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## ESSAYS

# Motility drives bacterial encounter with particles responsible for carbon export throughout the ocean

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## Scientific Significance Statement

Numerical abundance is often considered of primary importance when identifying microbial taxa that drive biogeochemical processes. However, there are a growing number of examples where numerically less abundant microbes carry out critical ecosystem processes. Here, we discuss a paradigmatic example and the mechanism that underpins it: how motility, by dramatically increasing encounter rate, allows otherwise rare microbes to be numerically dominant on particles that are responsible for vertical carbon export throughout the ocean.

Marine bacteria play central roles in the oceans' biogeochemical cycles. Quantifying the impact of their collective metabolism as well as the prevalence of different adaptations and the relative importance of different taxa remain topics of active research, and the answers will lie at the heart of our ability to model the role of the oceans in elemental cycling. In this context, numerical abundance is an important determinant of the significance of ecosystem members to the broader community and to ecosystem processes (Zehr et al. 2017). For example, *Prochlorococcus* represents the numerically dominant marine phototroph and is estimated to collectively fix as much carbon as global croplands (Billler et al. 2014). In other cases, numerically underrepresented groups of microbes dominate important components of biogeochemical cycles because of physiological or behavioral adaptations (Arrigo 2004). This is akin to apex predators driving trophic interactions in many ecosystems even though they occur in low

numbers. In freshwater microbial systems, *Chromatium okenii* can dominate carbon and ammonium uptake even though they represent only 0.3% of the community by cell number (Musat et al. 2008). It has been hypothesized that this disproportionate effect is due to *C. okenii's* ability to “move freely through the water column and find the best zones of nutrient availability and light intensity...” and to accumulate storage compounds (Musat et al. 2008). Here, we illustrate how microbial behavior serves to increase the relative functional importance of certain taxa disproportionately to their numerical abundance in the open ocean, where resources for microbial growth are sparse and copiotrophic behavior is often considered negligible. We demonstrate this by focusing on marine particles (Fig. 1)—the vector of vertical carbon export in the ocean's biological pump modulated by bacterial degradation (Azam and Malfatti 2007)—and comparing their rate of encounter with motile and nonmotile bacteria via a simple biophysical model.

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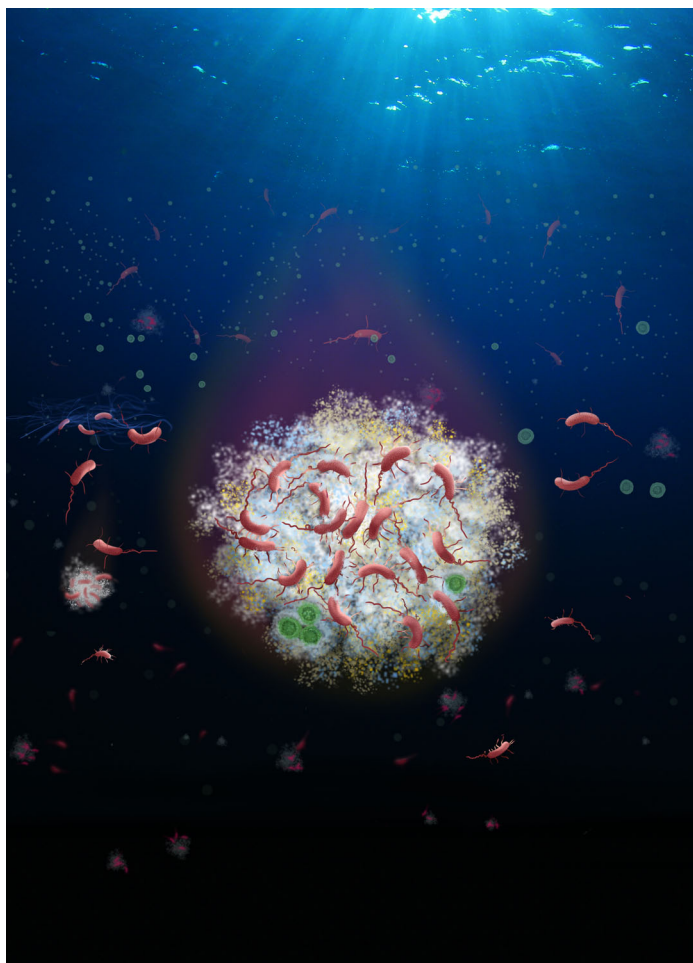
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## Motility and the oceans' biological pump

