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Science **338**, 628 (2012);
DOI: 10.1126/science.1208929

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Marine bacteria influence Earth's environmental dynamics in fundamental ways by controlling the biogeochemistry and productivity of the oceans. These large-scale consequences result from the combined effect of countless interactions occurring at the level of the individual cells. At these small scales, the ocean is surprisingly heterogeneous, and microbes experience an environment of pervasive and dynamic chemical and physical gradients. Many species actively exploit this heterogeneity, while others rely on gradient-independent adaptations. This is an exciting time to explore this frontier of oceanography, but understanding microbial behavior and competition in the context of the water column's microarchitecture calls for new ecological frameworks, such as a microbial optimal foraging theory, to determine the relevant trade-offs and global consequences of microbial life in a sea of gradients.

Twenty years ago much of microbial oceanography was based on the assumption that molecules and organisms are randomly distributed, with little regard for gradients and behavioral responses (1). There is now abundant evidence that nutrients are not homogeneously distributed at the scales relevant to the microorganisms and instead frequently arise as microscale hot spots. Many bacteria exploit heterogeneity by swimming toward the epicenter of hot spots, whereas others survive in low-concentration, uniform background conditions.

Although tools to interrogate the behavior of marine microbes at the level of single cells and their microenvironment have begun to be developed, the conceptual frameworks needed to evaluate the trade-offs and ecosystem implications of life in microscale gradients lag behind. Integrating microscale observations with ecological frameworks will shed light on important unexplored questions in microbial oceanography. What are the effects of gradients on microbial diversity in the ocean? How do they affect productivity? Do the consequences of heterogeneity simply average out, justifying mean-field descriptions based on bulk concentrations and a neglect of behavior, or do microscale gradients affect the rates and fluxes of biogeochemical transformation? This Review describes the nature and prevalence of microscale gradients in the ocean, the response of microbes to these gradients, and the putative mechanisms by which these processes can affect the marine ecosystem at a global scale.

At What Scales Do Marine Microbes Interact with Their Environment?

To understand the behavior of an organism, it must be studied in relation to its immediate environment. Marine microorganisms affect large-scale processes in the sea, including the cycling of most elements, the rates and fate of primary production, and the generation of climatically active gases (2), yet they live and interact with the ocean at the microscale. In terms of relative scale, environmental conditions at tens of meters resolution are to a microbe what the mean world temperature is to an African lion: a useful metric for global trends, but hardly a mechanistic ecological predictor.

How large, then, is a microbial microenvironment in the ocean? Rather than being a fixed volume (3), it depends on behavior and time, as simple calculations exemplify. For a nonmotile bacterium (or archaeon), cell size (~0.4- to 2-μm diameter) defines the microenvironment. For example, nutrient uptake occurs from a small region surrounding the organism, the diffusion boundary layer, which spans a few cell diameters. There is little motion of the cell relative to the surrounding water, with Brownian diffusion allowing a 0.4-μm–diameter cell to explore 45 pl of seawater (a ~35-μm cube) in 10 min and 80 nl (a ~430-μm cube) in a day.

In contrast, the microenvironment of a swimming bacterium is largely defined by its motility range. One can calculate that randomly swimming at 50 μm/s enables a bacterium to experience 0.5 μl (a ~0.8-mm cube) of new water every 10 min and 0.8 ml (a ~1 cm cube) every day. Chemotaxis (the ability to sense chemical gradients and direct motility accordingly) further increases the distance a microbe can traverse: a chemotactic velocity (the directional component of swimming) of 10 μm/s results in a net displacement of 6 mm in 10 min.

Microbial microenvironments can thus be large compared with cell size but are still tiny relative to most oceanographic sampling methods. With rare exceptions, these volumes remain difficult to interrogate in situ, owing to the small size and intermittency of microenvironments and the minuscule amount of matter they contain. We must gain better access to the marine microscale, in terms of tools and conceptual frameworks, if we are to understand the consequences of resource heterogeneity and microbial behavior on diversity, productivity, and biogeochemistry.

How Heterogeneous Is the Ocean at the Microscale?

