GOAL

To develop a basic intuition for selected small-scale biophysical processes among marine microbes → can in no way be complete

How did I get into this topic?

WANT TO LEARN MORE?

1. Ask questions and interrupt – anytime!

2. See the collection of video lectures from RS’s class “Physical ecology at the microscale”: techtv.mit.edu/collections/1-961videos

3. Recent good books
3. BOOKS


Some questions for you

1. how does the nutrient uptake by a cell scale with its radius?

2. How much does this uptake increase by, if a bacterium swims?

3. How far will a bacterium go (‘coast’) after it stops rotating its flagellum?
1. Life at low Peclet and Reynolds numbers

• The origin of diffusion: Brownian motion

• Diffusion-limited uptake: nutrient flux to osmotrophs

• When is it only diffusion: the Peclet number

• Swimming faster to get more food? The Sherwood number

• Low Reynolds numbers: counterintuitive fluid mechanics
  A world with no inertia: no Brazilian free kicks
  The perils of reversibility
Diffusion and its origins

Why start from diffusion?
A little history

The diffusion coefficient
(Einstein 1905)

\[ D = \frac{kT}{6\pi\mu a} \]

Another one: http://www.phy.ntnu.edu.tw/ntnujava/viewtopic.php?t=41
Brownian motion of 0.8 μm diameter latex spheres

Glassbowl in Aceton
Magn: 3200 X
Particle size 2 - 3 μm

Red Lead in Aceton
Slope: 6° - Magn: 800 x
Smallest visible particle: 1 μm
Brownian Motion

Dept. Microbiology & Immunology
University of Leicester, UK. 2001
Diffusion: a random walk
(molecules, viruses, bacteria, …)

Fig. 1.4. An x, y plot of a two-dimensional random walk of $n = 18,050$ steps. The computer pen started at the upper left corner of the track and worked its way to the upper right edge of the track. It repeatedly traversed regions that are completely black. It moved, as the crow flies, 196 step lengths. The expected root-mean-square displacement is $(2n)^{1/2} = 190$ step lengths.
Osmotrophs: nutrient uptake

Concentration of nutrients around cell
(question: can you predict the uptake?)

Flux $J$ of nutrients into the cell $\rightarrow$ Fick’s law: flux $= - \text{diffusivity} \times \text{gradient}$

At the cell surface ($r = a$) $\rightarrow$

$J(a) = - \frac{D \sigma_0}{a}$
Uptake rate

Uptake rate $U$

- $U = \text{flux} \times \text{area} = J \times 4\pi a^2 = (Dc_\infty / a) \times 4\pi a^2 = 4\pi Da c_\infty$

E.g. if $c_\infty$ is in mol$_C$/cm$^3$ and $a$ is in cm → Uptake rate $U$ is in mol$_C$/s

Note: $U \sim a$ (NOT $a^2$)

Volume-specific uptake rate

- $\text{Volume-specific uptake rate} = U / \text{Cell Volume} = 4\pi Dac_\infty / (4\pi a^3/3) = 3Dc_\infty / a^2 \sim 1/a^2$

→ small cells are strongly favored,
large cells are at a competitive disadvantage in oligotrophic waters
Maximum and optimum cell size

Fig. 2.6. Optimum and maximum cell size of an osmotroph. For diffusive supply, uptake rate increases linearly with cell radius, and the slope is proportional to the ambient nutrient concentration (dashed lines). Expenditure (metabolism) increases as a power function of cell size. The maximum possible cell size is the size at which uptake equals expenditure, i.e., where the uptake and expenditure lines intersect. Similarly, optimum cell size, where absolute growth (uptake minus expenditure) is the largest possible, is at the cell size where the difference between uptake and expenditure curves is the largest. Both optimum and maximum cell sizes increase with ambient nutrient concentration.

Kiorboe, 2008
Insect tracheae

Fig. 6.12 Spiracles (located on the sides of the abdomen) are the external openings to the locust's tracheae. Internally, the tracheae go through various bifurcations.

Fig. 6.13 Each tertiary tracheole supplies oxygen to a portion of muscle. The dimensions of the schematic tracheole-muscle system shown here allow us to calculate the maximal length of tracheae.

Air and Water, Denny 1993

- Muscles consume $\text{O}_2$ (most demanding) $H = 6.5 \text{ mol O}_2 \text{/ m}^2 \text{ s}$
- Air is delivered to cells via blind-ended pipes
- Length of tracheole up to 1 mm; diameter up to 0.2 μm

Is diffusion sufficient to deliver enough air?
Eggs

Why is an egg so fragile?

How porous must an egg of given size be?

Does this work in water?

