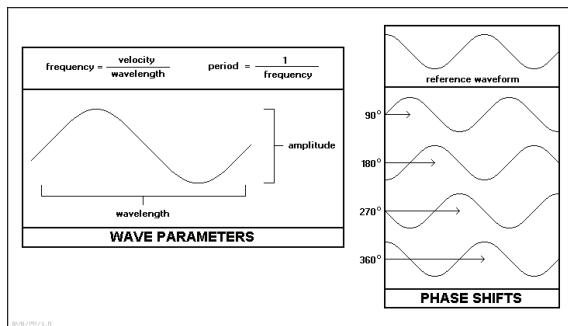


INSTRUCTIONS. Be sure to write your name above. Read the question carefully, think, then write your answer in the lined space (front and back of this page). Excessive length is not encouraged.

When finished, please hand in your answer separate from your exam booklet.

QUESTION. A bacterial flagella is very flexible. When the motor hook is rotating, it forms a helical coil shape, which then causes the bacteria to swim. Notably, because of its flexibility, a number of flagella --each attached to separate motors-- may intertwine to create a thick helical coil. But for this question, we will assume that the bacteria has only one flagellum

ONE. Would a bacteria swim faster if the flagellum was stiff, always in the shape of a helical coil as shown in the diagram? Explain.



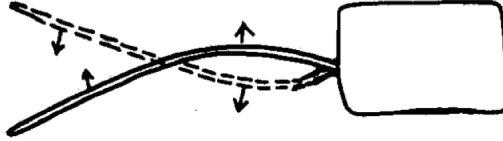
TWO. Could a bacteria swim if the flagellum was whipped back and forth by a reciprocating motor, to create a two-dimensional sinusoidal shape with constantly changing phase? Explain.

One. As long as the shape (length, wavelength and pitch angle) of the stiff flagellum is the same as the shape of the flexible flagellum, then the speed of the bacteria will be the same, since the net force available for propelling the bacteria will be the same. Work is required to 'shape' the flexible flagellum into a helical coil, because of its elasticity, so the propulsion efficiency of the stiff flagellum will be higher. A stiff flagellum has one major drawback: tumbling (to change the swimming direction) would not be possible. Reversing the motor would simply cause the bacteria to go backwards.

Two. In the required reading by Purcell, his fascinating exposition on *Life at Low Reynolds Number*, he argues that it would be possible if the flagellum was flexible: "You see, you

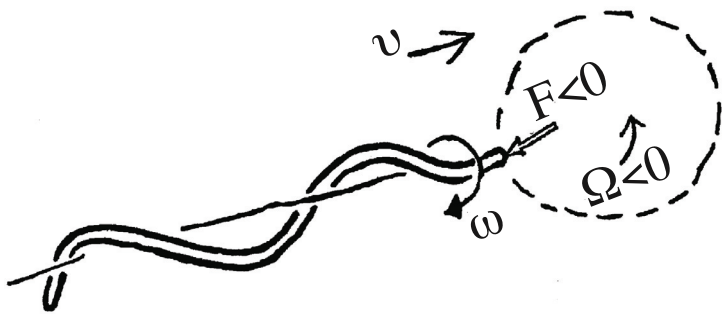
can't row a boat at low Reynolds number in molasses —if you are submerged— because the stiff

The flexible oar



oars are just reciprocating things. But if the oar is flexible, that's not true, because the oar bends one way during the first half of the stroke and the other during the second half. That's sufficient to elude the theorem that got the scallop [which cannot swim because it only has one hinge]".

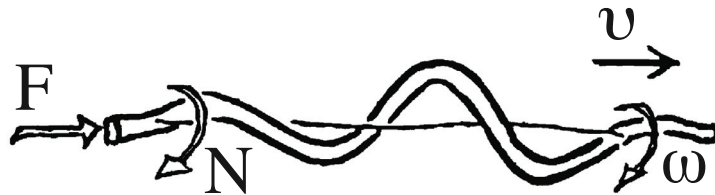
The Nobel Laureate Edward M. Purcell^[1] considered the mechanisms of propulsion for a bacteria. Much of his considerations are presented in a classic paper entitled “Life at low Reynolds number” (American Journal of Physics 45:3–11. 1977) (a required reading). The motility of the bacteria (with a velocity, v) relies upon the rotation of a helical shaped flagella rotating at a frequency ω , while the bacterial body counter-rotates at a frequency Ω in the opposite direction (hence the negative value).



