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The Influence of Cell Size on Marine Bacterial Motility and Energetics

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Abstract. The influence of Brownian motion on marine bacteria was examined. Due to their small size, marine bacteria rotate up to 1,400 degrees in one second. This rapid rotation makes directional swimming difficult or impossible, as a bacterium may point in a particular direction for only a few tens of milliseconds on average. Some directional movement, however, was found to be possible if swimming speed is sufficiently great, over approximately 100 μm sec^{-1}. This led to the testable hypothesis that marine bacteria with radii less than about 0.75 μm should exceed this speed. The result of the increased speed is that marine bacteria may spend in excess of 10% of their total energy budget on movement. This expenditure is 100 times greater than values for enteric bacteria, and indicates that marine bacteria are likely to be immotile below critical size-specific nutrient concentrations.

Introduction

There are commonly 10^5 to 10^6 or more bacteria in a milliliter of seawater [14], yet there are few published data on movement and motility of natural assemblages of marine pelagic bacteria. Bell and Mitchell [6] showed migration of marine bacteria to algal exudate, as measured from a few isolates from Vineyard Sound, Massachusetts, that had been grown on agar. Ferguson et al. [13] have since shown that less than one percent of pelagic bacteria grow in culture.

Many authors have pointed out that motility may be important where average nutrient concentrations are low because it allows cells to find micropatches of higher nutrient concentrations [3, 5, 16, 17, 26]. Alldredge and Cohen [3] have shown the existence of chemical micropatches surrounding particles that might

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attract or repel motile bacteria. Through in-depth simulation, Jackson [17] found that temporary clustering around nutrient sources was possible for marine bacteria, but that there were chemosensory limits to the bacterial response. The physical constraint that Brownian motion places on marine bacterial motility and the subsequent energetic consequences are examined here.

In moving toward a nutrient source a bacterium "measures" the concentration of an attractant during about 0.5 sec, then continues moving and measures the attractant concentration for another 0.5 sec and compares the two concentrations [7, 24]. If the concentration decreases or remains the same, the cell, after this first second, tumbles to randomly change its direction. If the concentration increases, the cell continues swimming for another second or so. This process is iterated, producing a biased random walk. The additional second is what gives a cell net directional movement, biasing the otherwise random walk towards the nutrient source. Purcell [30] points out there is a minimum distance a cell must swim before it can detect a change in a concentration gradient. This distance is influenced by the steepness of the gradient and the attractant concentration [9, 24, 30].

As a bacterium swims it is reoriented by rotational Brownian motion [7, 8, 16]. As a result, the direction a cell is swimming at the end of a run is different from the direction it was swimming at the beginning of that run. The amount of reorientation during a run depends on the cell size, temperature, and viscosity. Cell size is particularly important, as reorientation increases as a function of decreasing volume, i.e., the third power of the cell radius [7]. The practical implication of this, as shown here, is that Brownian motion accentuates the differences among groups of bacteria with regards to their ability to perform chemotaxis.

The reorientation by Brownian motion is continuous in a liquid, resulting in net migration velocities of a few micrometers per second when the swimming speed is 30 μm sec^{-1} [11, 16]. With the migration velocity only a fraction of the swimming speed, bacteria need to swim for long periods to reach or stay near their goal [9]. Experimental observation confirms this [23, 24].

Continual swimming places an energy demand on the cell, but this energetic cost has been shown to be negligible for *Escherichia coli* swimming 10 to 30 body lengths per second [7, 9, 30]. This conclusion is apparently based on the work of Adler [1, 2] and of Macnab and Koshland [24], where 0.1 to 200 mM motility medium was used. Ocean nutrient concentrations are more aptly measured in nanomolar concentrations. The energetic costs of swimming in medium and in the environment, however, are about the same for a given cell. The energetic cost of swimming relative to the available nutrients will be greater in an environment such as the ocean compared with that of medium. The work here is an analysis of how cell size influences these costs and the ability of marine bacteria to perform chemotaxis.

Methods

The equations used to calculate the influence of Brownian motion and cell size on marine bacterial movement and chemotaxis were the equations for translational and rotational Brownian motion

of spheres and ellipses, the power needed to overcome drag, the nutrient uptake by a cell, and the theoretical minimum distance a cell needs to swim to detect a change in concentration.