It has long been recognized that the water column is dotted with copious sources of microscale heterogeneity (Fig. 1). A ubiquitous case is the "phycosphere," the region surrounding a phytoplankton cell, which harbors gradients of dissolved organic matter [DOM; operationally defined as the organic material <0.7 μm in size (2)] and oxygen that attract heterotrophic bacteria (4, 5). This attraction can result in diverse ecological interactions between bacteria and algae, from symbiosis to parasitism, and can increase the fraction of primary production used by bacteria (6). Equally widespread are marine snow particles, aggregates that also contain gradients of DOM and oxygen (7) and emanate intense DOM plumes as they sink (8, 9). The particles and their plumes can attract and become growth hot spots for bacteria (9, 10). Strong gradients are further created by excretions from larger organisms, cell lysis, and sloppy feeding. These sources of heterogeneity, along with a multitude of particle types ranging from colloids to fecal pellets to exopolymers, can vary in size from micrometers to centimeters, and harbor resource concentrations orders of magnitude above background levels.

These processes have led to the view that even a milliliter of seawater is far from homogeneous (3). I suggest that microscale gradients are in fact considerably more pervasive than even these sources of heterogeneity indicate, for three reasons. First, the majority of inputs of microbial resources are heterogeneous at microbial scales: 10- to 1000-μm oil droplets originating from spills or natural seeps, 50- to 5000-μm gas bubbles released from natural vents or injected by breaking waves, sediment grains resuspended by currents, and dust particles of aeolian origin are all constituents of large-scale events that for marine microorganisms resolve into a patchy landscape peppered with discrete resources and microscale gradients.

Second, turbulence converts macroheterogeneity into microheterogeneity. In the process of mixing a solute such as DOM, turbulent whirls stir the solute into ever-finer sheets and filaments (see Box 1 and associated figure). This stretching and folding continues down to a scale below which molecular diffusion dissipates gradients to truly mix the solute. For typical marine turbulence levels, this scale, known as the Batchelor scale, ranges from 30 to 300 μm. Thus, irrespective of the size of the DOM source, turbulence produces a rich fabric of gradients at the scale of microbial microenvironments.

Third, chemical gradients are compounded by physical gradients. Microscale viscosity gradients can develop inside and around particles, but also

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in the bulk medium, where colloids and mucus sheets can form tangled polymer webs (*3*). Gradients in fluid velocity due to turbulent shear can occur at millimeter scales and result in subtle hydrodynamic interactions with cell shape (*11*). Salinity can equally vary on submillimeter scales, owing, for example, to pockets of interstitial fluid carried by porous particles sinking through the water column (*12*).

Likely as a consequence of this heterogeneity, bacteria are also heterogeneously distributed, with recorded variations in cell concentration of up to 20-fold over 10 to 30 mm (*13*). Thus, despite its superficial homogeneous appearance, the water column can have a rich physical, chemical, and biological microarchitecture, not unlike that of environments dominated by surfaces, such as sediments or animal hosts. In the following, I focus on a specific adaptation to this heterogeneity: chemotactic motility.

How Pervasive Are Behavioral Responses to Microscale Gradients?

Chemotactic motility is not only the most conspicuous adaptation to microscale chemical gradients, but also a de facto demonstration of their existence. A subtle distinction is in order: motility alone does not increase microbial nutrient uptake, whereas chemotaxis can. The description of marine bacteria as the "ultimate swimming stomachs" [J. Stern in (*14*)] should not be interpreted in the same manner as whales swimming open-mouthed to catch plankton: The uptake rate of a bacterium while it swims is the same as when it rests, except for very high molecular weight solutes (*15*). In contrast, cells can increase uptake by residing in high-concentration microenvironments, which they find by chemotaxing along gradients. Thus, chemotactic motility is intimately linked to microscale gradients. But how prevalent is motility among marine bacteria?

It contrast to phytoplankton, whose motility is a well-studied, distinguishing trait (e.g., in the competition between diatoms and dinoflagellates), or enteric bacteria, whose chemotaxis is among the best understood cellular processes, bacterial motility and its prevalence have been given less attention in the ocean. On one hand, we know that some numerically abundant organisms, such as *Pelagibacter ubique* of the SAR11 clade, are nonmotile (*16*). On the other hand, direct observation has shown that many marine bacteria are motile (*17*), and the fraction of motile cells can be as high as 20 to 60% (*18*, *19*). Further, metagenomic studies have revealed that genes for motility and chemotaxis can be common in the photic zone (*20*). Nutrient enrichment can elevate the motile fraction from <10 to >50% in 12 hours (*21*), which suggests either a lag time for the activation of motility or the occurrence of a rapid community shift upon episodic resource inputs.

Motility is typically associated with the ability to respond to gradients. Laboratory observations have shown that marine strains are capable of chemotaxing into the DOM plumes emanating from settling particles (*10*), to high phosphate concentrations in phosphate-limited environments (*22*), toward dimethylsulfoniopropionate to associate with algae (*23*, *24*), and toward lysing organisms (*5*) and cyanobacterial exudates (*25*). In a dynamic version of the phycosphere, they can even briefly pursue swimming algae (*26*).