Whether motile or nonmotile, bacteria live in a world dominated by diffusion. Swimming does not itself increase the instantaneous uptake rate for small microorganisms (Karp-Boss et al. 1996), but rather serves them in finding new nutrient sources (Purcell 1977). This year marks the 42<sup>nd</sup> anniversary of Edward Purcell's seminal realization that a bacterium “... does not move like a cow that is grazing a pasture—it moves to find greener pastures” (Purcell 1977). Purcell's original statement referred to chemotaxis—the ability to move up chemical gradients—but applies more generally to the



**Fig. 1.** Motile copiotrophic bacteria frequently dominate over small, nonmotile bacteria in communities inhabiting and degrading marine particles. They can thus play a dominant role in reducing the magnitude of the ocean's biological pump, the downward transport of vast quantities of carbon driven by sinking particles.

increase in encounter rate with sources of nutrients afforded by motility. For a heterotrophic marine bacterium, there are no greener pastures than particles rich in organic matter.

The role of sinking particles in driving the biological pump and of bacteria in attenuating the vertical flux has traditionally been considered in the context of productive coastal oceans (Muller-Karger et al. 2005), yet recently a comparable carbon export was found to come from the open ocean (Jahnke 1996; Muller-Karger et al. 2005). New approaches have revealed that particle concentrations in the open ocean can be much higher than those previously measured by sediment traps (Pilskaln et al. 2005), including conspicuous amounts of nonsinking organic particles (Baltar et al. 2010), and that aggregation of the characteristically small cells of the open ocean produces particles with sinking speeds similar to those in coastal waters (Richardson and Jackson 2007). This suggests that, even in the open ocean, particles are an important available niche for motile bacteria, with implications for carbon export dynamics throughout the ocean.

Particle-associated microbial communities are often found to be taxonomically and functionally distinct from their free-living counterparts (Ganesh et al. 2014; Fontanez et al. 2015). Physiologically, particle-attached bacteria are typically larger and exhibit greater uptake and exoenzyme production rates (Dang and Lovell 2016). Genes characteristic of a copiotrophic lifestyle, including motility genes, are enriched in the particle-associated fraction compared to the free-living population, in both coastal waters (Ganesh et al. 2014), and the open ocean (Fontanez et al. 2015; Guidi et al. 2016).

While small, nonmotile bacteria dominate by numerical abundance in the free-living fraction of open ocean waters, evidence is accumulating that the oceans' interior is rich in bacteria adapted to a particle-associated lifestyle (Lauro and Bartlett 2008; Herndl and Reinthaler 2013). Copiotrophic bacteria with large genomes are preeminent members of deep-sea particle-associated communities (Lauro and Bartlett 2008, Herndl and Reinthaler 2013) and sequenced genomes contain a large number of genes responsible for flagellar synthesis, signal transduction, and response to gradients (Lauro and Bartlett 2008). Together with the prevalence of dissolved, particle-degrading enzymes indicative of surface-attached communities (Herndl and Reinthaler 2013), this evidence points to an active community of particle-attached copiotrophic bacteria in the open ocean's interior, where bacteria colonize particles through motility and remineralize them.

### **Motility offsets low numerical abundance in the colonization of particles**

Swimming greatly increases the volume of water that bacteria explore in a given time and thus the rate at which they encounter particles. At the small scale of bacteria, the ability to explore and encounter corresponds to a diffusivity, which for motile bacteria is 100–8000 times greater than for nonmotile bacteria exploring the environment through Brownian motion alone. This can be seen through a simple calculation of the diffusivity of nonmotile and motile bacteria. A nonmotile bacterium with effective radius  $r = 0.5 \mu\text{m}$  has a diffusivity due to Brownian motion of  $D = kT/(6\pi\eta r) \approx 10^{-12} \text{ m}^2 \text{ s}^{-1}$ , where  $k$  is Boltzmann's constant,  $T$  is temperature, and  $\eta$  is the dynamic viscosity. The diffusivity of motile bacteria, originating from their random-walk behavior, is  $D \approx v^2\tau/3$ , where  $v$  is the swimming speed and  $\tau$  is the run time (Berg 1993). Motile strains isolated from particles were found to have  $D = (0.1\text{--}8) \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$  (Kj rboe 2008).