The rotation of a cell by Brownian motion is quantitatively described as

$$\langle \theta^2 \rangle = 4D_r t, \tag{1}$$

where t is time (sec), $\langle\rangle$ indicates the mean, θ is the angle in radians and D_r, the rotational diffusion ($cm^2\ sec^{-1}$), is

$$D_r = (kT)/(8\pi\eta a^3), \tag{2}$$

where k is Boltzmann's constant, T is temperature in °K, η is dynamic viscosity ($g\ cm^{-1}\ sec^{-1}$) and a is cell radius (cm) [7].

Cell size is the dominant factor in eq. (2) and important in eqs. (3), (5), (8), and (9). The size range for marine bacteria is well established [20, 22]. Lee and Fuhrman [20] found mean marine bacterial sizes to range from equivalent spherical radii of 0.2 to 0.25 μm, with the range of radii from 0.1 to 2 μm. Maeda and Taga [22] report most bacteria were between 0.4 and 0.8 μm in the longest dimension. For the calculations that follow, two bacterial sizes are used, i.e., radii of 0.2 and 1.0 μm. The radii are chosen to be illustrative of the size range of marine bacteria (0.1 to 1 μm). The upper value is the size usually used for *E. coli*. Cell size also figures prominently in translational diffusion, D_t ($cm^2\ sec^{-1}$), and is

$$D_t = (kT)/(6\pi\eta a), \tag{3}$$

where all terms are defined as in eq. (2) [7].

For calculating the role of cell shape on rotational velocity, the drag coefficients for an ellipse rotated around its minor axis was used and is

$$F_r = \frac{(8\pi\eta a^3)/3}{\ln(2a/b) - 0.5}, \tag{4}$$

where a and b are the radii of the major and minor axes, and F_r is the rotational frictional drag coefficient [7].

At the low Reynolds number (non-inertial) environment in which bacteria move, the major retarding force on the cell is drag and the power expenditure to overcome that drag is

$$P = 6\pi\eta a v^2, \tag{5}$$

where P is in ergs sec^{-1} and v is cell velocity ($cm\ sec^{-1}$) [7, 30, 32]. All calculations were done in cgs units. There are little data on motility of marine bacteria, so initially for calculating the cost of movement the velocity was assumed similar to that of enteric bacteria.

To find the minimum cost of chemotaxis, the minimum velocity at which chemotaxis can still be performed was used. This velocity was based on the minimum distance a cell must move to detect a change in the concentration of a dissolved compound [30]. This distance is

$$d \sim D/v, \tag{6}$$

or the equivalent

$$d \sim (Dt)^{1/2} \tag{6a}$$

where d is the minimum distance (cm), D is molecular diffusivity ($10^{-5}\ cm^2\ sec^{-1}$) and t is rotation time. Here, eq. (6a) was used. The cell must move d before it rotates 90° in time t, where t was obtained from eq. (1). The minimum velocity then is a minimum distance divided by the maximum time the cell is allowed to go that distance while still maintaining its orientation.

The flux of nutrients into the cell depends on active transport and is estimated using

$$J = \frac{J_{max} C}{K_m + C} \tag{7}$$

where J is the flux, J_{max} is the maximum flux, C is the concentration, and K_m is the half saturation constant. Values for J_{max}, C and $K_m + C$ are from Azam and Hodson [4] and Furhman and Furguson [15]. The total available molecules striking the cell surface is given as

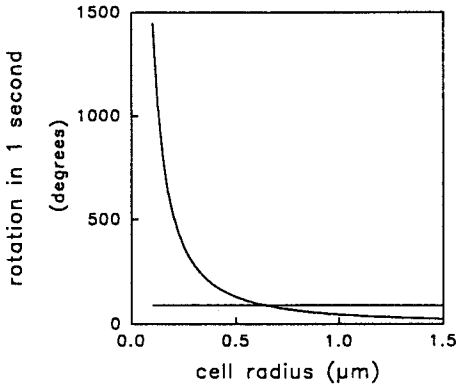

Fig. 1. The rotation of a cell as a function of its radius. The curved line is the cell rotation. The straight line marks 90° to indicate the rotation above which a cell traveling at 20 to 30 μm sec^{-1} must substantially increase its speed in order to be chemotactic. Both lines begin at 0.1 μm. The rotation is not around one axis. Instead the axis continually changes (Fig. 2), making compensation for rotation by steering impossible.

$$I = 4\pi CaD \tag{8}$$

where I is the number of molecules hitting the cell surface sec^{-1}, C is the concentration in nutrient molecules cm^{-3} [7].