Motility demarcates two evolutionary strategies among marine bacteria. These are broadly aligned with the dichotomy between oligotrophs and copiotrophs. Oligotrophs, such as *P. ubique*, are adapted to life in nutrient-poor conditions. Their minute size (~0.4 μm in diameter) allows them to maximize uptake per unit biomass and to extract nutrients at the minuscule bulk concentrations characteristic of the ocean (*27*). Their streamlined genome lacks many functional and regulatory genes, including those for motility and chemotaxis (*16*); The latter would be vain at any rate, because directed swimming is trounced by Brownian effects for cells <0.6 μm in diameter (*28*). Streamlining also implies poor metabolic plasticity and an inability to exploit high-resource conditions (*29*).

In contrast, copiotrophs are adapted to take advantage of rare, resource-rich conditions: Their abundance of motility and chemotaxis genes, together with fast uptake kinetics, indicate that their success is linked to an ability to exploit microscale gradients (*27*), and their abundance will be a reflection of the texture of the resource landscape. The metabolic flexibility of copiotrophs allows them to adapt rapidly to newly encountered microenvironments (*30*), for example, by disproportionately increasing protease activity upon attachment to particles (*31*), though their size and uptake kinetics would make them less competitive at low resource concentrations.

The numerical abundance of marine bacteria is often dominated by nonmotile oligotrophs, such as members of the SAR11 clade (*29*). However, to assess the importance of copiotrophs relative to oligotrophs—and therefore the importance of microscale gradients—in shaping large-scale ecosystem properties, one must go beyond abundance and consider activity. The relation between abundance and activity in the ocean remains unclear (*32*), but there is evidence that rare taxa have proportionately higher potential growth rates
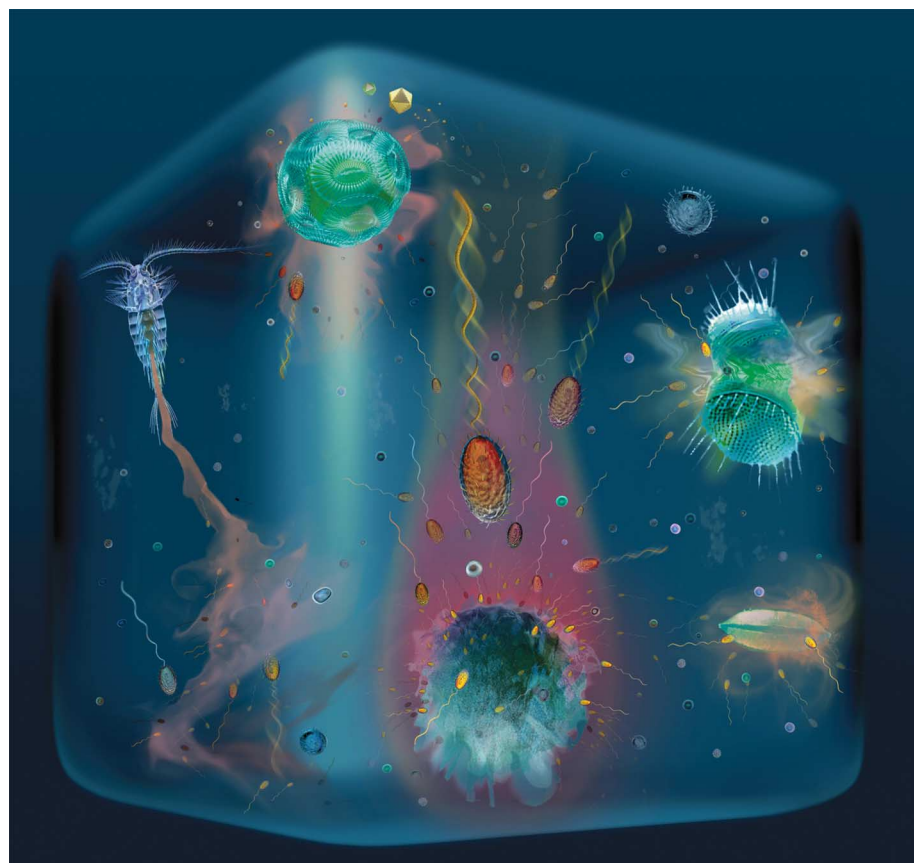

