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Microbes in flow

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Microbes often live in moving fluids. Despite the multitude of implications that flow has on microbial ecology and environmental microbiology, only recently have experimental tools and conceptual frameworks from fluid physics been applied systematically to further our knowledge of the behavior of microbes in flow. This nascent research field, which truly straddles biology and physics, has already produced important contributions to our understanding of the physical interaction between microbes and flow, both in bulk fluid and close to surfaces, at the same time revealing the richness and complexity of the resulting dynamics.

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Introduction

Fluid flow is a ubiquitous feature of microbial habitats. Marine and aquatic microorganisms are frequently exposed to turbulence, which can directly impact fundamental processes including motility, chemotaxis, and nutrient uptake [1,2]. Soil microorganisms are subject to laminar flow through the soil's porous matrix [3], with consequences for their transport and potentially their bioremediation capacity [4]. Bacteria belonging to the microbiome of humans and other animals experience flow in multiple regions of the body, including the intestine, stomach, urinary tract, mouth, and lungs [5,6]. In continuous stirred-tank bioreactors and photobioreactors [7,8] microorganisms are exposed to laminar and turbulent flows generated to enhance their growth and bioprocesses (like fermentation) by ensuring nutrient mixing, gas exchange, and optimal light exposure. In aquatic ecosystems, flows relevant to microorganisms can be generated by other organisms, such as the wake of swimming phytoplankton [9], the feeding currents of copepods [10], and the microvortices produced by coral cilia [11].

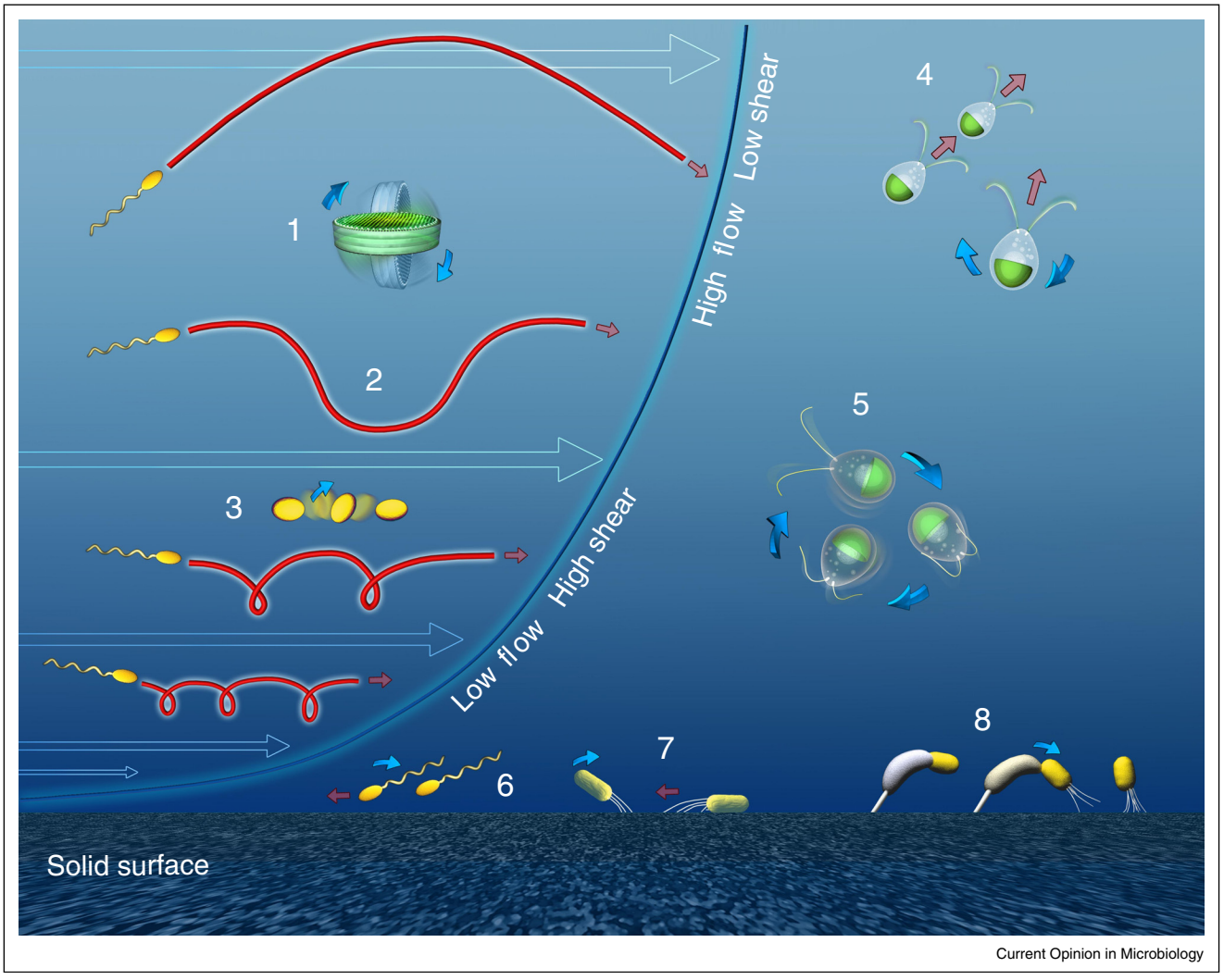
Common to all these flow environments are gradients in fluid velocity, which we here refer to as 'shear'. Shear is often generated near a solid surface (Figure 1), since fluid has to be at rest at the boundary (the 'no-slip' condition), or by the action of turbulence, which microorganisms experience as spatially smooth, temporally varying gradients in the fluid velocity. Shear is the mechanical feature of fluid flow that has the most direct and profound consequences on microorganisms. The physics of fluids at the scale of microorganisms is very different from its macro-scale counterpart, since viscous damping dominates over inertial forces (the so-called low-Reynolds-number regime). Thus, owing also to the nearly neutral buoyancy of most microorganisms, hydrodynamic processes such as sinking or rising, or the presence of lift forces that may deflect the trajectories of objects in flow and cause clustering, are negligible under the majority of flow conditions. Instead, shear creates torques on microorganisms that — when coupled with microbial phenotypes such as morphology, motility, or chemical sensing — generates a rich spectrum of dynamics with fundamental consequences on microbial ecology.

