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REVIEW

Microbial Behavior in a Heterogeneous World

Tom Fenchel

Most microorganisms are motile during at least part of their life cycle, because they need to find optimal conditions in a patchy world. The sheer volume of microorganisms in the biosphere means that their motile sensory behavior also contributes to the global transformation and cycling of matter. How microorganisms move and how they orient themselves using environmental cues are integral to understanding the complex structure and function of microbial communities, but although motility in response to external stimuli was first described more than 120 years ago, understanding of the cellular and molecular mechanisms involved has only been achieved more recently.

All motile species of microorganism respond to different kinds of chemical stimuli. Many also respond to light intensity and to mechanical stimuli, and a few even orient themselves in magnetic fields or in relation to the force of gravity (*1–5*).

Microorganisms swim using flagella and move on surfaces by gliding or by amoeboid movement. They may respond directly to ambient conditions or, more frequently, to temporal changes in stimulus intensity. Although microorganisms are too small to sense the direction of a chemical gradient directly, they can sense a change in intensity or concentration over time, because they have a short term "memory" with a time constant of 0.5 to 1 s (*6*). Cells respond to temporal changes in stimulus intensity by changing swimming direction or velocity. If, for example, changes in swimming direction are more frequent when an organism moves away from an attractant than when it swims toward it, the result is a biased random walk leading the organism toward the source of the attractant (*6*). Larger eukaryotic microorganisms can use greater precision in swimming to approach the source of a chemical attractant more directly, but essentially their orientation is also based on temporal gradient sensing (*7*). The small size and low swimming velocities of microorganisms mean that they live at low Reynolds numbers; that is, under conditions in which viscous forces dominate and molecular diffusion of solutes is often more important than advective transport (*8*).

The adaptive significance of particular types of sensory motile behaviors appears obvious in many cases. Nevertheless, the role of such behavior in natural habitats is only now being elucidated in detail, with the recognition that microbial communities are spatially and temporally complex. Moreover, in natural habitats, different physiological types of microorganisms closely interact, hence the insights derived from the behavior of pure cultures are often of limited relevance. Microorganisms respond to microscopic spatial and temporal heterogeneity, while simultaneously creating spatial heterogeneity resulting from the output of their own metabolic activities.

Recent progress in describing natural microbial communities stems from methodological developments, including the use of microsensors that can map chemical heterogeneity at a fine spatial scale, improvements in microscopy, in situ fluorescent treatment that labels particular microbial species or discloses their physiological state, and theoretical modeling. Together, these efforts have revealed microbial communities that may be as complex and intriguing as coral reefs and rainforests.

Chemotaxis in the Turbulent Water Column

Suspended motile organotrophic bacteria respond rapidly to point sources of dissolved low-molecular-weight organic matter (Fig. 1). These point sources may arise when protozoan or algal cells lyse as a result of viral attack or predation. Concentration gradients of dissolved organic molecules form around the lysed cell, and bacteria located in the surrounding few microliters accumulate within minutes. Because the dissolved substances eventually disappear by diffusion or are consumed by the bacteria, such patches of organic matter are short-lived (5 to 10 min), and eventually the bacteria redistribute. Such events can be modeled theoretically, using known values for diffusion coefficients and parameters for bacterial motile behavior.

Intuitively, it seems that concentration gradients could not develop in an oceanic water column that is exposed to turbulent mixing; however, the effect of turbulence vanishes at the small spatial scales at which these gradients develop. Thus, below the Kolmogorov minimum length scale, turbulence is replaced by linear shear caused by viscous forces. Depending on the rate of wind-driven energy dissipation, the range of the Kolmogorov minimum scale is between 0.6 and 3.5 cm, corresponding to rough and calm seas, respectively, and the shear strength ranges from 0.5 to 0.005 s^{-1} (*9*). In steady continuous shear, an initially spherical solute distribution (such as that arising from a point source) will be drawn into ellipsoid or disc-shaped distributions. The distortion caused

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by the effect of shear on a solute concentration distribution is difficult to predict, because shear is an intermittent phenomenon; its strength and direction change over time, and periods of relative calm will be punctuated by shorter bursts of more intense motion. It is likely that the time interval for changes in shear strength and direction is inversely proportional to shear strength and falls within 2 to 200 s. At length (L) scales below the Kolmogorov scale, the effect of shear diminishes, and at a scale $L < [D/E]^{1/2}$, where D is the diffusion coefficient of the solute and E is average shear strength, molecular diffusion dominates over advective transport; for $D \approx 10^{-5}$ cm^2 s^{-1} (typical for low-molecular-weight compounds), L will be within the range of 50 to 500 μm (*10*). Direct observation of bacterial accumulations around point sources of organic matter is probably impossible in turbulent water, but modeling shows that even in rough water, motile bacteria can still take advantage of point sources by using chemosensory motile behavior (*11*). Similar modeling has shown that bacteria may also be attracted to and use plumes of dissolved organic matter formed in the wake of sinking organic particles (*12*).