Equations (5) and (9) (Results) are in ergs sec^{-1}. To make a direct comparison between mechanical energy output and chemical energy potential, the ergs sec^{-1} were converted to molecules of glucose consumed sec^{-1}. For this conversion it was assumed that there were 1.8×10^{-11} ergs/glucose molecule (263 kcals mole^{-1}) [33], or the equivalent of 36 molecules of ATP produced per glucose molecule.

For simulations of chemotaxis in marine bacteria [16], glucose and galactose concentrations of 30 nM were used [12]. Total carbohydrate concentrations of up to 1 μM are known and used here, but it is not clear that this is available to the bacteria [28].

There are known losses of efficiency during the conversion of chemical to mechanical energy due to flagellar deformation and elasticity, motor wobble, cell vibration, and partial rotation of the cell instead of the flagella [10, 21]. The efficiency of the propulsion system is considered to be about 1% [9, 30].

Results

Cell rotation as a function of size is plotted in Fig. 1. For a cell with a radius of 0.2 μm, at a temperature of 10°C (283°K), the mean rotation is about 440° sec^{-1}, eq. (1). This rotation is not a spin in the sense that rotation is around a single axis. The axis shifts according to the unpredictable nature of Brownian motion, meaning that the cell cannot compensate for, nor anticipate the direction of rotation. In Fig. 2 the orientations at 10 msec intervals are connected by lines. Cell size decreases from top to bottom of the figure, with the concomitant increase in reorientation. Adding translational movement, motility, to the reorientations in Fig. 2 gave the paths of swimming cells (Fig. 3).

The increase in rotational motion with decrease in cell size means that a small cell must cover its minimum distance faster than a large cell if the rotation of the two is held to a maximum of 90°. A 1 μm cell has 3.8 sec to cover its minimum distance, whereas a small cell must cover its minimum distance in 42 msec (eq. [1]). This assumes the small cell can detect a gradient over this time, which appears possible given the work by Segall et al. [31]. For a 1 μm radius cell moving 30 μm sec^{-1} the minimum distance that must be swum to