This difference in diffusivity has direct implications for encounter rates. The rate at which a neutrally buoyant particle of radius  $r$  encounters bacteria is  $E = 4\pi rDB$  (Kj rboe 2008), where  $B$  is the concentration of bacteria and  $D$  is their diffusivity. The fraction of bacteria that are motile out of all bacteria encountering a particle (in terms of cell number) can be computed as the rate of encounter of motile bacteria divided by the combined rate of encounter of motile and nonmotile bacteria:

$$F_{\text{mot,particle}} = \frac{E_{\text{mot}}}{E_{\text{mot}} + E_{\text{non}}} = \frac{(D_{\text{mot}}/D_{\text{non}}) F_{\text{mot,bulk}}}{(D_{\text{mot}}/D_{\text{non}}) F_{\text{mot,bulk}} + (1 - F_{\text{mot,bulk}})}, \quad (1)$$

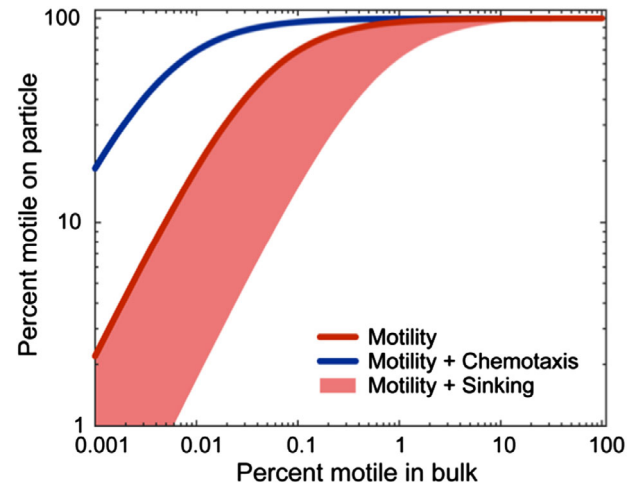
where  $F_{\text{mot,bulk}}$  is the relative abundance (i.e., fraction) of motile bacteria in the bulk water column. Motile bacteria are often chemotactic and we therefore also consider the role of chemotaxis in setting encounter rates. Because chemotaxis can occur only in the vicinity of the particle in response to gradients of dissolved organic matter originating from the particle, it can be seen as effectively increasing the size of the particle as a target of the bacterial encounter process. Here, we model chemotaxis as a 10-fold increase in the radius of the particle when bacteria are motile and chemotactic, based on recent observations (Smriga et al. 2016).

As a particle sinks through the water column, fluid motion relative to the particle continuously brings new bacteria into close proximity to the particle, where motility or Brownian motion can cause an encounter. The strength of this mechanism depends on the ratio of advection of bacteria with the flow to their diffusive transport (described by the Peclet number). As a result, the encounter rate becomes additionally proportional to  $D^{-1/3}$  (Kjørboe 2008), yielding the following expression for the fraction of bacteria that are motile out of all bacteria encountering a particle:

$$F_{\text{mot,sinking particle}} = \frac{1}{(D_{\text{non}}/D_{\text{mot}})^{2/3} (1 - F_{\text{mot,bulk}})/F_{\text{mot,bulk}} + 1}. \quad (2)$$

This simple model shows that, as a direct consequence of motility, swimming bacteria throughout the ocean encounter particles at disproportionate rates compared to nonmotile bacteria (Fig. 2), demonstrating that microbial behavior outweighs the numerical dominance of nonmotile bacteria. Faster encounter with particles, as favored by motility, will in turn favor the earlier hydrolysis of particles, thereby attenuating the magnitude of the biological pump. Strikingly, even when motile bacteria make up only 0.1% of bacteria in the bulk (e.g., Vergin et al. 2013), they will account for 70% of bacterial encounters with particles. From our results, it is also apparent that chemotaxis can play an additional important role over motility alone in the encounter between bacteria and particles, particularly when the relative abundance of motile bacteria is low in the background community. At a minute relative abundance of 0.001%, chemotaxis accounts for an increase in encounter rate of 18% over the encounter rate caused by motility alone. However, chemotaxis plays the critical role of increasing residence time near the particle surface and thus favoring attachment, irrespective of the abundance of motile bacteria.

