

# Lecture : Stirring by swimming organisms

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## 1 Introduction

The question of which factors contribute to mixing in the ocean has been the subject of many studies. The idea that organisms could play a role in affecting their environment through something like mixing first appeared in Darwin's last book, called "The formation of vegetable mould through the action of earth worms, with observations on their habits." (See figure 1.) This was suggested by his uncle and future father-in-law Josiah Wedgwood II, son of the famous potter. From Darwin's book:

In the year 1837, a short paper was read by me before the Geological Society of London, "On the Formation of Mould," in which it was shown that small fragments of burnt marl, cinders &c which had been thickly strewed over the surface of several meadows, were found after a few years lying at the depth of some inches beneath the turf, but still forming a layer. This apparent sinking of superficial bodies is due, as was first suggested to me by Mr. Wedgwood of Maer Hall in Staffordshire, to the large quantity of fine earth continually brought up to the surface by worms in the form of castings. These castings are sooner or later spread out and cover up any object left on the surface. *I was thus led to conclude that all the vegetable mould over the whole country has passed many times through, and will again pass many times through, the intestinal canals of worms.* [emphasis added] Hence the term "animal mould" would be in some more appropriate than that used of "vegetable mould."

The modern name for this phenomenon is 'bioturbation.' At the time, the idea that many small events could accumulate to create something much bigger was quite controversial (and still is to some people, in the case of evolution).

It was not until almost a century later that Walter Munk [8] seriously proposed marine organisms as a possible factor for mixing in the ocean. However, Munk discounted the effect as negligible. The idea lay dormant for forty years, until 2004 when Huntley & Zhou [3] analyzed the swimming of 100 species in a wide range of sizes, and concluded that for 11 representative species the turbulent energy production is  $\sim 10^{-5} \text{ W kg}^{-1}$ , the total of which would add up to an amount comparable to the energy dissipation by major storms. Another study on the magnitude of the mixing effect of the oceanic biosphere was performed by Dewar et al. [2], who estimated that the ocean's organisms take in a total

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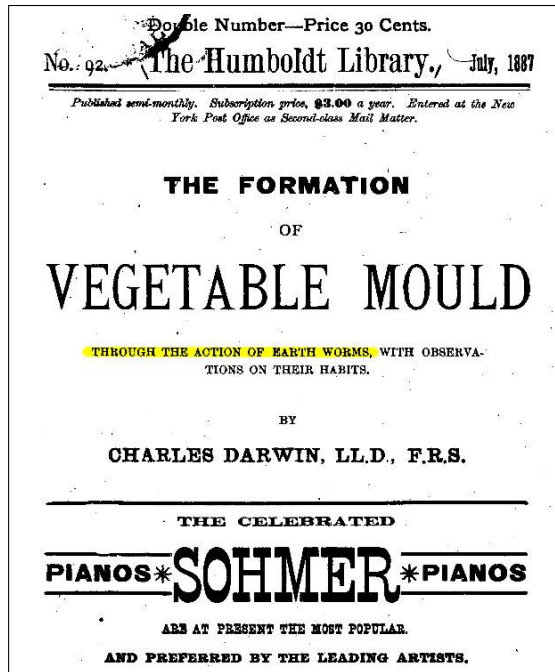


Figure 1: Darwin’s last book, “The formation of vegetable mould through the action of earth worms, with observations on their habits.”

power input of almost 63 TeraW. They assumed that about 1% of this amount is delivered as mechanical energy, which leads to a number comparable to the input of winds and tides [2]. An experimental study by Kunze et al. [5] showed that the level of turbulent activity in an inlet was elevated by 2 to 3 orders of magnitude during the day, due to swimming krill. (Though it must be mentioned that later studies were far less successful.)

In reaction to the papers mentioned above, Visser [10] argues that very small organisms such as zooplankton cannot produce sufficient mixing to overturn a stratified medium. The author points out that the efficiency of mixing is proportional to the ratio of the lengthscale of the organism ( $L$ ) and a buoyancy lengthscale, defined as  $B = (\epsilon/N^3)^{1/2}$ , where  $\epsilon$  is the rate of turbulent energy dissipation and  $N$  is the buoyancy frequency. When  $L < B$ , the mixing efficiency quickly drops by several orders of magnitude [10], rendering biomixing negligible. Katija and Dabiri [4] however suggest that it is not the scale of turbulence produced by the marine organisms that is the relevant quantity, but the net displacement of fluid particles they cause. This aspect will be discussed in these notes by constructing a simple model of stirring by swimming organisms, based on drift trajectories due to a moving object.

