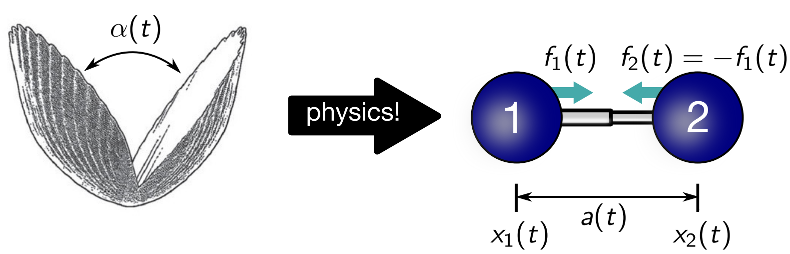
BIOREPS Problem Set #5
A tale of two scallops

Peer Fischer and his collaborators recently designed tiny scallop-like devices that can swim through non-Newtonian fluids, like those found inside the eye and in many other anatomical contexts [Nature Comm. **5**, 5119 (2014)]. These micro-scallops (with shells of size $\sim 300\ \mu$m) perform a periodic, reciprocal swimming stroke, which is the only kind possible when there is a single variable that controls body shape: the angle $\alpha(t)$ between the shells. By Purcell's scallop theorem, such a simple stroke could not lead to net displacement in a Newtonian fluid, but everything changes in a non-Newtonian fluid, where the viscosity η of the medium is no longer a constant independent of the swimming motion.

But what about Newtonian micro-scallops? Are they forever doomed to oscillate in place? Happily, even in Newtonian fluids, there is an interesting caveat to the Purcell theorem: it breaks down in the presence of a second micro-scallop, located not too far away from the first. By themselves they would get nowhere, but together they can very, very slowly drift in one direction. This scallopy action at a distance is due to long-range flow fields induced in the fluid by the reciprocal swimming strokes. The goal of this problem set is to show why there is no "Purcell many-scallop theorem", following an argument introduced by Eric Lauga and Denis Bartolo [Phys. Rev. E **78**, 030901R (2008)]. Hydrodynamic interactions can thus provide a way for micro-swimmers to achieve collective motion.

Part I: a micro-scallop spherical cow model



The fluid dynamics of real micro-scallops is non-trivial to model, so we will adopt an alternative system that is mathematically tractable, and is qualitatively very similar: two spheres of radius R connected by a thin, motorized linker. The motor inside the linker can exert forces on the spheres, $f_1(t)$ and $f_2(t)$, and thereby decrease or increase the distance $a(t) = x_2(t) - x_1(t) > 0$ between the sphere centers. By Newton's third law, $f_2(t) = -f_1(t)$, so there is really only one force function in the problem, which we will call $f_a(t) \equiv f_1(t) = -f_2(t)$. The variable $a(t)$ plays the same role as the scallop angle $\alpha(t)$: it determines the "body shape". Specifying the periodic functional form for $a(t)$ defines the stroke of the swimmer. From the Stokes drag law, we know that applying a force $f_i(t)$ to sphere i will lead to a velocity $\dot{x}_i(t) = f_i(t)/(6\pi\eta R) \equiv \mu f_i(t)$, where η is the viscosity of the surrounding fluid. The constant $\mu = 1/(6\pi\eta R)$ (generally called the *mobility*) is the inverse of the friction coefficient. Only the spheres are assumed to have drag: we will take the linker to be extremely thin, and thus it will not appear in the equations of motion, except indirectly through the fact that its motor applies the force $f_a(t)$ necessary to produce a certain pre-determined periodic cycle $a(t)$.

There is one aspect of motion through a fluid that we have not considered so far: the phenomenon of *long-range hydrodynamic interactions*. For simplicity, we have ignored these in our lecture discussions, but they will play a major role here. The physical basis of these interactions is simple: if you apply a force on an object, you will impart some velocity to that object, according to the Stokes drag law. But you will also create a fluid flow field in the vicinity, and if another object is present nearby, it will start to move as a result. Because this interaction is mediated by the flow field, and the velocity of the fluid decays with distance, this indirect speed transfer to a nearby object will be smaller than if you directly applied the force to that object. But to capture the full physics of the system, you cannot ignore it. In this exam, we will only consider systems of spheres moving along a single coordinate axis $\hat{\mathbf{x}}$ (for example the two-sphere micro-swimmer above). For a system of N spheres, the velocity of the ith sphere in the presence of hydrodynamic interactions is

