2. Motility and chemotaxis, in general and in the Ocean

• Why and how to swim?
  Rotating a corkscrew, cracking a whip or coordinating many hairs

• The costs of swimming: a Datsun in Saudi Arabia?

• E. coli’s run-and-tumble swimming

• Diffusion of a bacterial population

• Chemotaxis
  How it works
  Examples of taxis

• Recent work on motility and chemotaxis in the Ocean
Counterintuitive fluid mechanics

(2) Reversibility at low Re

http://web.mit.edu/fluids/www/Shapiro/ncfmf.html
The scallop theorem!
Costs and benefits of swimming for microbes

**Why** swim?
- Find food (encounter it more often (blindly), or actively exploit gradients)
- Find mates (in the same manner)
- Minimize death by predation (handling, *not* encounter)

**Why not?**
- Energy cost
- Signal to predator (you’re ‘moving water’)
- Higher encounter rate with predators and viruses
- It’s difficult to swim if you are small: Brownian reorientation

**How** to swim? → need to circumvent the scallop theorem!
1) Rotating a rigid, helical flagellum (bacteria)
2) Waving a flexible flagellum (eukaryotes, e.g. sperm, phytoplankton)
→ Both are non-reversible motions and give propulsion
Three types of swimming appendages

- Bacterial flagella
  - e.g. *E. coli*

- Cilia
  - e.g. *Paramecium*

- Eukaryotic flagella
  - e.g. spermatozoa

Lighthill, 1976
The eukaryotic flagellum

Flagellum is **flexible:**
→ cell propagates waves down the flagellum
→ from the base to the tip (mostly), like a whip

Waves can be
→ planar (2D)
→ helical (3D)

Powered by dynein molecular motors distributed along the length and circumference of the flagellum, driven by ATP
Eukaryotic flagella: phytoplankton

Leucocryptos marina, a marine dinoflagellate (Butcher 1967)

Chlamydomonas

http://www.uwlax.edu/biology/faculty/Howard/Research.htm

imbrickle.blogspot.com
Structure of the eukaryotic flagellum: the axoneme

- Protein: tubulin
- Diameter of the flagellum: 200 nm
- 9+2 structure
- Bending of flagellum: due to sliding between pairs of outer microtubules
The prokaryotic flagellum

- Helical and rigid: pitch ~ 2 μm, diameter ~ 20 nm
- Helical protein: flagellin
- Single motor at the base of each flagellum

Multiple polar flagella
One polar flagellum (monotrichous)
Many flagella, all over the body (peritrichous)
Flagella tuft
The molecular motor

Hook-basal body complex

Figure 9.3. A schematic diagram of the flagellar rotary motor, drawn to scale. Inset: Rotationally averaged reconstruction of electron micrographs of purified hook-basal bodies. Compare Table A.3. The signaling molecule CheY-P, which binds FliM, is shown at the lower left. FlgM (lower right) blocks the activity of a sigma-factor that activates late genes. FlgM is pumped out of the cell via the transport apparatus once the basal part of the motor is complete. (Image reconstruction courtesy of David DeRosier, Brandeis University.)

Motor: proton-driven or sodium-driven
Propulsion by cilia

- Cilia have many functions: locomotion, excretion, circulation, feeding, irritability, contractility, reproduction

- Structure: same as the eukaryotic flagellum (9+2)

- Basic idea: a “Stokesian parachute”

- Metachronal waves
Propulsion by cilia

Paramecium
Propulsion by cilia

Opalina
Figure 16. Approximate beat patterns for Opalina and Paramecium with the positions of an individual cilium at equal intervals in time on the left and the positions of an array of cilia at a given time on the right, showing the symplectic metachronism of Opalina and an antiplectic approximation to the metachronism of Paramecium.
Metachronal waves

*Figure 15* A scanning electron micrograph following rapid fixation of the ciliated protozoan *Paramecium* (from Tammi 1972). The metachrony of this specimen is dextroplectic and/or amphirotic. A-P, anterior-posterior axis; D-V, dorsal-ventral axis. (We are indebted to Dr. S. L. Tammi for this photograph.)


*Figure 14* A scanning electron micrograph following rapid fixation of the ciliated protozoan *Oxytricha* (from Tammi & Horridge 1970). As in the preceding figure, the in vivo metachronal wave orientation is reflected in the pattern over the fixed specimen. Arrows indicate the direction of the metachronal wave. The key difference between the two specimens is that this figure is limited to all or part of a single cell. (We are indebted to Dr. S. L. Tammi for this photograph.)

Energetic cost of swimming

- Power required for swimming ~ square of swimming speed
  (huge cost increase for fast swimmers, e.g. Mitchell)

- Efficiency: only ~1% !!

- Conversion:
  1 Joule ~ 5x10^7 glucose molecules

- A Datsun in Saudi Arabia??
  (Purcell 1977)
Bacterial cells swimming near a glass surface, then above the surface.