## 2 Displacement of a fluid particle due to a moving body

We will first discuss the displacement of a fluid particle due to a single moving body, and generalize this theory in the next section to multiple ‘kicks’ due to several moving bodies,

and ultimately to an effective diffusivity. For simplicity we will assume the moving body to be 2D and symmetric with respect to its direction of motion. (Axisymmetric about its direction of motion in 3D.) (See figure 2.) We only consider potential flow. The body moves along a straight line with constant velocity  $U$  for distance  $\lambda$ . The distance between the fluid particle and the straight line of motion is  $a$ , while the distance from the start of the trajectory to the point of closest approach (with respect to the initial position of the particle) is  $b$ . Together  $a$  and  $b$  are called impact parameters. Note that  $a$  is positive but  $b$  can have either sign, with a negative  $b$  indicating a swimmer that begins its trajectory already having passed the fluid particle.

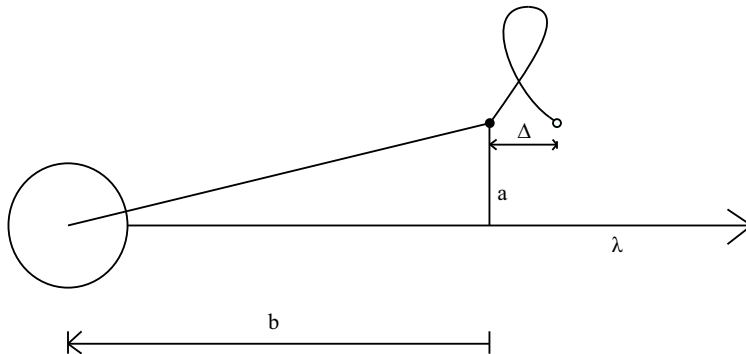


Figure 2: Displacement of a fluid particle by a swimming body.

Due to the movement of the swimming body, the fluid particle will have a net displacement  $\Delta = \Delta_\lambda(a, b)$ , known as *drift*. Although Maxwell [7] was the first to discuss the drift to a moving body, it is often referred as 'Darwinian drift' [1], due to Charles G. Darwin, great grandson of the other Darwin.

We first need to determine how much a fluid particle is displaced. We could solve this problem in a fixed frame centered around the moving cylinder, where the particle moves around the body (figure 3, left panel). It is however easier to work in a frame which is moving with the fluid particle (figure 3, right panel).

In the  $x$  direction, the displacement of the particle solely due the flow  $U$  would be  $b - \lambda$  ("free-streaming"). Because of the influence of the moving body, the fluid particle ends up at  $x_f$ , a distance  $\Delta x$  away from  $b - \lambda$ . Now we can define a travel time  $T$  it takes the fluid particle to go from  $b$  to  $x_f$ :

$$T = \frac{\lambda}{U} = \int_b^{x_f} \frac{dx}{u(x, y)} \quad (1)$$

where  $u(x, y)$  is the velocity felt by the fluid particle. This assumes that the horizontal component of the velocity field never vanishes. Using  $x_f = b - \lambda + \Delta x$ , this gives

$$\begin{aligned} \frac{\lambda}{U} &= \int_b^{b-\lambda+\Delta x} \frac{dx}{u} = - \int_b^{b-\lambda+\Delta x} \frac{dx}{|u|} = \int_{b-\lambda+\Delta x}^b \frac{dx}{|u|} \\ &= \int_{b-\lambda}^b \frac{dx}{|u|} + \int_{b-\lambda+\Delta x}^{b-\lambda} \frac{dx}{|u|}. \end{aligned}$$

If the particle is only lightly displaced and  $|b - \lambda|$  is large, then the velocity felt by the particle approximates the free-stream velocity ( $|u| \simeq U$ ) in the second integral. The second