The composition of bacterial communities on particles is certainly influenced by factors beyond encounter rates. The metabolic repertoire of particle-associated bacteria is one such



**Fig. 2.** In the colonization of particles, motile bacteria dominate even when their numerical abundance in the bulk is low. Shown is the percentage of bacteria that are motile (relative to total bacteria) encountered by a particle (red solid curve), as a function of the percentage of motile bacteria in the bulk, as predicted by a simple mathematical model. Also shown is the additional effect of chemotaxis (blue) and the effect of particle sinking (shaded red), the latter represented as an envelope to account for different sinking speeds. Motility and chemotaxis enhance the encounter rate of a particle with bacteria by orders of magnitude, leading to a disproportionate contribution of motile bacteria to particle colonization. Note that results are independent of particle size.

factor. This, however, is expected to often act to further favor motile bacteria, which are often copiotrophs capable of rapid growth and utilization of a broad range of substrates (Lauro and Bartlett 2008; Herndl and Reinthaler 2013; Dang and Lovell 2016). Although bacterial physiology plays a role in defining community composition, we argue that under a broad range of scenarios, the striking enhancement in encounter rates still makes motility a major determinant of which groups of bacteria are most abundant on particles, and thus likely to contribute to particle degradation and the fraction of particulate carbon sequestered vs. released to the atmosphere.

### Microbial foraging in sparse particle landscapes

Are distances between particles too large in the open ocean for motile bacteria to rely on them as nutrient sources? A calculation analogous to that from Kjørboe et al. (2002) shows that this is often not the case. Foraging bacteria encounter sinking particles of a particular radius  $r$  at a rate  $E = 4\pi r D C_p(r) \text{Sh}(r)$ , when the bacterium is much smaller than the particle.  $C_p(r)$  is the concentration of particles of radius  $r$  and  $\text{Sh}$  is the Sherwood number, which represents the relative enhancement in the encounter rate due to particle sinking. The Sherwood number is also a function of the particle radius, as  $\text{Sh}(r) = 1 + 0.619 (U(r)r/\nu)^{0.412} (\nu/D)^{1/3}$  (Kjørboe et al. 2002), where  $\nu$  is the kinematic viscosity of seawater ( $10^{-6} \text{ m}^2 \text{ s}^{-1}$ ) and we have adopted the empirical relation  $U(r) = 0.13r^{0.26}$  for the settling velocity  $U$  (in  $\text{cm s}^{-1}$ ) as a function of particle radius (Alldredge and

Gotschalk 1988). Considering a range of particle sizes, where the concentration of particles over a narrow band of particle radii  $dr$  is given by integrating the particle size spectrum  $N(r)dr$ , the total encounter rate is given by:

$$E_{\text{tot}} = \int_{r_1}^{r_2} 4\pi r DN(r) \text{Sh}(r) dr, \quad (3)$$

where  $r_1 < r < r_2$  defines the size range of particles being encountered.  $E_{\text{tot}}$  is the average number of particles with radii between  $r_1$  and  $r_2$  that one bacterium encounters per unit time. The inverse of  $E_{\text{tot}}$  is therefore the average search time ( $T_{\text{mean}}$ ) to encounter a particle in this size range. The time ( $T_{10}$ ) for the first 10% of bacteria to encounter a particle can be determined using the cumulative probability distribution  $P(t < T) = 1 - e^{-t/T_{\text{mean}}}$ , resulting in  $T_{10} = -T_{\text{mean}} \ln(0.9)$ .