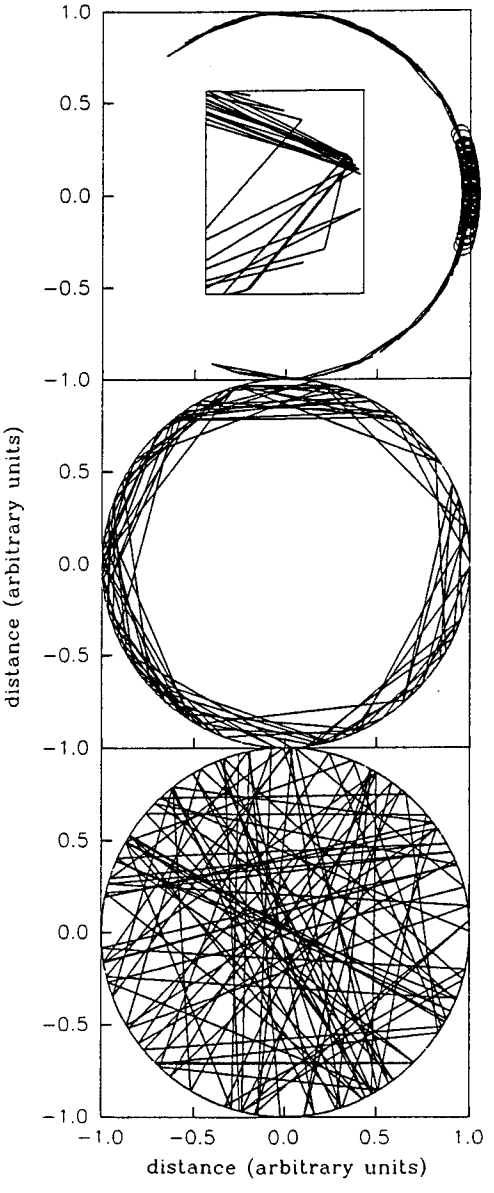

Fig. 2. Each graph follows a fixed point on the cell surface as that cell is rotated by Brownian motion. The lines connect the fixed point at 10 msec intervals. The longer the lines on the circle, the greater has been the reorientation during the 10 msec interval. Each graph is normalized to the individual cell radius so that "0" is the center and "1" is the edge of the cell. Small circles, instead of lines, were used to mark the fixed point at 10 msec intervals for the 1 μm cell (top panel) to emphasize that the fixed point does not move much; the cell points in about the same direction the entire time. For the insert in the top graph, lines have been substituted for the small circles to show, that when expanded, the distribution is similar to the other graphs. The arc of short lines in the top graph show the reorientation for a 0.6 μm cell. Reorientations for 0.4 and 0.2 μm cells are shown in the middle and bottom graphs, respectively. The simulation was done in 3 dimensions, but only 2 are plotted here.

detect a change in concentration is about 32 μm (eqs. [6] and [6a]). The small cell needs to swim only about 6 μm for its minimum distance. This is a short distance compared to the 32 μm for a larger cell, but because the allowed time is only 42 msec, a velocity of about 150 μm sec^{-1} is required. The smaller the bacterium the faster it must swim to move in a given direction and to detect a gradient in that direction.

For a fixed volume, changing cell shape did change the amount of rotation.

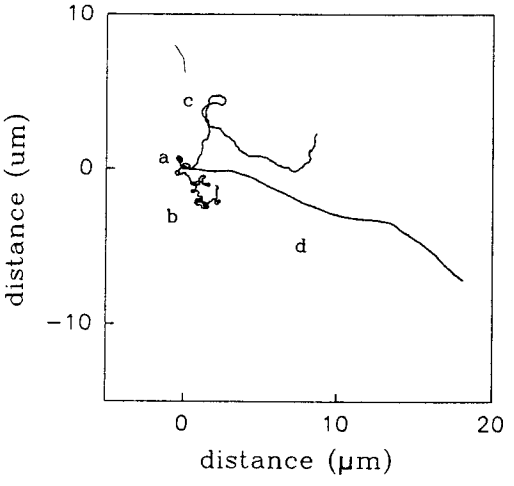

Fig. 3. The simulated paths of four different size cells during 1 sec. The reorientation of Fig. 2 has been combined with motility. The lines shown are one path length, and there are no tumbles. All cells began at the origin. a (the irregular dot), A path of a 0.2 μm cell; b, of a 0.4 μm cell; c, of a 0.6 μm cell; d, of a 1 μm cell. Cell speeds were 20 μm sec^{-1}.

Bacilli of a given volume rotate less than cocci of the same volume. For cells with axis ratios between 2 and 3 to 1 the reduction was found to be about 30%. For a bacterium with an equivalent spherical radius of 0.2 μm the reduction is from 440 to 300° in 1 sec, still greater than the 90°, the upper limit allowing taxis. For an *E. coli* sized bacterium with a volume equivalent to a spherical radius of 1 μm the reduction in rotation is from 30 to 21° in 1 sec. Among cells of similar volume, such a reduction might allow a rod-shaped cell to reach or approach a nutrient source before a spherical cell. The shape of a cell is not an important factor, however, when comparing cells with significantly different volumes, which is the interest here. Thus, the focus here is on spheres.

Assuming an equivalent spherical volume of 0.2 μm, the energy necessary to move 150 μm sec^{-1} was about 6×10^3 glucose molecules sec^{-1} (eq. [5]). From eq. [7] this was found to be about what the cell could take up living in approximately 1 μM glucose, when J_{max} was 3.6×10^{-9} moles $liter^{-1}$ $hour^{-1}$ and K_m + Concentration was 1.5×10^{-7} M [4]. The potential uptake under these J_{max} and K_m + Concentration, if the cell is a perfect absorber, is about 10^6 molecules sec^{-1} (eq. 8). The measured value is 0.6% of the potential. This discrepancy is explained in the Discussion.

Equations (1), (2), (3), (5), and (6a) were combined and power related directly to size with the net result

$$P_c = \frac{3kTD_t}{(a\theta)^2} \tag{9}$$

where P_c is the power required for a cell of a given size, a, to perform chemotaxis, with all other terms given in the Methods. A substitution diagram is given in Fig. 4. The results from the equation are given in Fig. 5.