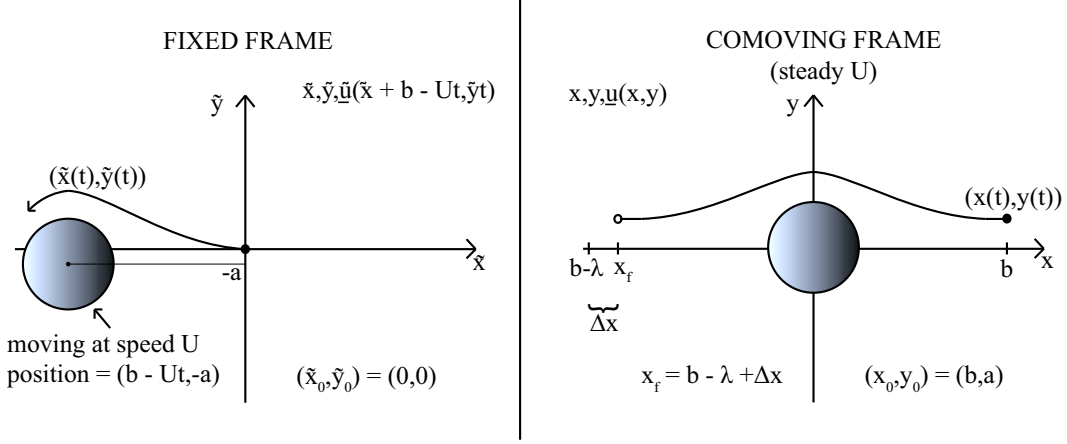


Figure 3: Left: displacement of the particle in a fixed frame. The particles starts in the origin. Right: displacement of the particle in a frame that moves with the particle. The moving cylinder is in the origin.

integral can then be approximated by  $\Delta x/U$ , which gives

$$\frac{\lambda}{U} \simeq \int_{b-\lambda}^b \frac{dx}{|u|} \iff \frac{\Delta x}{U} = \int_{b-\lambda}^b \frac{dx}{|u|} - \frac{\lambda}{U}$$

From this statement we can derive an equation for the approximate horizontal displacement of the fluid particle  $\Delta x$ :

$$\boxed{\Delta x \simeq U \int_{b-\lambda}^b \left( \frac{1}{|u|} - \frac{1}{U} \right) dx} \quad (2)$$

The displacement in the  $y$ -direction is trivial, as the fluid particle will follow a streamline of the flow in the comoving frame (assuming the flow is steady in that frame). Far away from the moving cylinder ( $\lambda \rightarrow \infty$ ,  $b - \lambda \rightarrow -\infty$ ) the displacement in the  $y$ -direction must therefore be zero:

$$\boxed{\Delta y = 0} \quad (3)$$

Note that both boxed expressions are only valid in the limit of large path length  $\lambda$ .

## 2.1 Example: A cylinder in potential flow

As an example, consider a cylinder in potential flow with stream function

$$\Psi(x, y) = -Uy \left( 1 - \frac{l^2}{x^2 + y^2} \right) \quad (4)$$

with  $l$  the radius of the cylinder and

$$u = \frac{\partial \Psi}{\partial y}, \quad v = -\frac{\partial \Psi}{\partial x}.$$

We will choose  $U = 1$  and  $l = 1$ .

### 2.1.1 Far away from the cylinder

It can be expected that the effect of a moving cylinder on a particle far away from the body is negligible. To test this statement, one can construct a qualitative order of magnitude for the displacement of such a particle. This displacement can be represented by  $\Delta x$  and  $\Delta y$ . We will assume the path length is infinite, so the displacement  $\Delta y$  vanishes identically.

First of all, let us calculate the maximum excursion in  $y$ ,  $\epsilon_{\max}$ . This can be calculated using the stream function in the fixed frame (figure 2). Here, the particle is located initially at  $(b, a)$ . Because the flow around the cylinder is steady, the particle moves along the stream line. Therefore, we can set up

$$-y + \frac{y}{x^2 + y^2} = -a + \frac{a}{a^2 + b^2} \simeq -a, \quad (5)$$

where  $a \gg 1$  is assumed such that  $\frac{a}{a^2 + b^2}$  can be neglected. Let  $y = a + \epsilon$ , where  $a \gg \epsilon$ . If we input this expression into equation 5, we obtain

$$-a - \epsilon + \frac{a + \epsilon}{x^2 + (a + \epsilon)^2} \simeq -a - \epsilon + \frac{a}{x^2 + a^2} \simeq -a.$$

Therefore,

$$\epsilon \simeq \frac{a}{x^2 + a^2} \quad (6)$$

Here,  $\epsilon_{\max} \simeq \max_x(\epsilon)$ , thus

$$\boxed{\epsilon_{\max} \sim \mathcal{O}(1/a)} \quad (7)$$

where we assume from now that  $x \ll a$ .