The water column of the open sea typically contains about 10^6 bacteria per milliliter as determined by direct counts, although probably not all are metabolically active or even viable. Most of these bacteria depend on dissolved low-molecular-weight organic matter occuring at very low concentrations, and then the rate of bacterial uptake is almost linearly proportional to concentration. Reasonable assumptions about the occurrence of such point sources in the water column indicate that motile chemosensory behavior may increase the rate of mineralization in the water column twofold, relative to the situation in which bacteria experience only the average bulk concentration of dissolved organic molecules. Bacterial chemotaxis thus affects the oceanic carbon cycle (*11*). The fact that a large fraction of plankton bacteria (20 to 70%, possibly representing the entire fraction of metabolically active cells) are motile (*13*, *14*) also suggests an adaptive role for chemotaxis in a heterogeneous environment.

Microbial Communities Associated with Surfaces

Suspended colloidal particles, or "marine snow," represent another aspect of spatial heterogeneity in the water column. The particles are composed of microbial mucus combining organic and inorganic particles such as diatom frustules, and ranging in size from less than a micrometer to several centimeters. The interest in marine snow has arisen because it offers a mechanism by which organic matter is transported from the photic zone of the water column to the sea bed. These particles are also foci of microbial activity and mineralization of organic matter in the water column, because they contain densities of bacteria and protists 100 to 2000 times greater than in the surrounding water (*15–17*). The microbial biota associated with suspended particles is distinct from that of the surrounding water, because the particles are dominated by adherent species belonging to particular taxonomic groups (*16*, *18*). As a result of a combination of chemosensory behavior, contact adhesion, and subsequent growth, complex microbial communities develop within a few days (*13*).

The microbial communities that form biofilms and microbial mats on solid surfaces and in sediments are even more complex than those of the plankton. Part of this complexity derives from the steep diffusion gradients of nutrients and metabolites and the rapid attenuation of light within the volume of the community structure. High densities of microorganisms will intensify intra- and interspecific interactions to influence quorum sensing and motility. Hence, spatial heterogeneity may result from differential growth of individual cells or of microcolonies under a local range of ambient environmental conditions.

Communities, such as those found in microbial mats and sediments have been described as a one-dimensional vertical zonation caused by the successive depletion of electron acceptors for respiratory metabolism. Thus, oxygen is typically depleted within millimeters below the surface by aerobic respirers and diffusional limitation of oxygen transport from above. Beneath the oxic zone, anaerobic metabolism depends on either fermentation or on respiration based on other, energetically less efficient, electron acceptors. For example, moving downward in a sediment, electron acceptors are exhausted in sequence from NO_3^- to Mn^{4+} to Fe^{3+} to SO_4^{2-}, and finally, when sulfate is depleted, methanogenesis, based on H_2 and CO_2, predominates. In shallow-water sediments and mats, the depth distribution of the different electron acceptor zones is not constant but varies diurnally. During the day, the oxic zone expands downward, owing to photosynthesis, and during the night, the anaerobic and reducing zone migrates upward again. However, this picture is an oversimplification because sediment structure is rarely uniform (*19*) (Fig. 2). The irrigated burrows of invertebrates create oxygenated microzones that penetrate anaerobic zones. There are also "hot spots" of photosynthetic or respiratory activity, each surrounded by zones of different types of microbial activity. The surface of sediments is rarely completely smooth, and small mounds or depressions lead to complex patterns of advective water flow several millimeters beneath the surface of porous sediments (*20*).