In calculating the above power requirements it was assumed that nutrient molecules were utilized aerobically. If regions were oxygen-depleted or anaerobic then the nutrient molecules would have to be fermented so that about 10

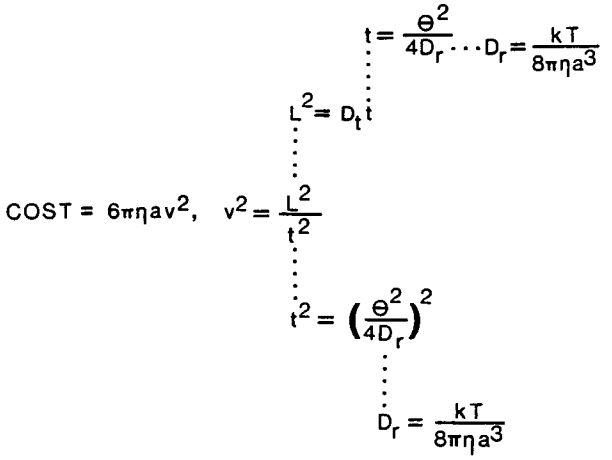

Fig. 4. Equation (9) is obtained with the substitutions in this diagram. Velocity is a length divided by time. For chemotaxis the length is the minimum length a cell must go to detect a change in concentration and is $(D_t t)^{1/2}$. Small t is the time the cell has to swim the minimum distance. The time to rotate 90° degrees is used here; if the cell takes more time than this it never reaches the minimum distance. Small t is defined as the angle squared divided by four times the rotational diffusion coefficient, D_r. This coefficient is the thermal fluctuation (kT) divided by the drag term $8\pi\eta$ and a^3, the cell radius cubed. In short, "1" is the distance the cell swims in a straight line. Returning to the definition of velocity, the small t in the denominator is again the rotation time as described previously. Small t is the amount of time the cell has before it rotates 90°. The complete substitution gives eq. (9). The time for rotation, t, may also be left explicitly in the equation.

times more molecules would be required to provide the energy to move at a given speed as compared to a fully oxic environment.

Discussion

Marine bacteria are small, rarely reaching 1 μm, with radii of 0.2 μm common [20, 22]. As a result Brownian motion quickly reorients these cells. To achieve forward displacement or to be chemotactic, such small cells must swim rapidly so that they move a significant distance before being rotated. Increased velocity increases the energy expenditure, and the cell, in effect, pays with nutrient molecules to compensate for Brownian motion. This discussion will focus on the possible strategies for reducing or circumventing the cost of being small. These strategies are slowing down, using internal energy stores, flagellar stabilization, and greater molecule uptake.

Can small cells lower the cost relative to the ambient nutrient concentration by slowing down? Apparently not. Cell rotation is independent of cell velocity (eq. [2]). This means that D_r does not specify the distance a cell can swim in a straight line, only the time it takes before a cell rotates through a given angle. Thus, if a cell slows down to reduce power consumption it rotates more in a given distance than it would if it had not slowed down. The 150 μm sec^{-1}

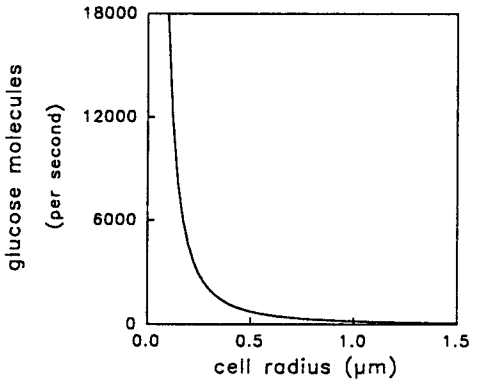

Fig. 5. The cost of compensating for Brownian motion during chemotaxis as a function of size. The curved line shows the cost for the cell in molecules of glucose per second.

swimming speed given above was the minimum allowable speed, and costs the cell the equivalent of all of the molecules it could take up in about 1 μM glucose.

The cost is reasonable if it is small compared with what the cell has stored as an energy reserve. To estimate the utility of storing an energy reserve for motility it is assumed that 1% of the cell volume is energy reserve in the form of glucose, allowing the other 99% for DNA, RNA, ribosomes, water, and proteins. It is also assumed that the reserve is respired aerobically and that 100% of the energy goes to drive the motors. The power consumption was calculated with eq. (9) at $\theta = 1.57$ rads and the maximum glucose density of 1.56 g cm^{-3} (crystalline). A 1 μm cell has a storage volume that is about 4×10^{-14} cm^3. This volume of stored material will propel the cell for 9 hours. For a 0.2 μm cell the storage volume is 3×10^{-16} cm^3. This volume of stored material will propel the cell for 4 min. The difference in time reflects the large difference in volumes between the large and small cells. If chemotaxis is required to keep the small cell in a patch then the patch nutrient concentration must be elevated well above 1 μM, because this is the swimming maintenance concentration and does not allow any excess for storage or other cellular processes.