$\Delta x$  can be calculated from equation 2. First, we can find  $u$  using the given streamfunction in the fixed frame and then construct an approximate expression for  $|u|^{-1} - 1$ . The velocity  $u$  is

$$u = \frac{\partial \Psi}{\partial y} = -1 + \frac{x^2 - y^2}{(x^2 + y^2)^2}.$$

Therefore, using  $x \gg y \gg 1$ , it follows that

$$\frac{1}{|u|} - 1 = \frac{1}{1 - \frac{x^2 - y^2}{(x^2 + y^2)^2}} - 1 \simeq 1 + \frac{x^2 - y^2}{(x^2 + y^2)^2} - 1 = \frac{x^2 - y^2}{(x^2 + y^2)^2}.$$

Let  $y = a + \epsilon$ , this gives

$$\frac{1}{|u|} - 1 \simeq \frac{x^2 - a^2}{(x^2 + a^2)^2} - \frac{2a\epsilon}{(x^2 + a^2)^2}.$$

Therefore,

$$\Delta x = \int_{-\infty}^{\infty} \left( \frac{1}{|u|} - 1 \right) dx \simeq \int_{-\infty}^{\infty} \frac{x^2 - a^2}{(x^2 + a^2)^2} dx - \int_{-\infty}^{\infty} \frac{2a\epsilon}{(x^2 + a^2)^2} dx.$$

Here, the first integral on the right hand side is

$$\int_{-\infty}^{\infty} \frac{x^2 - a^2}{(x^2 + a^2)^2} dx = -\frac{1}{a} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \cos 2\theta d\theta = 0,$$

where  $x = a \tan \theta$  is used. The second integral on the right hand side is

$$2a\epsilon \int_{-\infty}^{\infty} \frac{1}{(x^2 + a^2)^2} dx = \frac{2a\epsilon}{a^3} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \cos^2 \theta d\theta = \frac{\epsilon\pi}{a^2}.$$

Therefore,

$$\boxed{\Delta x \simeq -\frac{\epsilon\pi}{a^2}}. \quad (8)$$

Previously, we showed that  $\epsilon \sim O(a^{-1})$ , which leads to the conclusion that  $\Delta x \sim O(a^{-3})$ . Because  $a$  is much larger than 1, the displacement of the particle far away from the cylinder is negligible, which confirms our initial guess. However, note that the perturbation to the velocity field due to the moving object is of order  $a^{-2}$ , and the net displacement is smaller by another order of magnitude. Thus, drift trajectories far from the moving body are very nearly closed.

### 2.1.2 Close to the cylinder

A more interesting limit is the one very close to the cylinder ( $a \ll 1$ ). The path of the fluid particle can be subdivided into three regions (figure 4). In the first region the particle more or less follows the  $x$ -axis. In region 2 the fluid trajectory bends upwards and in region 3 it follows an almost circular path to the  $y$ -axis. On the other side of the moving body, the fluid particle follows the same path in reverse order.

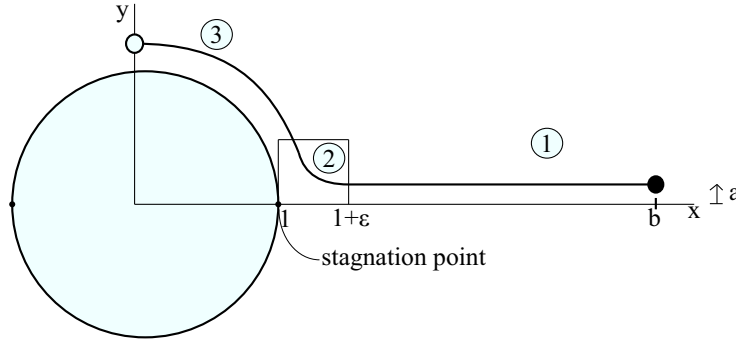


Figure 4: Path of a fluid particle close to the cylinder ( $a \ll 1$ ).