Fig. 1. Marine microbial microenvironments. Disparate processes contribute to make the ocean a sea of gradients, from the vantage point of microorganisms, including DOM exudation by phytoplankton (top), cell lysis events (top right), stationary or sinking detritus and marine snow particles (bottom center), and copepod excretions (left). Marine bacteria adopt one of two broad strategies: They can be motile, propelling themselves with corkscrewlike flagella to exploit microscale gradients, or nonmotile, optimizing uptake of solutes diffusing to them and saving the cost of swimming. [Modified from the cover of *Science*, 5 February 2010, with permission; original image credits: R. Stocker, J. R. Seymour, G. Gorick]

Box 1. The Batchelor scale in the ocean

The shape of a solute patch is affected by two transport processes: diffusion and turbulence. Turbulence stirs the patch into ever-finer filaments. As a filament thins, the associated gradient (the concentration contrast with the background, divided by the filament width) grows. This increases the effect of diffusion, which is proportional to the magnitude of the gradient, in erasing the gradient. There is, hence, a scale where the effects of turbulence and diffusion balance. This scale is the Batchelor scale (54), $(\nu D^2/\varepsilon)^{1/4}$, which in the sea ranges from 30 to 300 μm depending on the turbulent dissipation rate ε, the diffusivity of the solute D, and the kinematic viscosity of seawater, ν.
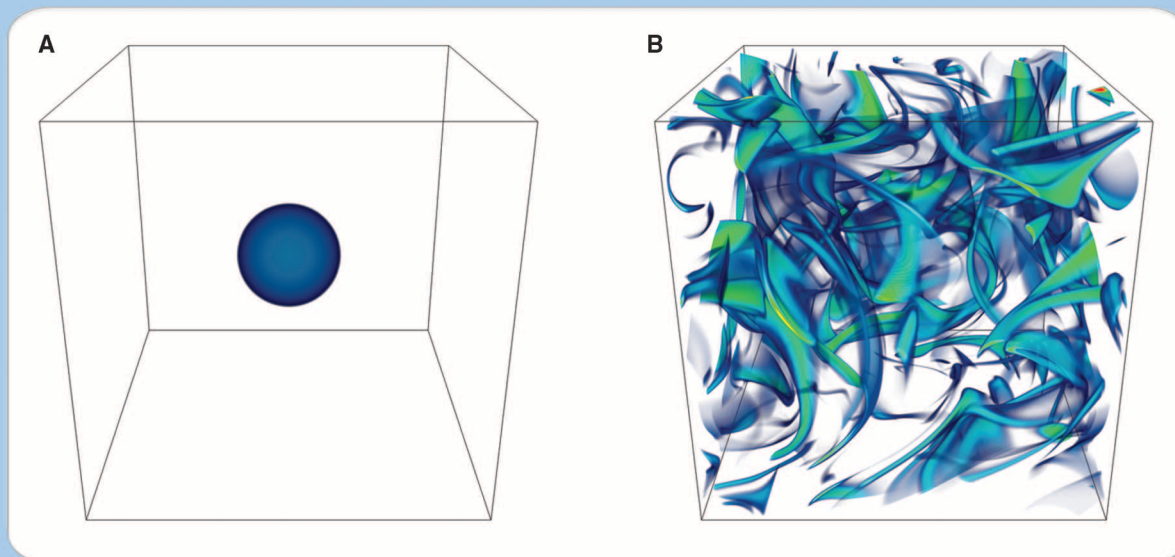
Turbulence stirs chemical resources of any size into a complex web of microscale gradients. Any source of a dissolved substance in the ocean (**A**), even if macroscopic, will produce a tangle of sheets and filaments (**B**). The characteristic scale of the resulting gradients is set by the Batchelor scale. The image on the right is the result of a direct numerical simulation modeling the fate of a centimeter-scale patch exposed to turbulence for 30 s (with a turbulent dissipation rate ε of 10^{-6} W/kg). [Image courtesy of J. R. Taylor]

than abundant taxa (32). Bacteria on particles are less numerous than free-living bacteria, but they are frequently larger and more active (30). In an example from a different aquatic environment, an oligotrophic lake, the large (270 μm³) motile bacterium *Chromatium okenii* was found to be responsible for >40% of total ammonium uptake and >70% of total carbon uptake, despite accounting for only 0.3% of the total cell number (33). In contrast, the small (1.2 μm³) nonmotile *Chlorobium clathratiforme* only contributed 15% to total ammonium uptake and 15% to total carbon uptake, despite having a 100-fold larger numerical abundance and a 10% larger total biovolume compared with *C. okenii*. Geographic distribution also matters: Copiotrophs are most abundant in the coastal ocean, where DOM inputs are greater (34) and impacts on biogeochemistry proportionally larger. Furthermore, the metabolic plasticity of copiotrophs suggests that they are the early responders to biogeochemical perturbations, as evidenced by increases in motility and chemotaxis after drastic events such as algal blooms (19) and nutrient enrichments (21). Whether these higher levels of activity and readiness to respond to change often exhibited by copiotrophs outweigh the numerical dominance of oligotrophs in shaping marine biogeochem-istry remains a fundamental open question in microbial oceanography.