Despite the widespread occurrence and implications of flow, its physical effects on microorganisms are rarely considered in microbial studies. In the past few years, however, thanks to growing interdisciplinary efforts and the advent of suitable technologies like microfluidics [12], this theme has come to the forefront. Here we review this recent body of work, with the aim of illuminating how pervasive the influence of fluid forces on microorganisms is and thus contributing to integrate this physical view of microorganisms into microbial ecology. We focus on the effects of flow on individual cells in dilute suspensions, both in the bulk and near surfaces, and will not cover the hydrodynamics of dense microbial assemblages, such as biofilms, bacterial turbulence and bioconvection.

The effects of flow on the swimming and spatial distribution of microorganisms

By exerting torques on microorganisms, shear causes them to undergo periodic rotations relative to the flow. These flow-induced rotations affect the microorganisms' direction of motion and, in turn, their ability to disperse, seek nutrients by chemotaxis, or reach surfaces. While the centroid of a non-motile microorganism faithfully follows the flow (i.e., the streamlines), its body rotates as a result of the fluid torque associated with shear: the resulting periodic rotations are known as Jeffery orbits [13]

Figure 1



Fluid flow can have a broad range of effects on microorganisms, both in the bulk fluid and in the vicinity of surfaces. White arrows and the blue line define the velocity profile of the flow. The flow velocity is zero at the solid surface (no-slip boundary condition), where shear is highest. Numbers refer to different flow–microbe interactions, as follows. (1) Periodic rotations ('Jeffery orbits') of non-motile phytoplankton cells, such as diatoms. (2) Trajectories of motile bacteria for different magnitudes of shear. (3) Jeffery orbits of a non-motile bacterium. (4) Gyrotaxis of phytoplankton. (5) Gyrotactic trapping of phytoplankton. (6) Upstream swimming of bacteria. (7) Upstream twitching of bacteria. (8) Surface colonization by a stalked, curved bacterium under flow.

(Figure 1). When microorganisms are elongated, the rotation rate is not uniform: considerably faster when the cell is oriented transverse to the flow and slower when it is aligned with the flow. As a result, elongated microorganisms spend most of their time aligned with the flow direction, flipping orientation periodically with a period that increases with the cell's aspect ratio and decreases with the magnitude of shear. Given that elongation is a feature of many microorganisms, particularly when propulsion appendages or the ability to form chains are factored into the calculation of the aspect ratio, this purely physical preferential alignment affects a broad range of microorganisms under many natural conditions.

Trapping of bacteria by shear

Jeffery orbits can have important ecological consequences. For non-motile plankton, the preferential alignment of elongated cells with flow has been estimated to affect light propagation in the ocean under certain conditions, because light scattering by cells depends on orientation [14]. For motile microorganisms, shear-induced rotational dynamics determine not only a microorganism's orientation, but as a consequence also its swimming direction. Mathematical models [15,16•] have been used to compute the trajectories of idealized microorganisms undergoing Jeffery orbits in laminar flow in closed conduits ('Poiseuille flow'), such as the urinary tract. Depending on the cell's aspect ratio and the flow strength, a bacterium is predicted to either swim

pointing against the flow by 'swinging' around the conduit's centerline (the region of highest flow velocity and lowest shear) or to constantly tumble in the regions of higher shear nearer to the conduit sidewalls. These trajectories have been observed experimentally [17••] by tracking individual, smooth-swimming *Bacillus subtilis* cells in microfluidic flows (Figure 2a). Geometrical properties of the cells can further affect these dynamics. In particular, the chirality of bacterial flagella has been observed to introduce a bias in the swimming direction in the presence of flow, owing to a complex interaction between chirality and shear [18,19].