We want to know the displacement  $\Delta x$  (equation 2). With  $U = 1$  the integral for  $\Delta x$  becomes

$$T \simeq \int \left( \frac{1}{u} + 1 \right) dx$$

where we now use the travel time  $T$  instead of distance  $\Delta x$  to match the units ( $T$  has the same numerical value as  $\Delta x$  for  $U = 1$ ). We can split the integral into the three regions. For the third region one can use the full stream function, but for the first two it is easier to

use an approximate form. The stream function in the three region is

$$\Psi_1 \simeq - \left(1 - \frac{1}{x^2}\right) y \quad (y \ll 1) \quad (9a)$$

$$\Psi_2 \simeq -2(x-1)y \quad (x, y \ll 1) \quad (9b)$$

$$\Psi_3 = - \left(1 - \frac{1}{x^2 + y^2}\right) y. \quad (9c)$$

We can now calculate the travel time in each of the three regions.

### Region 1

$$u_1 = \frac{\partial \Psi}{\partial y} = - (1 - x^{-2})$$

$$T_1 = \int_b^{1+\epsilon} \left(\frac{1}{u} + 1\right) dx = \int_b^{1+\epsilon} \frac{dx}{1-x^2}$$

Using  $\epsilon \ll 1$  and  $b \gg 1$  this can be approximated by

$$T_1 \simeq \frac{1}{2} \log\left(\frac{2}{\epsilon}\right) + \frac{\epsilon}{4} - b^{-1} + \mathcal{O}(\epsilon^2, b^{-2})$$

### Region 2

For region 2 we first need to specify the boundaries of the region. Let us rewrite the approximate streamfunction as

$$\Psi_2 \simeq -2(x-1)y = -2XY$$

where  $X = x - 1$  and  $Y = y$ . The fluid particle enters region 2 at  $(X_0, Y_0)$ . At that point

$$\Psi_0 = -2X_0Y_0 = - (1 - b^{-2}) a.$$

As  $X_0 = \epsilon$  and  $b \gg 1$ , this is approximately

$$-2\epsilon Y_0 = -a \implies Y_0 = \frac{a}{2\epsilon}.$$

Because the stream function is hyperbolic and the domain of region 2 is of size  $\epsilon$  by  $\epsilon$ , it follows that  $(X_1, Y_1) = (a/2\epsilon, \epsilon)$ . The travel time in region 2 is thus

$$T_2 = \int_{X_0}^{X_1} \left(\frac{1}{u} + 1\right) dx = \int_{\epsilon}^{a/2\epsilon} \left(\frac{1}{-2x} + 1\right) dx = -\frac{1}{2} \log\left(\frac{a}{2\epsilon^2}\right) + \frac{a}{2\epsilon} - \epsilon$$

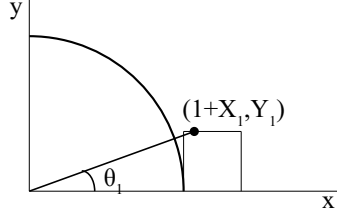


Figure 5: Close-up of the path of the fluid particle in region 3.

### Region 3

From the full stream function the velocity  $u$  is

$$u(x, y) = \frac{\partial \Psi}{\partial y} = -1 + \frac{x^2 - y^2}{(x^2 + y^2)^2}$$

In polar coordinates ( $x = r \cos \theta$ ,  $y = r \sin \theta$ ) this can be written as

$$u(r, \theta) = -1 + \frac{\cos 2\theta}{r^2}$$

Figure 5 shows a sketch of the path of fluid particle in region 3. We define  $\theta_1$  as the (small) angle between the x-axis and the point  $(1 + X_1, Y_1)$ . The travel time in region 3 is then

$$T_3 = \int_{\theta_1}^{\pi/2} \left( \frac{1}{u} + 1 \right) \frac{dx}{d\theta} d\theta = \frac{1}{2} \int_{\theta_1}^{\pi/2} \frac{\cos 2\theta}{\sin \theta} d\theta = -1 + \frac{1}{2} \log 2 - \frac{1}{2} \log \theta_1 + \mathcal{O}(\theta_1^2)$$

using  $dx/d\theta = -r \sin \theta$ . From figure 5 one can derive

$$\tan \theta_1 = \frac{Y_1}{1 + X_1} = \frac{\epsilon}{1 + \frac{a}{\epsilon}} \simeq \epsilon \left( 1 - \frac{a}{\epsilon} \right) = \epsilon - a$$

The travel time in region 3 is thus approximately

$$T_3 \simeq -1 + \frac{1}{2} \log 2 - \frac{1}{2} \log \epsilon + \frac{a}{2\epsilon} + \mathcal{O}\left(\left(\frac{a}{\epsilon}\right)^2\right).$$