Mermaid's purse

Fig. 6.15 An embryonic bird exchanges gases with its surroundings through pores in its shell.
The Peclet number

Now let the cell move, relative to the fluid → we will call this ‘advection’
→ ‘advection’: many different types of flow (e.g. swimming, sinking, turbulence, …)

D : diffusivity of the solute (often $\sim 10^{-9}$ m$^2$ s$^{-1}$ in water)

Why do we like to use dimensionless numbers?
→ Rapid classification of, and intuition about, the physical regime
The Peclet number

\[
\frac{\text{Advection}}{\text{Diffusion}} = \frac{\text{advecive flux}}{\text{diffusive flux}} = \frac{C_0 U}{D \sigma} = \frac{U \sigma}{D} \cdot \text{Re} = \text{Peclet Number}
\]

- \( \text{Re} \ll 1 \) → diffusion dominates, advection negligible.
- Swimming organisms: \( U = 10 \, \mu m \) [in meters and seconds]

\[
\text{Re} = \frac{10 \, \mu m^2}{10^{-2} \, \mu m^2/s} > 1 \quad \text{for} \quad a > 10 \, \mu m
\]
The Sherwood number

\[ Sh = \frac{\text{Flux by advection} + \text{Flux by diffusion}}{\text{Flux by diffusion}} \]

• How to think about the Sherwood number (catching mosquitoes)

• No simple, a priori expression for \( Sh \) (like there is for \( Pe \))

• Instead, \( Sh \) actually measures (rather than estimates) the relative importance of advection and diffusion

• Diffusion only \( \rightarrow Sh = 1 \) (\( Pe = 0 \))

• \( Sh \) can be computed as a FUNCTION of the Peclet number, where the choice of the function depends on which flow one is considering (e.g. sinking or turbulence)
Uptake gain due to swimming (or sinking)

Advection doubles the uptake

Sh = 1.2 at Pe = 1

How this works: compute Pe → get Sh from the graph (for THIS flow)
Uptake gain due to swimming
Examples of Sherwood numbers

<table>
<thead>
<tr>
<th></th>
<th>U (μm/s)</th>
<th>Pe</th>
<th>Sh</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5 μm bacterium</td>
<td>20</td>
<td>$10^{-2}$</td>
<td>1.00</td>
</tr>
<tr>
<td>5 μm flagellate</td>
<td>200</td>
<td>1</td>
<td>1.22</td>
</tr>
<tr>
<td>500 μm algal colony</td>
<td>800</td>
<td>400</td>
<td>5</td>
</tr>
</tbody>
</table>

So, why would bacteria want to swim??
Enhancement of nutrient uptake by *sinking*

### Phytoplankton

<table>
<thead>
<tr>
<th>Radius, μm</th>
<th>Sinking velocity, cm s⁻¹</th>
<th>Re ( (= \text{aw/v}) )</th>
<th>Pe ( (= \text{aw/D}) )</th>
<th>Sh²</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>2.3 × 10⁻⁴</td>
<td>1.1 × 10⁻⁵</td>
<td>1.1 × 10⁻⁴</td>
<td>1.00</td>
</tr>
<tr>
<td>5</td>
<td>3.4 × 10⁻⁴</td>
<td>1.7 × 10⁻⁵</td>
<td>1.7 × 10⁻²</td>
<td>1.01</td>
</tr>
<tr>
<td>50</td>
<td>5.0 × 10⁻³</td>
<td>2.5 × 10⁻³</td>
<td>2.5 × 10⁸</td>
<td>1.41</td>
</tr>
<tr>
<td>500</td>
<td>7.5 × 10⁻²</td>
<td>3.8 × 10⁻¹</td>
<td>3.8 × 10³</td>
<td>5.06</td>
</tr>
</tbody>
</table>

### Marine snow aggregates

<table>
<thead>
<tr>
<th>Radius, mm</th>
<th>Sinking velocity, cm s⁻¹</th>
<th>Re ( (= \text{aw/v}) )</th>
<th>Pe ( (= \text{aw/D}) )</th>
<th>Sh²</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>0.039</td>
<td>0.039</td>
<td>39</td>
<td>2.6</td>
</tr>
<tr>
<td>1</td>
<td>0.071</td>
<td>0.71</td>
<td>710</td>
<td>6.4</td>
</tr>
<tr>
<td>10</td>
<td>0.13</td>
<td>13</td>
<td>1300</td>
<td>18.8</td>
</tr>
</tbody>
</table>

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3. \( u \ (\text{cm s}^{-1}) = 2.88 \cdot 1₀ \ (\text{cm})^{1.37} \). Calculated from Stokes' law taking the declining cell density with cell size into account (Jackson 1989).  
4. \( Sh \) calculated using eq. 3.5 assuming \( D = 10^{-4} \text{cm}^3 \text{s}^{-1} \).  
5. \( u \ (\text{cm s}^{-1}) = 0.13 \cdot 1₀ \ (\text{cm})^{0.28} \) (Allsopp and Gotschalk 1983).  
6. \( Sh \) calculated using eq. 3.6, assuming \( v/D \) equal to 1000.  