$$\dot{x}_i(t) = \sum_{j=1}^{N} H_{ij} f_j(t) \qquad \text{where} \quad H_{ij} = \begin{cases} \mu & i = j \\ \frac{\nu}{|x_j(t) - x_i(t)|} & i \neq j \end{cases} \tag{1}$$

where the form of the matrix H is valid assuming the distances $|x_j(t) - x_i(t)|$ between spheres are always much larger than the sphere radius R (which will always hold in our case). Here $f_i(t)$ is the internal force on the ith sphere (applied by a motor, for example), and the constant $\nu = 1/(4\pi\eta)$. The diagonal elements of the matrix H are $H_{ii} = \mu$, and just reflect Stokes drag law as described above. The off-diagonal elements are the new part: the contribution to the velocity of sphere i due to the flow fields created by forces acting on spheres $j \neq i$. The distance in the denominator reflects the fact that these flow fields decay as you go away from the point of force application.

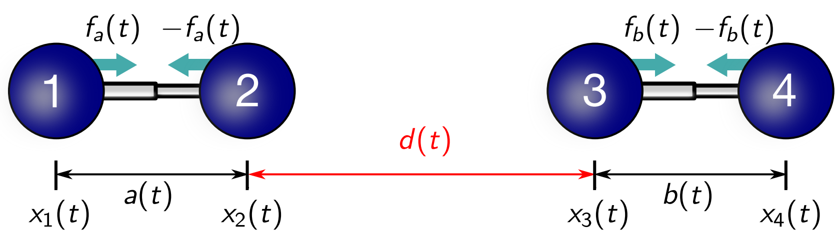
An immediate question arises: for a single micro-swimmer at low Reynolds number in a Newtonian fluid, does Purcell's theorem still apply when we include hydrodynamic interactions between the parts of the swimmer? As it turns out, the answer is yes, because Eq. (1) preserves the linear relationship between forces and velocities that was at the core of the theorem's proof. However, it is instructive to test this explicitly for the case of our two-sphere micro-swimmer.

a) Using Eq. (1), write down equations for $\dot{x}_1(t)$ and $\dot{x}_2(t)$. Rewrite everything in terms of the variables $x_a(t) \equiv (x_1(t) + x_2(t))/2$ and $a(t) = x_2(t) - x_1(t)$, which represent the center-of-mass position of the micro-swimmer and its length. Derive equations for $\dot{x}_a(t)$ and $f_a(t)$ that depend only on $a(t)$, $\dot{a}(t)$, or constants. In particular, you should find that:

$$\dot{x}_a(t) = 0, \quad f_a(t) = \frac{a(t)\dot{a}(t)}{2(\nu - \mu a(t))} \tag{2}$$

As you can see, the zero center-of-mass velocity $\dot{x}_a(t)$ means that the scallop goes nowhere, regardless of the stroke function $a(t)$. Purcell's theorem is safe (for now).

Part II: a micro-scallop pas de deux



Now consider another micro-scallop in the picture: two spheres of radius R at positions $x_3(t)$ and $x_4(t)$, with body variable $b(t) = x_4(t) - x_3(t)$. The separation from the first scallop is $d(t) = x_3(t) - x_2(t)$. Given a set of periodic stroke functions $a(t)$ and $b(t)$, can each micro-scallop exploit the fluid velocity field induced by the other in order to achieve net motion?

b) Using Eq. (1), write down equations of motion for $\dot{x}_i(t)$, $i = 1, \ldots, 4$. Assume $d(t)$ is much larger than all the other distances in the problem, and simplify expressions involving $d(t)$ in your equations by Taylor expanding for small $1/d(t)$, keeping terms up to and including order $1/d^2(t)$.

c) Just like in part a), switch to swimmer center-of-mass variables $x_a(t) = (x_1(t) + x_2(t))/2$ and $x_b(t) = (x_3(t) + x_4(t))/2$, and length variables $a(t)$ and $b(t)$. Derive equations for $\dot{x}_a(t)$, $f_a(t)$, $\dot{x}_b(t)$, and $f_b(t)$. You should find that $f_a(t)$ is the same as in Eq. (2), but $\dot{x}_a(t)$ is no longer zero. The center-of-mass velocities should have the form:

$$\dot{x}_a(t) = \frac{\nu b^2(t)\dot{b}(t)}{2d^2(t)(\nu - \mu b(t))}, \qquad \dot{x}_b(t) = -\frac{\nu a^2(t)\dot{a}(t)}{2d^2(t)(\nu - \mu a(t))} \tag{3}$$

where $d(t)$ in the center-of-mass/length variables is: $d(t) = x_b(t) - x_a(t) - a(t)/2 - b(t)/2$.