For the displacement of the fluid particle we need the total travel time, which is twice the sum of the travel time in region 1, 2, and 3. Adding up the leading orders of the travel times gives

$$T = T_1 + T_2 + T_3 = \left( \frac{1}{2} \log \left( \frac{a}{\epsilon} \right) - b^{-1} \right) + \left( -\frac{1}{2} \log \left( \frac{a}{2\epsilon^2} \right) \right) + \left( -1 + \frac{1}{2} \log 2 - \frac{1}{2} \log \epsilon \right).$$

The  $\epsilon$ 's cancel out. To leading order, the total transit time for half the particle path is then

$$T = -\frac{1}{2} \log a - 1 + \frac{3}{2} \log 2 - b^{-1}. \quad (10)$$

For small  $a$ , the first term dominates the travel time, i.e., the particle tends to get stuck near the stagnation point in region 2 for a while. As  $a \rightarrow 0$ , we see that  $T \rightarrow \infty$ . In general,

for a moving body of any shape in 2D potential flow it turns out that the coefficient of  $\log a$  is given by the sum over the linearization coefficients for each hyperbolic stagnation point encountered, as long as  $a$  is small. The displacement of a fluid particle close to a moving body in potential flow due to this moving body is thus well-approximated by

$$\Delta_\lambda(a, b) = \begin{cases} -\log a & 0 \leq b \leq \lambda \\ 0 & \text{otherwise.} \end{cases} \quad (11)$$

The cutoff for  $b < 0$  and  $b > \lambda$  is due to the fact that since the displacement is mostly due to the stagnation points, the particle must at least reach the stagnation point. (We take the size of the body itself as negligible.)

### 3 Displacement of a fluid particle due to multiple kicks

In previous section an expression for  $\Delta_\lambda(a, b)$  was obtained. Based on this information we can derive an effective diffusivity. Here, we have four constants and two random variables:  $U$  is the mean velocity of the cylinder,  $l$  is the length scale,  $\lambda$  is the mean free path of the cylinder, and  $n$  the number density. The position of the particle is coordinated by two random variables,  $a$  and  $b$ , which were described in the previous section. If we pick a point,  $(x, y)$ , in Cartesian coordinates, the probability measure of the point is simply represented as  $(1/V)dxdy$ , where  $V$  is the total volume. Instead of  $(x, y)$  space, we have to use  $(a, b)$  space for representing the PDF of the particle distribution. Considering that  $a$  is positive and neglecting the edge of the domain, we find

$$\frac{1}{V} dxdy = \frac{2}{V} dadb. \quad (12)$$

A similar relation can be found in 3D. In this case, the probability measure can be expressed as

$$\frac{1}{V} dxdydz = \frac{2\pi a}{V} dadb. \quad (13)$$

Now, assume that our target particle is kicked by a swimmer. For  $N$  steps or kicks,

$$\mathbf{x}_N = \mathbf{x}_0 + \sum_{k=1}^N \Delta_\lambda(a_k, b_k) \hat{\mathbf{r}}_k, \quad (14)$$

where  $a_k$ ,  $b_k$ , and  $\hat{\mathbf{r}}_k$  are random variables. Their choices at each step are independent. In particular,  $\langle \hat{\mathbf{r}}_k \cdot \hat{\mathbf{r}}_l \rangle = \delta_{kl}$ . The direction of a swimmer is chosen independently. Without loss of generality, we can assume that  $\mathbf{x}_0 = 0$ . Since  $\langle \hat{\mathbf{r}}_k \rangle = 0$ , it follows from equation (14) that  $\langle \mathbf{x}_N \rangle = 0$ . To calculate the effective diffusivity, the second moment must be considered:

$$\langle |\mathbf{x}_N|^2 \rangle = \sum_{k=1}^N \langle \Delta_\lambda^2(a_k, b_k) \rangle + \text{vanishing cross terms.}$$

The cross terms vanish because  $\langle \hat{\mathbf{r}}_k \cdot \hat{\mathbf{r}}_l \rangle = \delta_{kl}$ . Each step of the target particle caused by the swimmers is independent such that the particle movement can be considered to be a

random walk. Since the variables are identically distributed, we get

$$\sum_{k=1}^N \langle \Delta_\lambda^2(a_k, b_k) \hat{r}_k \hat{r}_k \rangle = N \langle \Delta_\lambda^2(a, b) \rangle = \frac{N}{V} \iint \Delta_\lambda^2(a, b) 2dadb.$$