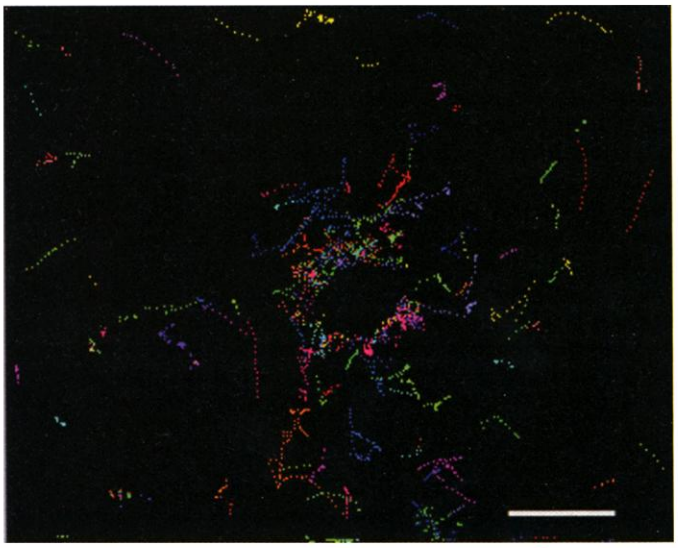

Fig. 1. Swimming tracks of bacteria around a lysed ciliate (center, not visible because only moving objects are included) in a sample of seawater 2 min after lysis and recorded for 4 s. The scale bar is 50 μm, and the time interval between the dots is 40 ms. The video recording was made with dark-field illumination, and the data were transferred to a computer for analysis of swimming parameters, as described in (*11*).

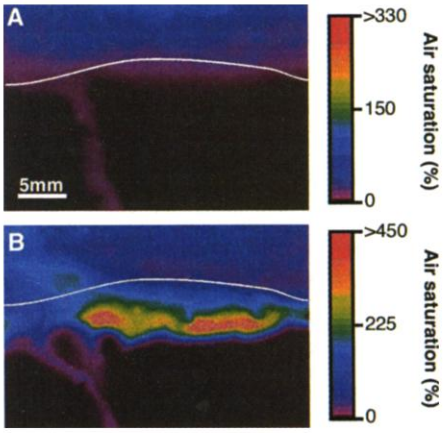

Fig. 2. The in situ oxygen tension (as percent of atmospheric saturation) in a vertical section of the upper 2 cm of a shallow (1 m) sandy marine sediment during the night (**A**) and at noon (**B**), recorded as described in (*39*). The white line indicates the approximate position of the sediment surface. The transect was close to a burrow of the polychaete *Nereis diversicolor* (left side), and patches of especially intense photosynthesis are seen in the daytime record. Extremely steep oxygen gradients are also shown, ranging from approximately 300% supersaturation to anoxia over a distance of only 2 mm.

Motile Responses in Oxygen Gradients

All motile microorganisms studied so far show a chemosensory response to oxygen, often displaying a very narrow range of preferred oxygen tensions between 2 to 20% of atmospheric saturation (*21*, *22*) (Fig. 3). Of course, oxygen is a repellent at all concentrations for most obligate anaerobes, although some prefer a very low oxygen tension rather than absolute anoxia. The adaptive nature of this is probably multifaceted: Microaerophilic preferences mean that the organisms can dispense with some of the energetic costs of defenses against oxygen toxicity; and for some phagotrophic protozoa, a given oxygen tension may be a cue for the presence of prey organisms. Furthermore, differential oxygen preferences will lead to niche separation of otherwise competing species.

The large colorless sulfur bacteria offer striking examples of responses to oxygen tension. These organisms inhabit the transition zone between aerobic and anaerobic regions. They make a living from the oxidation of reduced sulfur compounds (such as sulfide and elemental sulfur) with oxygen or nitrate and often form a macroscopically visible white film on the surface of organically rich sediments. Their preference for an oxygen tension of about 4% atmospheric saturation concentrates the cells in a narrow zone where sulfide and oxygen are simultaneously available. As they consume both oxygen and H_2S, the organisms themselves create steep concentration gradients of these compounds (*23*). The large filamentous *Beggiatoa* continuously slide up and down within the sediments, turning whenever oxygen concentration becomes intolerable (*24*). Some species store NO_3^- in their vacuoles when they are at the surface of the sediment, transporting it down into the sulfide zone, where the nitrate is used for sulfide oxidation (*25*).

Similarly, the large spherical *Thiovulum majus*, the fastest swimming bacterium known, orients itself in oxygen gradients by helical klinotaxis, a mechanism otherwise known only in eukaryotic microorganisms (*26*). Under optimal conditions, these bacteria attach to solid surfaces by a stalk of mucus, and as their flagella remain active, they pump oxygenated water toward them from above. Below the bacterial film, the oxygenated water is mixed with anaerobic sulfide-containing water. This bacterial film characteristically consists of a single layer of regularly spaced cells cells that are anchored 50 to 100 μm above the sediment surface by their stalks. The film is punctured by openings allowing the return flow of anoxic water from below. This spatial self-organization is the only example known so far of bacteria that overcome diffusion-limited substrate uptake by generating advective water flow (*27*).