*Escherichia coli* swimming

(H. Berg)
Bacteria

Pseudoalteromonas haloplanktis
Berg’s 3D tracking microscope

Figure 4.1. The tracking microscope, circa 1974. The lenses, mirrors, and fiber-optic assembly used to dissect the image of a cell was built into the rectangular box extending back from the top of the binocular. Just below the objective is a thermostatted enclosure containing a small chamber in which the bacteria were suspended, mounted on a platform driven by three sets of electromagnetic coils (similar to loudspeaker coils) built into the assembly at the left. (From Berg, 1978, Fig. 2).

E. Coli in Motion, Howard C. Berg 2004
The flagellar bundle → a ‘run’

http://en.wikipedia.org/wiki/Flagella
*E. coli*'s ‘run and tumble’ swimming

Bundled flagella (CCW rotation)

Flagella bundled (CCW rotation)

Tumble—flagella pushed apart (CW rotation)

Peritrichous
→ a random walk!
→ expect diffusion
A population of bacteria “diffuses”
(time scale 15 min; length scale 1 mm)
A population of bacteria “diffuses”

Diffusion coefficient $D = 0.5 \times 10^{-10} \text{ m}^2/\text{s}$
Run-and-tumble

\textit{E. coli}'s flagella are in fact polymorphic

\textbf{Figure 5.6.} A schematic drawing of the events that usually occur during a tumble. A cell with a bundle of two flagellar filaments is shown swimming from left to right. The cell alters course as the motor driving one filament changes its direction of rotation and the filament undergoes a normal to semicoiled transformation. This change in course defines the tumble interval, which, according to both the tracking and video data, takes 0.14 second, on average. As the cell begins to move along its new track, the filament undergoes a semicoiled to curly 1 transformation. Both the normal and curly 1 filaments generate forward thrust, but the curly one at a smaller magnitude. Finally, after the direction of flagellar rotation changes again, the filament reverts to normal. As it does so, it rejoins the bundle, and the cell resumes its initial speed. The time from the initial disruption of the bundle to its reconsolidation is defined as the reconsolidation interval. According to the video data, this takes 0.43 second, on average.
Other strategies

- **Reversible flagella**
  - CCW rotation → CW rotation

- **Unidirectional flagella**
  - CW rotation → Cell stops, reorients → CW rotation

- **Polar**
Different swimming behaviors (mutants)
Synechococcus swimming
*E. Coli* swims on the right

(DiLuzio et al, Nature, 2005)
Chemotaxis: introduction

The capillary assay
Receptors

Fig. 5.5 Absorbing disks (a model for receptors or ion channels) scattered on a non-absorbing sphere (a model for a cell).
Chemotaxis in *E. coli*: delay tumble when conditions are getting better.

*Temporal* vs. *spatial* gradient sensing.
Examples of different taxis in bacteria
Aerotaxis

(Pseudoalteromonas haloplanktis)

First taxis discovered (Engelmann 1883, while studying photosynthesis)
Aerotaxis

OXYGEN BUBBLE

accumulation

depletion

B. subtilis

background concentration

(KESSLER & HILL, 1995)
Phototaxis
Bacterial waves
(chasing the gradient)

Ahmed & Stocker, unpublished
pH taxis

*H. pylori*: away from the stomach lumen, towards the epithelium

Do marine bacteria do this? (ocean acidification)
Figure 1 Transmission electron micrograph of *Magnetospirillum magnetotacticum* showing the chain of magnetosomes inside the cell. The magnetite crystals incorporated in the magnetosomes have cuboctahedral morphology and are ca. 42 nm long. The magnetosome chain is fixed in the cell and the interaction between the magnetic dipole moment associated with the chain and the local magnetic field causes the cell to be oriented along the magnetic field lines. Rotation of the cellular flagella (not shown) causes the cell to migrate along the field lines. Bar equals 1 micron.

- move preferentially North in N-hemisphere and South in S-”
- geomagnetic field inclined downwards in both cases
- 1-D random walk towards optimum O₂
Recent insights on motility and chemotaxis in the Ocean
Bacterial motility in the sea and its ecological implications

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Fig. 1. Motility in natural bacterial assemblages (% motile) in surface waters off Scripps from August 1997 to June 1998. Samples were counted by dark-field microscopy (for details see 'Materials and methods')

Fig. 2. Diel pattern of motility in natural bacterial assemblages (% motile) in surface waters off Scripps on 23 to 25 October 1997. Samples were counted by dark-field microscopy (for details see 'Materials and methods')
Microscale Nutrient Patches in Planktonic Habitats Shown by Chemotactic Bacteria