Based on particle abundances and size spectra from the North Pacific (Pilskaln et al. 2005; Kostadinov et al. 2009; Lambert et al. 2019) and focusing on particles of radius ranging from 20  $\mu\text{m}$  to 2.5 mm, the time for a fast motile bacterium (i.e., one with a high diffusivity,  $D = 8 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$ ; Kiørboe 2008) in the open ocean to find a particle is 3.3–27.3 h on average, but 10% of the bacteria find a particle in 20–170 min and 1% find one in 1–16 min. For slower bacteria (i.e., ones with a low diffusivity,  $D = 8 \times 10^{-10} \text{ m}^2 \text{ s}^{-1}$ ; Kiørboe 2008), the time increases approximately 10-fold, yet many bacteria still find a particle within a day. In laboratory settings, bacteria have been observed to swim for 20–72 h in depleted environments (Malmcrona-Friberg et al. 1990; Seymour et al. 2010). Furthermore, motility does not need to result in success for every individual as long as a significant fraction of a clonal population survives. The feasibility of the search for particles is of course not uniform across the open ocean. For example, at the highly oligotrophic center of the South Pacific gyre, where particle abundances can be 100-fold lower than in the North Pacific (Stemmann et al. 2008), even the top 10% of bacteria would have to search for 3.6 d to find a particle, making motility less viable. Contributing to this variability is the heterogeneity in particle “quality”, which determines the growth return a bacterium obtains from a particle (Fernandez et al. 2018). What appears clear from combining the above calculations is that particle hopping is a viable strategy where a sufficient concentration of particles exists, namely in the regions of the open ocean that most contribute to carbon export, and that motile bacteria are expected to play a major role in modulating carbon flow in those regions because of their high encounter rates with particles.

Through literature data and a simple mathematical model, we demonstrated that particles are encountered disproportionately often by motile bacteria, even when these are numerically rare in the bulk seawater. This increased encounter rate is compounded by chemotaxis, which enables bacteria to find particles from greater distances and reside near the surface for longer timescales. These factors together

enhance the ability of motile bacteria to encounter, attach, and subsequently dominate particle-associated communities. Dominance on particles will be further influenced by factors such as metabolic capacity and microbial interactions (which often further favor motile bacteria because of their copiotrophic adaptations (Herndl and Reinthaler 2013; Dang and Lovell 2016)), but the 1000-fold enhancement in colonization rate highlighted in our model provides motile bacteria a significant starting advantage. Our calculation therefore supports previous reports—though these are limited in number for the oligotrophic ocean—that motile bacteria often dominate particle communities (Fontanez et al. 2015). As a result, we put forward the hypothesis that motile bacteria are key agents in determining the magnitude of the biological pump, not only in coastal waters but also in the open ocean.

### Future directions

Throughout the oceans, there exist diverse nutritional niches for bacteria, allowing for both oligotrophic and copiotrophic strategies. Small, nonmotile bacteria such as *Pelagibacter ubique* and *Prochlorococcus marinus* numerically dominate in the surface of the open ocean, where sunlight dominates as an energy source and photosynthate provides a relatively steady if low nutrient supply to heterotrophs. Below the sunlit ocean, the situation changes rapidly and particulate organic matter becomes a central component of the deep-sea microbial loop (Herndl and Reinthaler 2013). In light of current oceanographic evidence and biophysical modeling results, we put forward that motile bacteria dominate particle dynamics even when numerically rare overall—because they encounter particles at disproportionate rates through swimming—and thus directly impact critical biogeochemical fluxes, including particulate carbon export to the depths of the oceans. Advancing our understanding of the role and relevance of bacterial groups in the ocean necessitates us to reexamine ecosystem processes with a focus on microbial activity and functional impact, and to go beyond numerical abundance alone. Constructing this view will require tools capable of measuring the metabolism and behavior of microbial cells at temporal and spatial scales relevant to the environment they inhabit (Hunter-Cevera et al. 2014; Ottesen et al. 2014; Ribalet et al. 2015; Lambert et al. 2017), application of these tools across a variety of oceanic regions, and the development of ecological theory for aquatic microbes to generate and test hypotheses specific to the dynamic nutrient environments these cells inhabit. Altogether, there exist rich opportunities across many scientific disciplines to contribute, making this one of the most exciting frontiers in microbial ecology.

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### Conflict of Interest

None declared.

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