Rotation of small cells will be decreased by the stabilizing influence of the flagellum or flagellar bundle. Stabilization reduces the velocity needed for taxis and this in turn reduces the cost of motility. The influence of flagellar stabilization, however, appears small. Measured rotation of *E. coli* is about 27° in 1 sec [8]. Values for the theoretical rotation of an equivalent volume sphere are 28° [27] and 30° [7]. The stabilization for *E. coli* is about 3 to 10% of the total rotation. There are no rotational diffusion measurements of small bacteria. Recent measurements [27] on large cells (radii were 2 to 3 μm) support the observations on *E. coli* that flagella stabilize rotation by a few percent of the cell rotation.

If the flagella are arbitrarily long, however, rotation can be decreased to effectively zero. The stabilizing influence of flagella is approximated here by adding the rotational drag coefficients of the flagella and cell,

$$f_{rt} = f_{rs} + f_{rf} \tag{10}$$

where f_{rt} is the total rotational drag coefficient, f_{rs} is the rotational drag coefficient of the sphere

$$f_{rs} = 8\pi\eta a^3. \tag{11}$$

All variables are defined as above, and f_{rf} is the rotational drag coefficient of a flagellum or flagellar bundle

$$f_{rf} = \frac{(8\pi\eta a_f 3)/3}{\ln(2a_f/b) - 0.5} \tag{12}$$

where a_f and b are the major and minor axes of a flagellum, assumed to be an ellipse [7]. The radius of the equivalent spherical volume of the cell is 1 μm, the flagellar bundle radius is 0.02 μm, and the length 5 μm, with all calculations made in cgs units. The rotation is calculated from eqs. (10), (11), and (12) as

$$D_r = kT/f_{rt} \tag{13}$$

where all terms are as previously defined. The theoretical rotation for *E. coli* then is 21° in 1 sec, compared with the measured rotation of 23° in 0.86 sec (standard deviation = 1.18 sec) [8]. Given the relatively large standard deviation compared with the mean, the 21 and 23° rotations appear to be similar.

Repeating the process of the previous paragraph for a 0.2 μm cell we find that it needs a flagellum greater than 2 μm long to stabilize its rotation to below 90° and a flagellum slightly longer than that of *E. coli* to obtain the same amount of stabilization. For the 0.2 and 1 μm radius bacteria the flagella provide most (>99 and >85%, respectively) of the stabilization against rotation.

If the two different size cells are to have flagella of approximately the same length for the same rotational stabilization, then the synthesis of a flagellum is going to be a much greater portion of the total biosynthetic capacity of the smaller cell. To estimate the amounts of protein in a cell and flagellum we begin by noting that a log phase *E. coli* cell contains about 160 fg of protein [29]. A flagellum is a cylinder about 20 nm in diameter with an internal channel about 7 nm in diameter. This translates to roughly 0.41 fg of protein μm^{-1} of flagellum, so that a 5 μm flagellum is about 1.3% of the total protein in a 1 μm cell. If the same proportion of protein to volume found in *E coli* occurs in the 0.2 μm cell it then contains about 0.53 fg of protein. The 5 μm flagellum needed to stabilize the 0.2 μm cell is then about 390% of the protein found in the cell. A 2 μm flagellum is 150% of the protein in the cell. A flagellum that is sufficiently long to stabilize a small cell against Brownian rotation requires a large investment in protein.

In addition to a large biosynthetic investment, a long flagellum also represents a large energetic investment, as there is more translational drag on a 5 μm flagellum than there is on a 0.2 μm cell, about 4.2×10^{-8} versus 1.2×10^{-8} dynes. This difference of 3.5 times increases linearly as the flagellum becomes longer. This indicates that the value of 6×10^3 glucose molecules sec^{-1} found at the end of the Results section must be at least doubled to account for the presence of flagella.