Do Gradients Drive Specific Adaptations Among Marine Microbes?

The abundance of oligotrophs testifies to the stringent trade-offs in the utilization of microscale gradients in the ocean. Because most hot spots are ephemeral, chemotaxis is a race against time, which suggests selection for advanced chemotactic strategies. Evidence for specific adaptations for exploiting microscale gradients includes the discovery of the high swimming speeds of many marine bacteria, whose mean velocities, often exceeding 60 to 80 μm/s (10, 21, 22, 24), dwarf the 15 to 30 μm/s of *Escherichia coli* and allow fast chemotactic responses and large increases in potential nutrient uptakes (10, 24).

Rapid swimming has major energetic implications. The persistent viewpoint that motility is inexpensive for bacteria was developed for slow swimmers (*E. coli*) in nutrient-rich (e.g., enteric) environments (35) and is unlikely to apply in the ocean, where nutrients are orders of magnitude scarcer and the required propulsive power, proportional to speed squared, is more than 10 times as great. A model of competition for a nutrient patch between motile and nonmotile bacteria revealed a trade-off between the additional uptake afforded by swimming toward nutrient-rich filaments (see the Box) and the energetic cost of motility to find and reach filaments (36). Optimal predicted swimming velocities (~60 μm/s) fall within the observed range, which suggests that bioenergetic trade-offs are important in determining adaptations to microscale gradients.

Given the high energetic cost of motility, cells might have evolved adaptive strategies to exploit gradients, for example by activating motility only when the resource landscape justifies it. The question is "Can marine bacteria actively modulate motility, and over what time scales?" Recorded lags of several hours (21) suggest that motility is not tunable over the lifetime of an individual patch (~10 min), but can be resumed after episodic nutrient inputs. Yet, other evidence suggests that motility is highly intermittent at time scales of tens of seconds (19).

Another potentially ocean-specific adaptation is the hybrid swimming pattern of some monotrichous (i.e., having a single flagellum) marine bacteria, such as *Vibrio alginolyticus* and *Pseudoalteromonas haloplanktis*. These bacteria deviate from *E. coli*'s prototypical swimming behavior, alternating reversals in direction with strong reorientations caused by a rapid "flick" of the

flagellum (37). This is likely a strategy that guarantees effective turning, while requiring the synthesis of only a single flagellum, again highlighting that microbial motility in the ocean might be best understood in a cost-benefit framework.

Do Microscale Gradients Affect Species Composition and Diversity?

Gradients can provide a fitness advantage to motile cells. Mathematical models predict that growth rates increase 50% for cells that cluster around nutrient patches (38) and up to 10-fold for those chemotaxing into DOM plumes (9). These estimates are consistent with microfluidic experiments, which revealed a fourfold increase in potential uptake rates for bacteria responding to plumes over those that cannot (10).

Likely as a result of the fitness implications of gradients, microenvironments can affect species

composition. For example, bacteria on particles are taxonomically different from free-living bacteria (39), and laboratory manipulations have shown that the dominant phylotypes change during a diatom bloom (40). Can gradients, i.e., the intricacy of the microscale nutrient landscape, also affect species diversity? Because spatial and temporal gradients in the nutrient landscape represent two formidable dimensions in niche space, it seems plausible that the diversity of motile bacteria is, on average, larger than the diversity of nonmotile bacteria. On the one hand, the high diversity among copiotrophs such as *Vibrios* and the association of clusters of closely related *Vibrionaceae* with distinct microenvironments (41) is in line with this prediction: Could chemotactic motility, widespread among *Vibrios*, have contributed to determine these diversity patterns? On the other hand, it remains difficult to compare

the degree of diversity among clades and thus to determine whether microscale gradients represent a fundamental determinant of diversity and whether the diversity of copiotrophs is in general larger than the diversity of oligotrophs. These questions represent exciting targets for future molecular investigations.

Can Microscale Gradients Affect Ocean Biogeochemistry?