Complexity of Microbial Behavior

Microbial responses to particular environmental cues are not stereotypical, and they are often modified by other stimuli or by the physiological state of the cells. For example, photosynthetic purple bacteria respond to sulfide, oxygen, and light. In light, they prefer anaerobic conditions and perform anoxygenic photosynthesis, but in the dark they seek microaerobic conditions, where their energy metabolism is based on aerobic respiration (*28*).

Syntrophic interactions involve two or more different physiological types (species) of bacteria that are interdependent, in that a metabolite from one species forms a substrate for another species, and vice versa. The classical example comes from fermenting bacteria that produce hydrogen as a metabolite, and this is used by methanogens that oxidize it to CH_4, with CO_2 as an electron acceptor. The complete fermentation of carbohydrates to acetate and H_2 requires a low ambient hydrogen tension for the process to be thermodynamically possible. Hence, hydrogen consumption by methanogens drives the metabolism of the fermenting bacteria, resulting in mutual interdependence (*29*). This type of mutualistic interaction requires close physical contact between the partners, because the transfer of solutes occurs by molecular diffusion. In colonies of syntrophic pairs, the partners are arranged in specific geometric configurations, so that cells belonging to one species have neighbors belonging to the other species. *Chlorochromatium* is a compound organism consisting of a central motile heterotrophic bacterium, surrounded by green photosynthetic sulfur bacteria (Fig. 4). The green sulfur bacteria use sulfide as an electron donor and produce elemental sulfur. Until recently, it was believed that the central bacterium oxidizes organic matter (probably at least in part derived from the photosynthetic bacteria), using the elemental sulfur as an oxidant, and recycles sulfide to the surrounding green bacteria (*30*). Recent findings (*31*) however, have questioned whether the central bacterium is a sulfur reducer, but it has been established that it receives organic matter from the photosynthetic symbionts; these in turn probably profit from the motility of the host cell (green sulfur bacteria are otherwise not motile). Under all circumstances, the assembly of such syntrophic consortia must involve chemosensory behavior, but the details have yet to be worked out.

Many eukaryotic microorganisms harbor endosymbiotic microorganisms, and many of these associations are based on syntrophic interactions that have profound effects on host behavior. For example, because of their photosynthetic requirements, endosymbiotic green algae in ciliates have been shown to

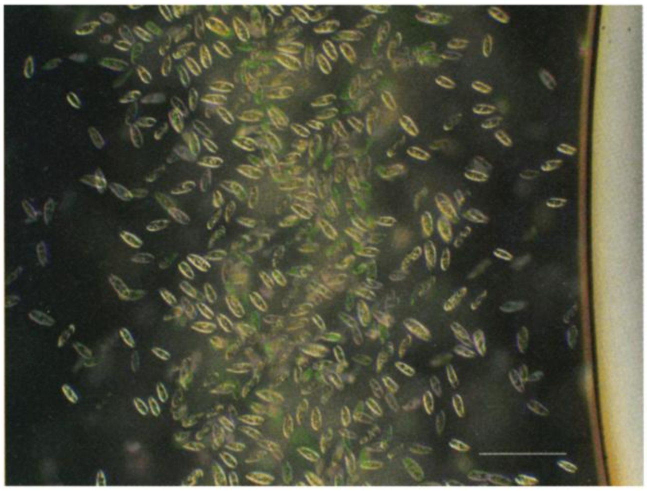

Fig. 3. The ciliate *Uronema nigricans* forming a band around an air bubble injected in anoxic seawater. At the meniscus (at right), the oxygen tension is atmospheric saturation and a diffusion gradient forms around the bubble. This gradient is maintained at a steady state owing to the respiration of the ciliates. The species has a preference for an oxygen tension of 10% atmospheric saturation. Scale bar, 100 μm.