Nicholas Blackburn,* Tom Fenchel, Jim Mitchell

www.sciencemag.org  SCIENCE  VOL 282  18 DECEMBER 1998
Long Lag Times and High Velocities in the Motility of Natural Assemblages of Marine Bacteria

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The motility characteristics of natural assemblages of coastal marine bacteria were examined. Initially, less than 10% of the bacteria were motile. A single addition of tryptic soy broth caused an increase in the motile fraction of cells but only after 7 to 12 h. Motility peaked at 15 to 30 h, when more than 80% of cells were motile. These results support the proposal that energy limits motility in the marine environment. Cell speeds changed more than an order of magnitude on timescales of milliseconds and hours. The maximum community speed was 144 μm s⁻¹, and the maximum individual burst velocity was 407 μm s⁻¹. In uniform medium, speed was

FIG. 2. Mean speed of motile cells as a function of time. (a) High-resolution sampling over a 50-h period. (b) Daily sampling over 9 days, with new bottles opened each day. Speed measurements were made in the center of the chamber away from surfaces. Zero values indicate that no motile cells were observed in these treatments. Sample sizes ranged between 10 and 25 cells for samples. Samples were assayed in triplicate. Error bars are 95% CI. Symbols in panel a show concentrations of TSB (wt/vol).
Rapid chemotaxis, 10-fold increase in nutrient gain
Adaptation to aquatic nutrient landscape?

Stocker et al, PNAS 2008
Bacterial tracking of motile algae

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Super-effective chemotaxis?
Hydrodynamic effect? (Locsei & Pedley 2009)
Colonization of particle plumes

“The response of bacteria to sinking organic particles has a big influence on the oceanic carbon cycle” (Azam & Long, Nature 2001)

Plume: ecological niche for bacteria?

(Smith et al., Nature 1992)

Chisholm, Nature 2000
Marine snow, organic solute plumes, and optimal chemosensory behavior of bacteria

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Abstract
Leaking organic solutes form an elongated plume in the wake of a sinking aggregate. These solutes may both be assimilated by suspended bacteria and guide bacteria with chemokinetic swimming behavior toward the aggregate. We used modifications of previously published models of the flow and concentration fields around sinking aggregates and of chemokinetic behavior of bacteria to identify the behavior that optimizes aggregate colonization and plume utilization. The optimal solution is governed by physical constraints and is a trade-off between a high sensitivity to chemical signals and a long signal integration time. For a run-and-tumble swimming behavior, the predicted tumbling frequency is between 1 and 10 s\(^{-1}\), similar to that reported for marine bacteria. The predicted optimal sensitivity to chemical signals is similar to or greater than that known for Escherichia coli. The optimal behavior was used to examine the potential contribution of aggregate-generated solute plumes for water column bacterial production. Despite occupying only a small volume fraction, the plumes may provide important growth habitats for free bacteria and account for a significant proportion of water column bacterial production at typical concentrations of marine snow aggregates.
Sea snow microcosmms
Farooq Azam and Richard A. Long

Marine bacteria can respond to organic particles in sea water, creating hotspots of bacterial growth and carbon cycling. This microscale behaviour should be included in models of the oceanic carbon cycle.

Figure 2 Carbon fluxes in the ocean involving marine snow. The marine snow (aggregated phytoplankton and dead material) can sink into the deep ocean, thereby removing it from the upper ocean, or it can become involved in nutrient cycling. The first step is colonization by bacteria, which produce enzymes that turn the marine snow into dissolved organic matter (DOM). The colonizing bacteria produce DOM faster than they can use it, so the sinking snow releases a plume of material containing carbon (C), nitrogen (N), silicon (Si) and iron (Fe). Other free-living bacteria (red) are attracted to the plume and grow rapidly. Colonizers may also release their progeny (blue) into the plume. High concentrations of bacteria attract protozoa, which in turn attract larger animals (metazoa). The marine snow and the plume may thus become the focus of a complex food web.
Accumulation in the plume
Ideal for studying microbial processes:

- **Low Reynolds number**: the flow regime of microbes
- **Accuracy**: geometry (~5 μm), flows (μm/s), chemical gradients (low Re)
- **Transparent**: track single bacteria
- **Versatile experimental platform**

Microfabrication

- Design channels (CAD)
- Print mask (transparency)
- Spin-coat photoresist on wafer (thickness = channel depth)
- Align mask and expose to UV
- Develop wafer (wash off unlinked photoresist)

Soft lithography (Whitesides et al 2001)

UV light

Mask

Photoresist

Silicon wafer

Mask (transparency)

Silicon wafer

Developed wafer
**Microfabrication**

- Cast PDMS and cure in oven
- Peel PDMS off wafer
- Make holes (inlets and outlets)
- Bond to glass slide (oxidized)
- Connect tubing and syringe
- Videomicroscopy

Syringe

PDMS

Silicon wafer

25 mm

Phase-contrast inverted microscope
Foraging in turbulent waters