The consequences of microscale gradients on biogeochemical dynamics and productivity are less intuitive. The most naïve interpretation is that microscale interactions simply average out. Several pieces of evidence indicate that this is not the case, but a consistent framework is lacking.

Macroscopic dynamics in patchy environments can differ significantly from mean-field descriptions based on bulk seawater concentrations. For
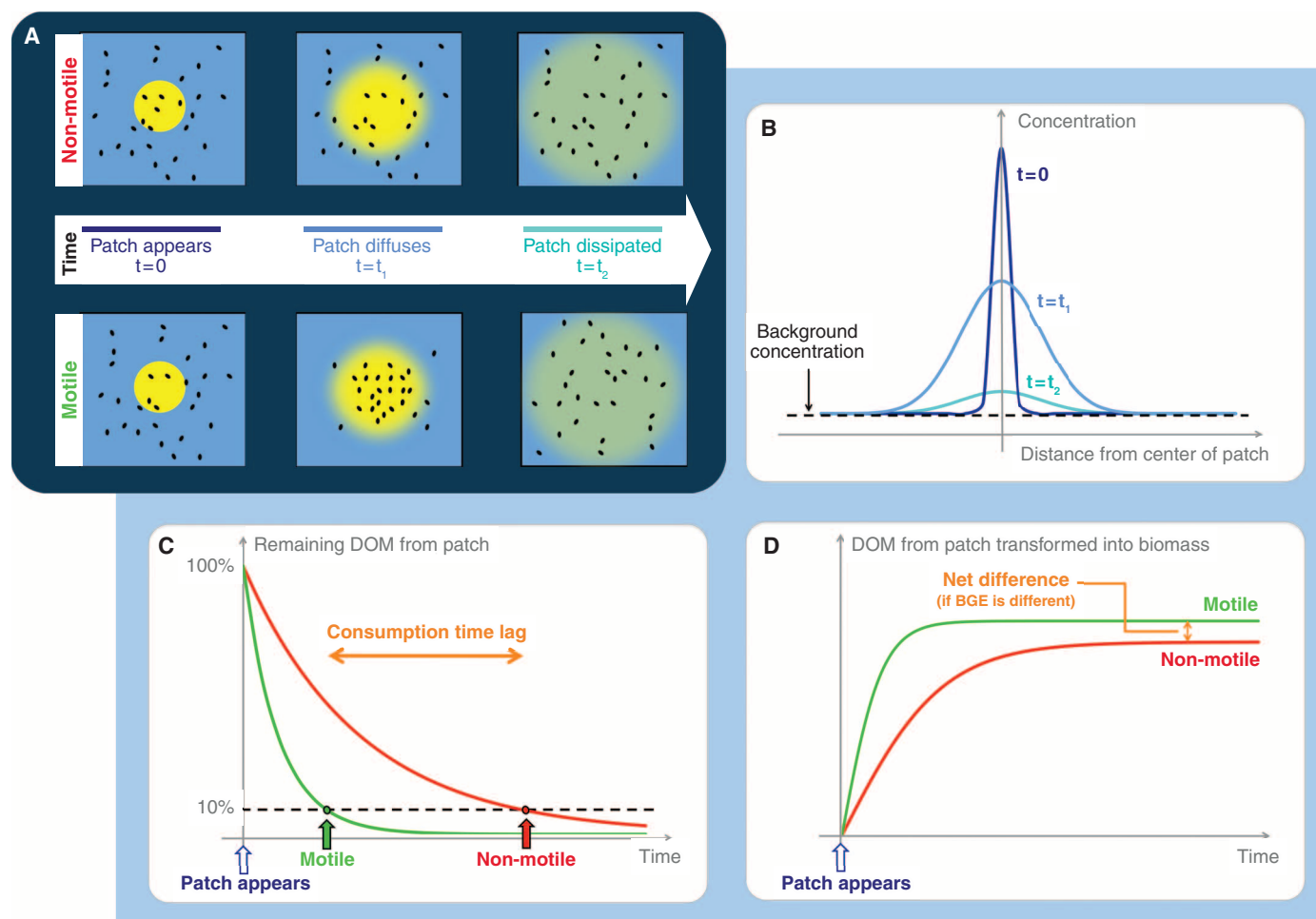