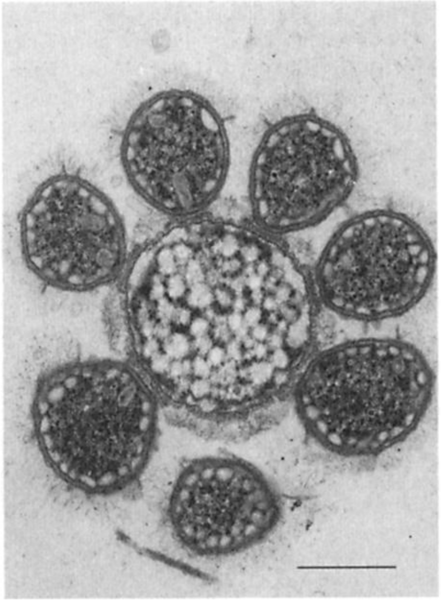

Fig. 4. A transverse section of *Chlorochromatium* in the electron microscope. The central cell is an anaerobic heterotroph, and the seven peripheral cells are green sulfur bacteria showing their photosynthetic vesicles in the cell periphery. Scale bar, 0.5 μm.

control the host's motile behavior in relation to light intensity and ambient oxygen tension; this control is probably mediated by the rate of oxygen production by the symbionts (*32*).

The functional significance of syntrophic interactions is only understood in relatively few cases. For instance, sheaths of filamentous cyanobacteria are often covered by attached heterotrophic bacteria, but attempts to grow the cyanobacteria axenically (in the absence of any other microbial species) have so far failed. So the association must be vital to the cyanobacteria, but the nature of the interaction is unknown (*33*). A recent study has shown that in a mixed culture of two species of organotrophic bacteria (*Pseudomonas* sp. and *Burkholderia* sp.), each grew in separate species-specific colonies when provided with a certain organic substrate (citrate). But when citrate was replaced with 3-chlorobiphenyl, the cells only grew in mixed colonies, because the *Pseudomonas* cannot use 3-chlorobiphenyl directly but it can use a metabolite of the other species, thus engaging in a sort of syntrophic interaction (*34*).

The discovery that some bacterial species communicate by extracellular signals adds further complexity to the study of microbial motile behavior. Thus, in response to increased cell density (quorum sensing) or diminishing substrate supplies, bacteria may excrete signal molecules that induce swarming or change in colony morphology (*35*, *36*). The role of these types of mechanisms remains to be studied in natural communities.

The study of microbial motile behavior will lead to a deeper understanding of how microbial communities are assembled in nature. A particularly exciting aspect for the near future is the meeting of ecology and molecular biology, linking gene expression directly with the biological and the nonbiological environment. Such attempts have already been initiated with laboratory systems (*37*, *38*); transferring these techniques to the study of natural systems will not only provide increased ecological insight but also serve to show the unity of biological research.

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REVIEW

Geomicrobiology: How Molecular-Scale Interactions Underpin Biogeochemical Systems

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Microorganisms populate every habitable environment on Earth and, through their metabolic activity, affect the chemistry and physical properties of their surroundings. They have done this for billions of years. Over the past decade, genetic, biochemical, and genomic approaches have allowed us to document the diversity of microbial life in geologic systems without cultivation, as well as to begin to elucidate their function. With expansion of culture-independent analyses of microbial communities, it will be possible to quantify gene activity at the species level. Genome-enabled biogeochemical modeling may provide an opportunity to determine how communities function, and how they shape and are shaped by their environments.

Life and Earth have coevolved since their beginning. So intimate has this relation been that if one seeks to discover a part of Earth that has not been fundamentally affected by life, it may be necessary to penetrate hundreds of kilometers into the mantle. Yet even at these great depths, the chemistry of the mantle may have been modified by the slow but steady subduction of sediments with elemental and isotopic features arising from biological activity. Although multicellular organisms such as fungi, algae, higher plants, and humans have made a significant mark on Earth's geochemistry, averaged over geologic time, it is clear that the most important geochemical agents by far have been unicellular microorganisms (e.g., *Bacteria*, *Archaea*, and single-celled *Eucarya*).

Microbes have changed Earth in a number of ways. They have altered the chemistry of the atmosphere via oxygenic photosynthesis, nitrogen fixation, and carbon sequestration (*1*); they have modified the compositions of oceans, rivers, and pore fluids through control of mineral weathering rates or by inducing mineral precipitation; they have changed the speciation of metals and metalloids in water, soils, and sediments by releasing complexing agents and by enzymatically catalyzing redox reactions; they have shaped the physical world by binding sediments, precipitating ore deposits, and weathering rocks; and they have sustained communities of higher organisms through primary production and by remineralizing organic carbon. And most remarkably, they perform these functions in