The uptake of 6×10^3 glucose molecules sec^{-1} is only 0.6% of the potential uptake. This percentage is consistent with previous work [18, 19]. The percentage can be increased by increasing receptor affinity and abundance. The affinity of the system was already high [4]. In studying receptor uptake, Berg

and Purcell [9] showed that the increase in uptake slowed as the receptor number increased beyond the ratio of the cell radius to the receptor radius. The optimum number of receptors was approximately equal to the ratio of the cell radius to the receptor radius. For the 0.2 μm radii cell considered here that number is 400. The total number of receptors on a cell is about 20 as calculated (not shown) from Berg and Purcell [9] for uptake as a function of receptor abundance and cell size. To increase receptor number by a factor of 10 or 20 to reach near optimum or optimum uptake may reduce the number of compounds a cell can take up, and more importantly requires increased biosynthesis, which in a nutrient limited environment may be prohibitive.

The conclusion here is that high speed motility is necessary for the small cells of the marine environment to be chemotactic, but that such taxis is energetically and biosynthetically expensive. Circumventing the cost of being small is difficult. Slowing down is an effective strategy only if a cell can increase its size and thus reduce Brownian rotation. Internal energy stores allow a cell to move for few minutes, but only if store is spent only on movement. Lengthening flagella to stabilize the cell against rotation results in greater than 99% of cell protein being in the flagella, in a large drag on the cell, and in loss of movement when the cell turns on the motor while the flagella remain stationary. Increasing molecular uptake appears promising, but conflicts with existing data and is biosynthetically expensive. Work on a cultured marine *Vibrio* indicates motility in a starving population decreased by 95% in one day and that the chemotactic response of this population differed from normal cells [25].

The size of a bacterium or size distribution of a population probably provides information about their strategy for obtaining nutrients. Bacteria with radii much less than say about 0.75 μm (Fig. 1) may rely on minimizing their size and so maximizing their Brownian diffusivity. These small bacteria would be adapted to low nutrient environments, where volumes of concentrated nutrients were seldom encountered. Their higher diffusivity would increase the rate at which they contacted large macromolecules and minimize the amount of material required to make a new cell. They would become motile only in response to a strong environmental signal. Motile cells with radii larger than about 0.75 μm would be adapted for encountering and responding to concentrated patches of nutrients. If cell volume is limited by resource limitation, the effects of Brownian motion on motile cells could be reduced 50% if the volume was rod-shaped. Drag and hence cost might also be reduced by lubricating surface polymers on bacteria, but there is currently no evidence for such polymers, and their influence on rotational motion would be unknown.

The overall result of this analysis is that it is more expensive for small bacteria to be chemotactic than for large bacteria. This seems counter-intuitive, but can be made intuitive if the reader realizes that each cell pays a price for taxis, but that small cells pay an additional price to compensate for Brownian motion.

For small bacteria in marine environments, nutrient concentrations are orders of magnitude lower than in motility media, and the increased influence of Brownian motion on small cells means they must increase speed to travel any distance in a straight line. These two factors indicate that, unlike the situation for enteric bacteria, the energetic costs to marine bacteria must be weighed against the benefits. Determination of whether marine bacteria are

usually motile or whether they diffuse awaits insight into the motility characteristics of natural assemblages of marine bacteria.