Kiorboe, 2008
Fig. 2. Effect of speed relative to host’s body length on contact rate with viruses for different particle sizes. Numbers shown are for particle diameter, arrows indicate swimming speed calculated by Eq. 11. Not only are larger hosts more sensitive to movement, they are very sensitive to small movements. Sh calculated from Eq. 5.
The Reynolds number

\[ \text{Re} = \frac{Ua}{v} \]

\( v \): kinematic viscosity of the fluid (10^{-6} \text{ m}^2 \text{ s}^{-1} \text{ for water})

\[ \text{Re} = \frac{\text{inertial forces}}{\text{viscous forces}} \quad \text{(dimensionless)} \]

Glaciers, pumping oil and swimming spermatozoa
When is the Reynolds number small?

\[ \text{Re} = \frac{Ua}{v} \]

- SMALL
- SLOW
- SMALL
- VISCOS

Note: all these processes are governed by the same fluid dynamics!!
UNIVERSAL PHYLOGENETIC TREE. This tree is derived from comparative sequencing of 16S or 18S RNA. Note the three major domains of living organisms: the Bacteria, the Archaea, and the Eukarya. The evolutionary distance between two groups of organisms is proportional to the cumulative distance between the end of the branch and the node that joins the two groups. See Sections 11.4–11.8 for further information on ribosomal RNA-based phylogenies. Data for the tree obtained from the Ribosomal Database project http://rdp.cme.msu.edu
# The Reynolds number

<table>
<thead>
<tr>
<th>Organism</th>
<th>Body Length (µm)</th>
<th>Speed (mm/s)</th>
<th>Lengths/Time s⁻¹</th>
<th>Reynolds Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bacterium, <em>Escherichia coli</em></td>
<td>3.0</td>
<td>0.03</td>
<td>10</td>
<td>0.00009</td>
</tr>
<tr>
<td>Sperm, <em>Lytechinus</em> (sea urchin)</td>
<td>5.1</td>
<td>0.16</td>
<td>31</td>
<td>0.0008</td>
</tr>
<tr>
<td>Flagellate, <em>Chlamydomonas</em></td>
<td>13.</td>
<td>0.06</td>
<td>4.6</td>
<td>0.0008</td>
</tr>
<tr>
<td>Flagellate, <em>Euglena</em></td>
<td>50.</td>
<td>0.08</td>
<td>1.6</td>
<td>0.004</td>
</tr>
<tr>
<td>Ciliate, <em>Tetrahymena</em></td>
<td>70.</td>
<td>0.48</td>
<td>6.9</td>
<td>0.03</td>
</tr>
<tr>
<td>Ciliate, <em>Paramecium</em></td>
<td>210</td>
<td>1.0</td>
<td>4.8</td>
<td>0.21</td>
</tr>
<tr>
<td>Ciliated flatworm, <em>Convoluta</em></td>
<td>2,000</td>
<td>0.60</td>
<td>0.3</td>
<td>1.2</td>
</tr>
</tbody>
</table>

Sources: Data from Holwill 1975, 1977; Brennen and Winet 1977; Sleigh and Blake 1977; Berg 1993.

US WALKING: 2 \times 10^6  2 \times 10^3  1  4 \times 10^5
Counterintuitive fluid mechanics

(1) No inertia, no coasting, no Brazilian free kicks

Example of soccer ball

How long does it take for a bacterium to come to rest after it stops propelling its flagellum? (e.g. soccer ball)
No inertia (no coasting) $\rightarrow$ particles/organisms faithfully follow streamlines (no Brazilian free kicks among microbes)

\[
\ln U = -\frac{t}{\tau} + k
\]

\[
U(t) = U_0 e^{-\frac{t}{\tau}}
\]

Time scale to come to rest:

\[
\tau = \frac{2}{3} \frac{R^2}{V} = \frac{\tau}{2} \cdot \left(\frac{\text{10^{-6} m}}{\text{10^{-3} m}^{2/3}}\right) < 1 \mu s
\]

Stopping distance:

\[
l = U_0 \tau = \frac{60 \mu m}{1} 
\]

At low forces, motion exists only while force (friction) acts

(Anscombe's prediction?)
Counterintuitive fluid mechanics

(2) Reversibility at low Re

http://web.mit.edu/fluids/www/Shapiro/ncfmf.html

The scallop theorem!