Fig. 2. The fate of the DOM from a patch. In order to understand the consequences of motility and the utilization of microscale gradients, it is useful to consider two scenarios: an ocean of nonmotile bacteria and one of motile (and chemotactic) bacteria. (**A**) A patch of DOM appearing within a suspension of bacteria can attract motile cells, whereas nonmotile cells remain randomly distributed. (A and **B**) DOM eventually diffuses into background concentrations, typically over time scales of minutes. (A and **C**) Chemotaxis into the patch can result in faster DOM consumption by motile bacteria, compared with nonmotile bacteria. Ultimately, however, the entire DOM from the patch is consumed in both cases, unless other processes intervene to reduce the bioavailability of DOM during the short (~minutes) time lag in DOM consumption between nonmotile and motile bacteria (see text). (**D**) Consumption by motile bacteria could increase the fraction of DOM that is transformed into biomass, if motile bacteria have higher BGE than nonmotile bacteria. Differences in BGE would have direct effects on the flow of carbon through the microbial loop and on biogeochemical fluxes and, thus, represent an important target for experimental quantification.

example, bacterial chemotaxis to microscale DOM gradients has been predicted to increase remineralization rates twofold (*42*). For phytoplankton, modeling predicts that productivity is several times larger in heterogeneous than in homogeneous conditions (*43*). Similarly, observations of phytoplankton growth in the face of nondetectable levels of limiting nutrients have been attributed to intermittent nutrient pulses (*44*).

To identify potential effects of microscale gradients on biogeochemical fluxes, it is instructive to consider how a small DOM patch affects bacteria, for nonmotile bacteria and for chemotactic bacteria (Fig. 2A). Only a minuscule fraction of the bacteria will initially find themselves by chance inside the patch, yet typically, most are within 100 to 1000 μm of the next patch (*45*). As the patch diffuses (Fig. 2, A and B), nonmotile cells remain randomly distributed, whereas many motile cells cluster inside the patch within tens of seconds (*5*, *10*, *24*). Does this behavior affect the total amount of DOM transformed into bacterial biomass? We need to consider that the entire DOM from the patch, which diffuses to uniformity within minutes, might ultimately be consumed in both the motile and the nonmotile scenarios, in which case DOM consumption may simply be accelerated if perpetrated by motile bacteria (Fig. 2C). In other words, do responses to microscale gradients purely change the time scale over which DOM is remineralized or also the total amount of DOM that is remineralized?

There are several mechanisms by which differential gradient utilization may affect total amounts, not only time scales. A first mechanism relates to the bacterial growth efficiency (BGE), the fraction of carbon taken up that cells incorporate as biomass (the remainder, they respire). BGE increases with growth rate and with resource concentration when measured across different marine provinces (*6*). Given the higher concentrations within patches and the higher maximum growth rates of copiotrophs, might copiotrophs have larger BGEs than oligotrophs? If metabolic studies were to verify this hypothesis, then DOM uptake by copiotrophs would channel more carbon into the microbial loop than uptake by oligotrophs (Fig. 2D).

A second mechanism concerns the feedback between primary production and remineralization. By clustering near phytoplankton (*4*), motile bacteria may not only accelerate remineralization of algal DOM but also enhance the productivity of phytoplankton by supplying them with inorganic nutrients. Evidence for the pervasiveness of these associations has come from atomic force microscopy measurements, which recently revealed that heterotrophic bacteria and cyanobacteria are "conjoint" on average 30% of the time (*46*). Calculations predict that motile bacteria have orders-of-magnitude higher chances of ending up conjoint than nonmotile bacteria and that this propinquity markedly increases solute fluxes between heterotrophs and autotrophs. A further example is the remineralization of organic matter

on sinking marine snow particles, which favors the retention of limiting elements in the upper water column and thereby stimulates primary production and the formation of more marine snow. Motility can enhance this process by increasing particle colonization rates up to fivefold (*9*).

Finally, the time lag in DOM consumption by nonmotile bacteria compared with motile bacteria (Fig. 2C), which are faster at locating DOM patches, may reduce the metabolic accessibility of DOM, because the latter becomes increasingly refractory over time (*3*, *47*). It remains to be de-
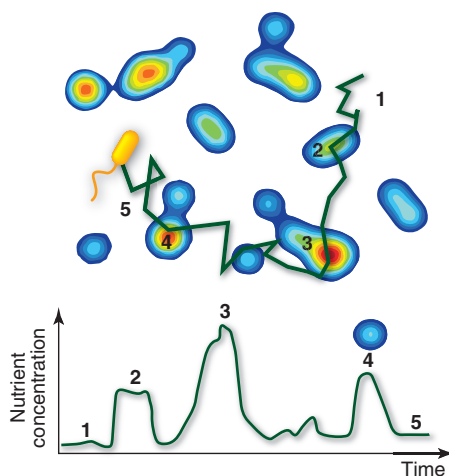

