

## OCEANS

# How microbes survive in the open ocean

Ubiquitous nonmotile marine microorganisms access dilute nutrients via diffusion

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A drop of seawater contains almost a million small cells, including genetically diverse bacteria, archaea, and protists, as well as viruses (1). Typical microscopic views of this diversity give the impression of a dense environment (see the first figure), but they are preceded by filtration and concentration steps that mask the remarkable distances between individual cells in the ocean, where hundreds of micrometers separate cells that themselves are less than a micrometer in size. Yet despite their microscopic size and relative isolation, marine microbes catalyze chemical transformations at rates that are critical for maintaining Earth's habitability. Viewing the open-ocean microbial world through the interwoven threads of space, time, and diffusion is critical for understanding how microbial interactions shape the biogeochemical cycles of one of the largest habitats on Earth.

Marine microbes were largely ignored in early considerations of marine food chains until epifluorescence microscopy showed that microbes are very abundant; typically, there are on the order of 1 million microbial cells per milliliter of surface seawater. The concept of the microbial loop (2) made explicit the roles of microbes in recycling nutrients and funneling matter and energy into protists and larger organisms of the oceanic food web. Early studies suggested that ocean algae (phytoplankton) grow at or near maximal growth rates despite extremely low concentrations of inorganic nutrients (3). One explanation was that microscale heterogeneities or patches, such as those made by grazing protists or zooplankton, provide high local concentrations of nutrients that could be rapidly taken up by phytoplankton to support high growth rates in the ocean

(4). This view of the microbial world as patchy and heterogeneous was extended to organic molecules and heterotrophic microbes (which require organic matter for carbon and energy) (5); more recently, it formed the basis of microscale experimental systems with bacteria (6).

This conceptualization of the microscale environment as a complex milieu of microbes and organic molecules in "hotspots" has become a common way of presenting the oceanic microbial world. These hotspots can result from exudation of organic molecules from active photosynthetic phytoplankton cells (7, 8) and can

science and is a dominant component of the microbial loop.

To emphasize the remarkable balance between cellular needs and supply, consider that open-ocean concentrations of ammonium ions—the preferred inorganic source of nitrogen for *P. marina*—are often 10 nanomolar (nM) or less. Thus, ammonium molecules are distributed at a distance  $l$  of about 0.6  $\mu\text{m}$ . A seawater volume of  $\sim 0.5 \mu\text{m}^3$ , equivalent to a large microbial cell of radius 0.5  $\mu\text{m}$ , would thus contain less than five ammonium ions. Yet, one smaller *P. marina* cell requires  $4 \times 10^8$  N atoms per day to divide. In other words, to reproduce, a microbial cell

needs to harvest the ammonium from hundreds of millions of times its cell volume (see the second figure).

Two mechanisms could expose individual cells to this number of ammonium molecules from a large volume of surrounding seawater: active swimming or passive movement via Brownian motion (9). A microbe with a radius of 0.3  $\mu\text{m}$ , swimming for 1 day at a velocity  $v$  of 30  $\mu\text{m/s}$ , would access  $\sim 0.7$  nl of seawater containing  $\sim 4 \times 10^6$  ammonium molecules (at 10 nM concentrations)—less than 1% of its daily requirement (see the supplementary materials). Brownian motion is vastly more effective than this at bringing cells into contact with dilute nutrients.

The stirring number—defined by  $(lv)/D_{\text{mol}}$ , where  $D_{\text{mol}}$  is the molecular diffusivity of the ammonium ions (10)—provides a benchmark for comparing the encounter efficiency of swimming to that of molecular diffusion. At low stirring numbers, there is little to no enhancement of nutrient uptake by swimming. For ammonium at 10 nM concentration with intermolecular spacing of  $l = 0.6 \mu\text{m}$ , molecular diffusion is over 50 times more efficient—as measured by the stirring number—than is cellular swimming at  $v = 30 \mu\text{m/s}$ . Molecular diffusion alone generates a potential flux of  $\sim 2 \times 10^9$  nitrogen atoms per day per cell—four times the daily nitrogen requirement for *P. marina* (see the supplementary materials). Thus, diffusive processes alone can fuel the growth and productivity of abundant, free-living unicellular microorganisms in the open ocean.

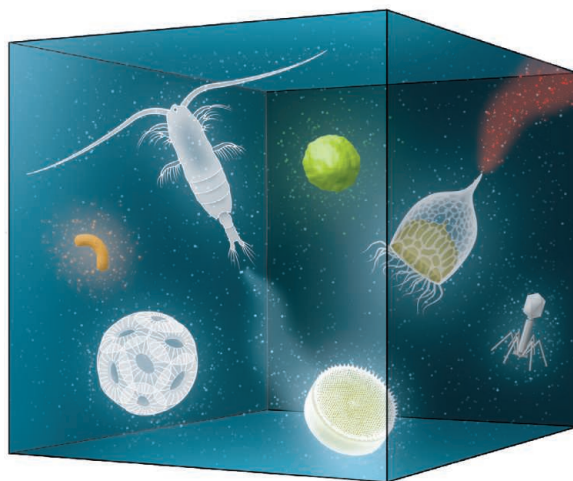


Illustration of the diverse components of the oceanic food web.