d) Use the results of Eq. (3) to derive an equation for $\dot{d}(t)$, and show that to leading order in the limit of large $d(t)$ this equation has the form $\dot{d}(t) \approx -\dot{a}(t)/2 - \dot{b}(t)/2$. The corresponding solution is:

$$d(t) = d(0) - \frac{a(t) - a(0)}{2} - \frac{b(t) - b(0)}{2} \tag{4}$$

e) By plugging Eq. (4) into Eq. (3), we now have expressions for $\dot{x}_a(t)$ and $\dot{x}_b(t)$ which depend solely on $a(t)$, $\dot{a}(t)$, $b(t)$, $\dot{b}(t)$, and constants. Let us check whether we can get net motion. The simplest case is when the scallop stroke functions are identical, $b(t) = a(t)$, so they do their motions perfectly in phase. The function $a(t)$ is periodic with period τ, so $a(0) = a(\tau)$. Argue that in this case $\Delta x_a \equiv x_a(\tau) - x_a(0) = 0$, $\Delta x_b \equiv x_b(\tau) - x_b(0) = 0$, so there is no displacement at the end of one period. We have thus ruled out all hope for a micro-scallop synchronized swim team. *Hint:* Integrate both sides of the $\dot{x}_a(t)$ and $\dot{x}_b(t)$ expressions from $t = 0$ to τ, and change integration variables from t to a in the integrals on the right-hand side.

f) What about out-of-phase swimming? Assume the scallop stroke functions are sinusoidal,

$$a(t) = L + A \sin\left(\frac{2\pi t}{\tau}\right), \qquad b(t) = L + A \sin\left(\frac{2\pi t}{\tau} + \phi\right)$$

for constants $L = 1$ μm, $A = 0.5$ μm, $\phi = \pi/2$ and period $\tau = 1$ ms. Each sphere has radius $R = 0.1$ μm, the viscosity of water is $\eta = 0.89$ pN/μm$^2 \cdot$ ms, and the initial separation is $d(0) = 3$ μm. Numerically integrate Eq. (3) (with the substitution of Eq. (4)) from $t = 0$ to $t = \tau$ to find the net displacements Δx_a and Δx_b. What are the mean velocities $\Delta x_a/\tau$ and $\Delta x_a/\tau$ of each scallop, and how do they compare to a typical swimming speed, i.e. 30 μm/s for *E. coli*? As you can see, the speeds of micro-scallop pairs are not exactly breathtaking. But at least they are getting somewhere! *Hint:* The quickest numerical integration scheme is just to sum the right-hand side of Eq. (3) from $t = 0$ to 1 ms in steps of $dt = 0.001$ ms, and then multiply the total by dt.

g) As one might imagine, this method of propulsion is not necessarily the most fuel-efficient. The power expended by the motor of the first micro-scallop is $P_a(t) = \dot{x}_1(t) f_1(t) + \dot{x}_2(t) f_2(t) = -\dot{a}(t) f_a(t)$, and similarly for the second micro-scallop $P_b(t) = -\dot{b}(t) f_b(t)$. For the parameters above, calculate the total energy used per period, in units of $k_B T$:

$$\frac{E}{k_B T} = \frac{1}{k_B T} \int_0^\tau dt \, (P_a(t) + P_b(t))$$

where $k_B = 1.3 \times 10^{-23}$ J/K and $T = 298$ K. To get a sense of how efficient or inefficient this energy expenditure is, we can make a baseline comparison: using the Stokes drag law, calculate the external force f_{ext} required to keep an isolated sphere of radius $R = 0.1$ μm moving at the same mean speed as you found in part f). Now calculate how much energy would be expended by this external driving over a duration of 1 ms, and multiply this number by 4 since we have 4 spheres in our system. Let us denote this total value, in units of $k_B T$, as $E_0/k_B T$. How do $E/k_B T$ and $E_0/k_B T$ compare? Clearly the indirect mechanism of propulsion through hydrodynamic interactions is very inefficient, since it requires much more energy to maintain the same average speed versus direct application of an external driving force. Where is the extra energy going? The vast majority is being expended through drag friction during the oscillatory motion of the scallop spheres. With each period, the center-of-mass has moved a tiny amount Δx_a, but the motor has moved the spheres back-and-forth across an amplitude $A \gg \Delta x_a$ to achieve this slight displacement.