Fig. 3. Optimal foraging. The nutrient concentration encountered by marine bacteria varies considerably over time scales as short as seconds to minutes, owing to pervasive chemical and physical gradients in their immediate environment. For motile bacteria, which actively exploit nutrient gradients, this variability is greater than for nonmotile bacteria. Optimal foraging frameworks—where utilization of nutrient patches is weighted against the cost of motility but also, e.g., against the increased risks of predation and viral infection—promise to help determine the dominant foraging strategies of marine bacteria as a function of the environmental conditions. These frameworks will require new information on bacterial metabolism, including, for example, the dependence of uptake kinetics and BGE on nutrient concentration, to determine to what extent the behavioral responses of bacteria to microscale gradients affect ocean ecosystem-level properties.

termined whether this degradation affects DOM bioavailability on the time scale (~minutes) of the consumption lag.

Behavioral responses to microenvironments can also have indirect effects on biogeochemistry. The attachment of heterotrophic bacteria to diatoms can favor diatom aggregation by stimulating the production of sticky extracellular polymers (*48*). Aggregation accelerates sinking and, thus, the efficiency of the biological pump in transporting carbon from the surface ocean to depth. Bacterial attachment to diatoms, in turn, could be strongly favored by algal exudate gradients and

bacterial motility, particularly during the algae's stickier senescent phase (*4*).

Outlook: Shrinking Our Fields of View While Expanding Our Ecological Frameworks

Advances in microbial oceanography have been repeatedly triggered by new tools, from the fluorescent staining of cells to flow cytometry to metagenomics. As we begin to appreciate how heterogeneous and diverse the world of marine microbes is, there is now scope for techniques that probe this world at the scale of single cells and microenvironments. Bulk sampling techniques, where liters of water are collected and homogenized, provide valuable information on the mean microbial environment but cannot capture the local conditions experienced by microbes. To do so, we must shrink our operational field of view. Exciting opportunities are in sight on a number of fronts: Genomics is reaching single-cell resolution (*49*), secondary ion mass spectrometry (nanoSIMS) is revealing the chemical signature of individual cells (*50*), atomic force microscopy is shedding light on the spatial organization of marine microbes (*46*), and microfluidic technology is unveiling microbial behavior within realistic microenvironments (*10*, *24*, *25*, *51*). Yet, it remains difficult to interrogate microenvironments in situ, owing to their small volumes and intermittent nature: There is "plenty of room at the bottom" for measurements of microbial behavior and the microscale chemical concentration gradients that shape it.

Tools, however, are not the sole limiting factor in our understanding of microbial ecology in the context of a heterogeneous microlandscape. We also lack quantitative ecological frameworks to rationalize and scale up microenvironmental processes. Unraveling the relation between gradients and motility; between patchiness and diversity; and between behavior, uptake kinetics, and biogeochemical fluxes calls for theoretical ecologists to dive into microbial oceanography. Microbes' fast generation times, vast numbers, disparate interactions, and rich spatial organization make microbial oceanography an intriguing, yet underappreciated, model system for testing ecological theory. Glimpses of this trend can be seen in microbial biogeography, where predictions for taxa-area relations and longitudinal gradients in species abundance have been recently tested on marine microorganisms (*52*).

In contrast, little ecological theory has been applied at the scale of microbial microenvironments. Fitness-based models can provide unifying frameworks to evaluate the role of specific adaptations, such as high swimming speeds, hybrid locomotion, and metabolic plasticity. For example, the bacterial nutrient quest in a sea of microscale patches is a quintessential optimal foraging problem (Fig. 3). Optimal foraging theory predicts the movement behavior that maximizes the fitness of an organism whose resources are heterogeneous (*53*). Motile marine bacteria live in a dynamic equilibrium between disparate micro-

environments: What strategies do they adopt to optimize foraging and fitness? Might only a minority of cells stumble upon the right combination of nutrient patches and survive, i.e., is the mean motile bacterium a dead bacterium? How are gene expression and uptake kinetics tuned to the intermittency of nutrient encounters? How do episodic events, such as blooms and spills, and top-down controls, such as predation and viral lysis, play into the competition and succession between oligotrophs and copiotrophs? If new approaches to quantify the metabolism and behavior of marine bacteria at the level of single cells can be brought to bear onto these questions and if the resulting insights can be integrated into comprehensive ecological frameworks, we will achieve a deeper understanding of the functions of bacteria in the oceans and, ultimately, improve our ability to predict the dynamics of Earth's biosphere.

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