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References

1. Adler J (1966) Chemotaxis in bacteria. Science 153:708–716
2. Adler J (1969) Chemoreceptors in bacteria. Science 166:1588–1597
3. Alldredge AL, Cohen Y (1987) Can microscale chemical patches persist in the sea? Microelectrode study of marine snow, fecal pellets. Science 235:689–691
4. Azam F, Hodson RE (1981) Multiphasic kinetics for D-glucose uptake by assemblages of natural marine bacteria. Mar Ecol Prog Ser 6:273–222
5. Azam F, Ammerman JW (1984) Cycling of organic matter by bacterioplankton in pelagic marine ecosystems: Microenvironmental considerations. In: Fasham MJR (ed) Flows of energy and materials in marine ecosystems. Plenum, New York, pp 345–360
6. Bell W, Mitchell R (1972) Chemotactic and growth responses of marine bacteria to algal extracellular products. Biol Bull 143:265–277
7. Berg HC (1983) Random walks in biology. Princeton University Press, Princeton, NJ
8. Berg HC, Brown DA (1972) Chemotaxis in *Escherichia coli* analysed by three-dimensional tracking. Nature 239:500–504
9. Berg HC, Purcell EM (1977) Physics of chemoreceptors. Biophys J 20:193–219
10. Berg HC, Turner L (1979) Movement of microorganisms in viscous environments. Nature 278:349–351
11. Dalquist FW, Lovely PS, Koshland DE Jr (1972) Quantitative analysis of bacterial migration in chemotaxis. Nat New Biol 236:120–122
12. Degens ET, Reuter JH, Shaw KNF (1964) Biochemical compounds in offshore California sediments and sea waters. Geochim Cosmochim Acta 28:45–66
13. Ferguson RL, Buckley EN, Palumbo AV (1984) Response of bacterioplankton to differential filtration and confinement. Appl Environ Microbiol 47:49–55
14. Fuhrman JA, Azam F (1982) Thymidine incorporation as a measure of heterotrophic bacterioplanktonic production in marine surface waters: Evaluation and field results. Mar Biol 66: 109–120
15. Fuhrman JA, Ferguson RL (1986) Nanomolar concentrations and rapid turnover of dissolved free amino acids in seawater: Agreement between chemical and microbiological measurements. Mar Ecol Prog Ser 33:237–242
16. Jackson GA (1987) Simulating chemosensory responses of marine microorganisms. Limnol Oceanogr 32:1253–1266
17. Jackson GA (1989) Simulation of bacterial attraction and adhesion to falling particles. Limnol Oceanogr 34:514–530
18. Koch AL (1971) The adaptive responses of *Escherichia coli* to a feast and famine existence. Adv Microb Physiol 6:147–217
19. Koch AL, Wang CH (1982) How close to the theoretical diffusion limit do bacterial uptake systems function? Arch Microbiol 131:36–42
20. Lee S, Fuhrman JA (1987) Relationships between biovolume and biomass of naturally derived marine bacterioplankton. Appl Environ Microbiol 53:1298–1303
21. Lowe G, Meister M, Berg HC (1987) Rapid rotation of flagellar bundles in swimming bacteria. Nature 325:637–640
22. Maeda M, Taga N (1983) Comparison of cell size of bacteria from four marine localities. La Mer 21:207–210
23. Macnab RM (1987) Motility and chemotaxis. In: Neidhardt FC, Ingraham JL, Low KB, Magasanik B, Schaechter M, Umbarger HE (ed) *Escherichia coli* and *Salmonella typhimurium*:

Cellular and molecular biology, Vol. 1. American Society for Microbiology, Washington, DC, pp 732–759
24. Macnab RM, Koshland DE (1972) The gradient-sensing mechanism in bacterial chemotaxis. Proc Natl Acad Sci USA 69:2509–2512
25. Malmcrona-Friberg K, Goodman A, Kjelleberg S (1990) Chemotactic responses of marine *Vibrio* sp. strain S14 (CCUG 15956) to low-molecular-weight substances under starvation and recovery conditions. Appl Environ Microbiol 56:3699–3704
26. Mitchell JG, Okubo A, Fuhrman JA (1985) Microzones surrounding phytoplankton form the basis for a stratified marine microbial ecosystem. Nature 316:58–59
27. Mitchell JG, Martinez-Alonso M, Lalucat J, Esteve I, Brown S (1991) Velocity changes, long runs, and reversals in the *Chromatium minus* swimming response. J Bacteriol 173:997–1003
28. Mopper K, Dawson R, Liebezeit G, Ittekkot V (1980) The monosaccharide spectra of natural water. Mar Chem 10:55–66
29. Neidhardt FC (1987) Chemical composition of *Escherichia coli*. In: Neidhardt FC, Ingraham JL, Low KB, Magasanik B, Schaechter M, Umbarger HE (ed) *Escherichia coli* and *Salmonella typhimurium*: Cellular and molecular biology, Vol. 1. American Society for Microbiology, Washington, DC, pp 3–6
30. Purcell EM (1977) Life at low Reynolds number. Am J Physiol 45:3–10
31. Segall JE, Manson MD, Berg HC (1982) Signal processing times in bacterial chemotaxis. Nature 296:855–857
32. Vogel S (1981) Life in moving fluids: The physical biology of flow. Princeton University Press, Princeton, NJ
33. Werner R (1983) Essentials of modern biochemistry. Jones and Bartlett, Boston