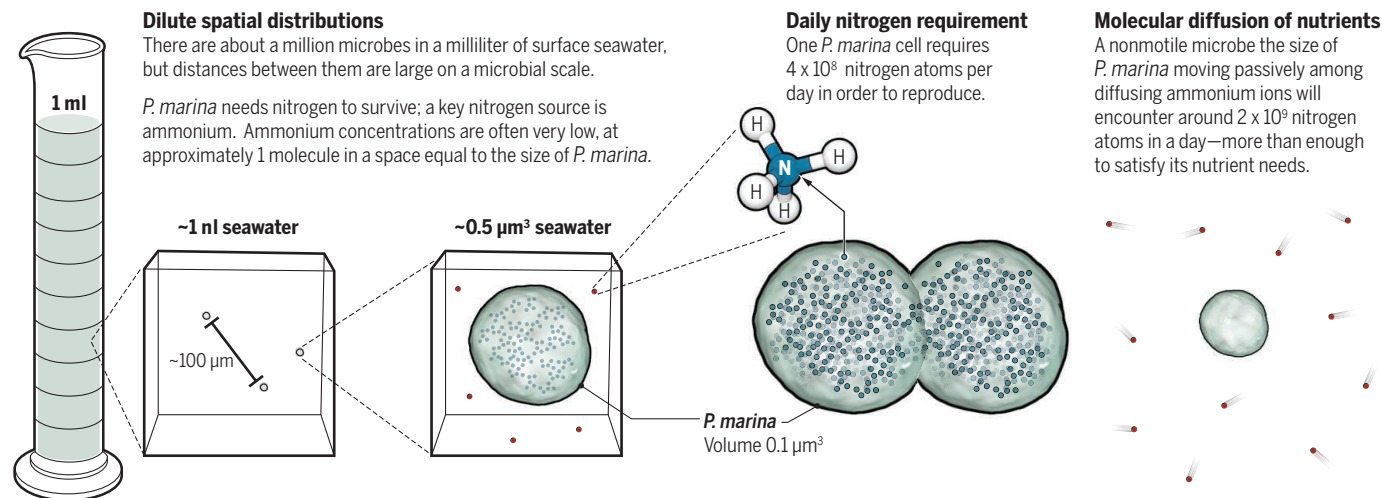
allow motile or particle-bound microorganisms to rapidly take up locally elevated concentrations of organic matter (9). Yet for many, if not most, microbial cells in the open-ocean habitat, such hotspots or patches are football fields away, if considered on a human scale.

In the open ocean, bacterial and cyanobacterial communities are dominated by nonmotile cells of two ubiquitous species: *Prochlorococcus marina* and *Pelagibacter ubique*. *P. marina* is Earth's smallest free-living phototroph (that is, it uses light for energy to fix carbon dioxide into organic matter). It is typically present at abundances on the order of a hundred thousand cells per milliliter and is responsible for  $\sim 25\%$  of the global photosynthetic production of oxygen. *P. ubique* is one of the most abundant microbes in the ocean known to

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## Getting enough nutrients in the sea

Space, time, and diffusion explain how nutrient molecules meet the survival needs of nonmotile marine microbes in a nutrient-limited open ocean. One of the most ubiquitous marine bacteria, *P. marina*, is exemplified below. Ammonium ions are not drawn to scale.



Diffusion-driven uptake can resolve the problem of how individual cells can grow in the nutrient-limited open ocean but does not fully explain how these cellular-scale processes cascade to transform ecosystem functions, including global biogeochemical cycles. Sources of inorganic nutrients are primarily recycled by bacteria or grazers that decompose organic matter and liberate ammonium.

The potential adaptive benefit of swimming toward patches for microbes of similar size to those of *P. marina* and *P. ubique* can be reassessed given recent estimates of micrograzers' sizes, which are smaller than those assumed in early modeling studies (11). For example, a micrograzer with a diameter of  $3 \mu\text{m}$ , swimming at  $100 \mu\text{m/s}$  and feeding and recycling ingested particulate nitrogen at a rate commensurate with one doubling per day, might leave a plume of remineralized nitrogen of only 5 to 60 nM, assuming that the plume is not dispersed (see the supplementary materials). The nitrogen concentrations in such a plume do not nearly overcome the over 50-fold advantage of molecular diffusion of the background ammonium (which is also partially derived from micrograzers) relative to swimming to patches in the oligotrophic ocean. Similarly, the nonmotile *P. ubique* depends on diffusion of organic molecules needed for food.

The nature of molecular diffusion also provides a mechanistic explanation for why the most abundant organisms in the open ocean, *P. marina* and *P. ubique*, are nonmotile (12). In essence, swimming toward temporary hotspots is not the dominant mechanism for supporting pro-

ductivity of small cells living in nutrient-depleted environments, the situation most common in the open ocean.

The above example of nitrogenous nutrients and *P. marina* demonstrates the importance of considering space, time, and diffusion in understanding major microbial processes of the dilute ocean. But these types of interactions have wider implications for the evolution and ecology of microbial life in the open ocean. Phosphorus and iron compounds are in much lower concentrations, and therefore the distances between molecules are much greater. Furthermore, recent studies suggest that metabolic exchanges between species are important in microbial interactions in the marine microbiome (13); such exchanges are also constrained by the space-time considerations described here. Population-level mutualisms that reshape the environment and provide energetic advantages to organisms may help to explain long-term evolutionary adaptations linking the behavior of ubiquitous autotrophs such as *P. marina* and heterotrophs such as *P. ubique* (14).

Many questions remain, including the interplay between viruses and grazers, the extent of the leakiness of the microbial loop, and in turn, the export of carbon to the deep ocean (15). Even without microscale complexity, chemotaxis, and motility, it is essential to understand how the abundant microorganisms in the dilute habitat of the open ocean adapt and how they interact with hotspots and motile microorganisms. To do so requires that we recognize how dilute spatial distributions and molecular diffusion, at scales relevant

to marine microbes, act in ways that may not seem intuitive yet are critical for understanding how the oceans and the global Earth system work. Recent discoveries, new techniques for measuring rates of chemical transformations at the microscale, genetic and genomic analyses of single cells, and visualization and experimentation at the scale of milliliters rather than liters will make it possible to examine the microscale processes in the open ocean that affect oceanic biogeochemical processes. ■

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