“A propeller in the shape of a right-handed helix connected to a spherical cell, both moving to the right at velocity v . The propeller and cell rotate in opposite directions, at angular velocities ω and Ω , respectively. The external force F acting on the propeller is directed to the left^[2].”

This can be simplified somewhat by removing the bacterial cell from consideration, leaving just the ‘propeller’, and revealing the combination of force and torque.

“An isolated propeller, subjected to an external force F and an external torque N . It rotates at angular velocity ω and translates at velocity v ^[2].”



The force and torque are intertwined. This is usually described by a matrix that arises from the formal inter-relations:

$$F = Av + B\omega$$

$$N = Cv + D\omega$$

That is, both velocity and rotation contribute to both the force and torque.

where the 2×2 matrix comprised of the constants (A , B , C and D , all proportional to the viscosity and the size and shape of the ‘propellor’) is called the propulsion matrix \mathbf{P} :

$$\mathbf{P} = \begin{bmatrix} A & B \\ C & D \end{bmatrix}$$

^[1]1952 (with Felix Bloch) “for their development of new methods for the nuclear magnetic precision measurements and discoveries in connection therewith”

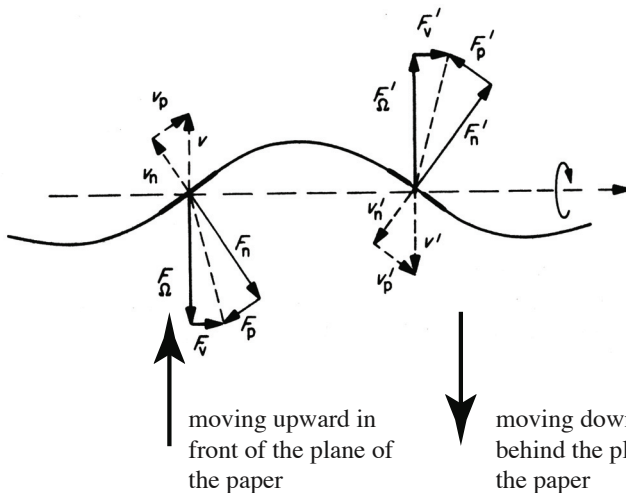
^[2]Source: Purcell, EM (1997) The efficiency of propulsion by a rotating flagellum. Proceedings of the National Academy of Science USA 94:11307–11311.

It's important to emphasize that the inter-relations between torque and force (and the propulsion matrix relating the two) are constrained by the low Reynolds number of the bacterial 'universe'. In the context of Newton's laws for translation and rotation, inertia is a dominate force. Not so for the small bacteria as described before. The basic equations –

Pure Translation (fixed direction)		Pure Rotation (fixed axis)	
Position	x	Angular Position	θ
Velocity	$v = dx/dt$	Angular Velocity	$\omega = d\theta/dt$
Acceleration	$a = dv/dt$	Angular Acceleration	$\alpha = d\omega/dt$
Mass	m	Rotational Inertia	I
Second Law	$F_{net} = m \cdot a$	Second Law	$\tau_{net} = I \cdot \alpha$

From Halliday, Resnick and Walker (2005) Fundamentals of Physics 7th edition. John Wiley and Sons. Chapter 10

– must be reconsidered in the context of the viscous drag encountered by the bacteria as it swims. Not only viscous drag on the translational movement, which must be counteracted by constant acceleration. But also viscous drag on the rotating flagella, which generates first the helical shape of the rotating structure, and then, because of the distribution of counteracting forces along the helical flagellar structure caused by frictional drag, the net translational motion of the bacterium.



The velocities of each segment (v) is decomposed into velocities normal (v_n) and parallel (v_p) to the segment. The frictional drag forces are also normal (F_n) and parallel (F_p). When F_n and F_p are decomposed into components normal and parallel to the helical axis, the net force F_v , contributes to the forward velocity^[1].

Intuitively, it is like turning a corkscrew through a soft material, such that rotation causes the forward motion of translation.

^[1]Source: Berg, HC (1993) Random Walks in Biology. Princeton University Press. pp. 79