$N$  is introduced as the number of time steps. Physically,  $N$  can be understood as the number of collisions between the particle and the swimmers. It can be represented as  $t/T$ , where  $t$  is an elapsed time and  $T$  is the mean free time, the average time for a swimmer to collide with the particle. Hence,  $t/T$  is the average number of collisions during the time  $t$ . Here,  $T$  can be represented as  $\lambda/U$ , where  $\lambda$  is the mean length which a swimmer proceeds before changing its direction, so that  $N$  can be written as  $Ut/\lambda$ . Hence,

$$\langle |x(t)|^2 \rangle = \frac{Ut}{\lambda} \frac{1}{V} \iint \Delta_\lambda^2(a, b) 2dadb,$$

where  $x(t)$  is used instead of  $x_N$ . To eliminate  $V$  from the equation, observe that the above equation is for one swimmer, so  $n = 1/V$  is the number density. Therefore,

$$\langle |x(t)|^2 \rangle = \frac{2Unt}{\lambda} \iint \Delta_\lambda^2(a, b) dadb = 4\kappa t, \quad (15)$$

where  $\kappa$  is the effective diffusivity.  $4\kappa t$  comes from the result of random walk (see previous lecture). The above expression is for a two-dimensional system, but can be easily generalized for 3D. We obtain finally

$$\kappa = \begin{cases} \frac{Un}{2\lambda} \int \Delta_\lambda^2(a, b) dadb, & 2D \\ \frac{\pi Un}{3\lambda} \int \Delta_\lambda^2(a, b) a dadb, & 3D \end{cases} \quad (16)$$

Recall our approximate form for displacement due to a cylinder, including dimensions:

$$\Delta_\lambda(a, b) = \begin{cases} -l \log(a/l) & 0 \leq b \leq \lambda \\ \text{negligible} & \text{otherwise} \end{cases},$$

the calculation of  $\kappa$  becomes

$$\kappa \simeq \frac{Un}{2\lambda} \lambda \int_0^l l^2 \log^2(a/l) da.$$

Using  $\int_0^1 \log^2 x dx = 2$ , we obtain

$$\kappa \simeq Unl^3. \quad (17)$$

Note that this result is completely independent of  $\lambda$  (for  $\lambda$  large).

Another relevant case is a swimmer with a ‘bubble wake,’ that is, a region enclosed by streamlines that follows the swimmer, often called the *atmosphere* of the swimmer. If there is a bubble wake behind a swimmer, a particle inside the bubble wake will follow the swimmer until the swimmer changes its direction. Therefore, the particle trapped inside the bubble moves by  $\lambda$ . Our approximate expression of  $\Delta_\lambda(a, b)$  is

$$\Delta_\lambda(a, b) = \begin{cases} \lambda & 0 \leq b \leq \lambda \\ 0 & \text{otherwise.} \end{cases} \quad (18)$$

Swimmer	$\lambda$ -dependence	far/near field dominance
potential (slip)	none	near
viscous (squirmers)	none	far
viscous (no-slip)	$\log \lambda$	near
trapped bubble	$\lambda$	near

Table 1: Dependence of displacement on path length and whether the displacement is dominated by far or near field, for various swimmer models.

In this case, our calculation of  $\kappa$  is

$$6\kappa = \frac{2Un}{\lambda} \int_{\text{bubble interior}} \lambda^2 da db = Un\lambda V_{\text{bubble}},$$

where  $V_{\text{bubble}}$  is the total volume of the bubble. Therefore,

$$\kappa = \frac{1}{6}Un\lambda V_{\text{bubble}}. \quad (19)$$

Now, unlike the potential flow case, the effective diffusivity depends explicitly on path length  $\lambda$ . This  $\kappa$  can be much larger than that for untrapped fluid.

More complexity could come in if we consider viscous swimmers with a boundary layer. In this case, some simple estimates [9] suggest  $\kappa \sim \log \lambda$ . For micro-organisms in the Stokes flow approximation, the transport is larger and is dominated by far-field (a few body lengths) hydrodynamics [6]. The dependence on flow characteristics and boundary conditions is summarized in Table 1, but it should be noted that the details of this table are still the object of active research.

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