteria either motionless or rotation lists and soon. So, you can go back and look at these paper as to how people actually calculate these A B Ds, but once they calculate those ABs and Ds.

Then the method use is exactly the same, they just plug these A s Bs and Ds back into Purcell's calculation enough to obtain the efficiencies. And this you can do for whatever organism or bacteria that you are interested ok. So, that is all that I have.