By altering the cells' swimming direction, shear can affect the spatial distribution of microbial populations, triggering microscale heterogeneities in cell concentration. This was recently demonstrated [17••] for *B. subtilis* and *Pseudomonas aeruginosa*, using image analysis to determine the positions of thousands of individual bacteria in microfluidic devices. These experiments were made possible by the flexibility of microfluidics to generate accurate fluid flows, in this case a parabolically varying velocity profile in the plane of observation. This study revealed that, within a few seconds, regions of lower shear in the center of the channel were depleted of bacteria by up to 70% and that bacteria accumulated in the regions of higher shear towards the channel sidewalls (Figure 2a). This spatial heterogeneity was found to stem from the competition between the shear-induced alignment of the bacteria, which are highly elongated, and the random reorientations due to active tumbling and passive Brownian rotational diffusion. Thus, bacteria are free to swim in all directions where shear is low and become trapped and accumulate where shear is high. This 'shear-trapping' phenomenon applies to a broad range of flows occurring in microbial habitats and to a broad range of swimming microorganisms, since the presence of flagella automatically implies a high aspect ratio (e.g., ~10 for *B. subtilis* [17••]).

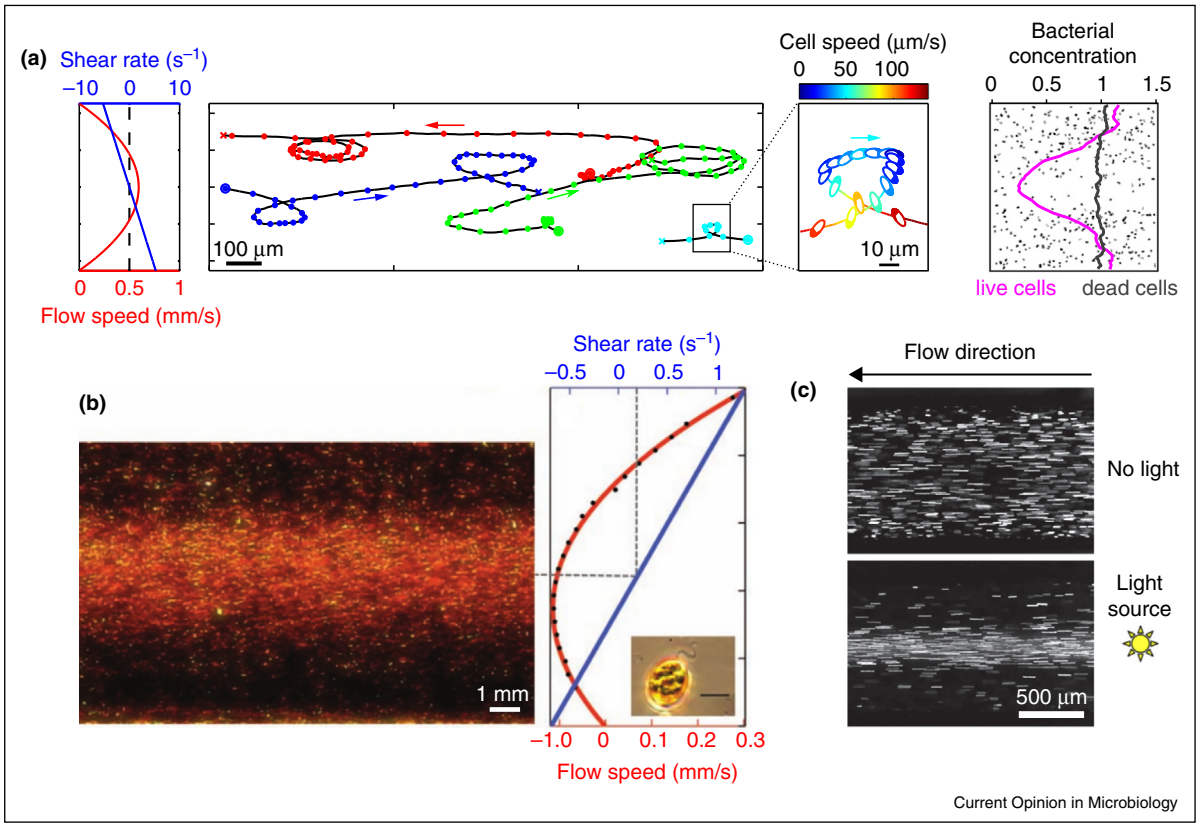
Mechanical properties of the cells, such as the flexibility of eukaryotic but possibly also of bacterial flagella [20,21], or active responses to shear can further affect the spatial distribution of microbial populations in flow. Recent microfluidic experiments (Barry *et al.*, in press) with motile phytoplankton revealed accumulation patterns similar to those observed in bacteria for species with a high aspect ratio, but an opposite trend — consisting in the accumulation of cells in low-shear regions — for two species, *Chlamydomonas reinhardtii* and *Dunaliella tertiolecta*. These two species have a more spherical morphology and a breaststroke motion ('puller-like') that is different both in the kinematics of the flagellar motion and in the resulting hydrodynamics from the propulsive system of a bacterium ('pusher-like'). These unexpected observations cannot be explained by the shear-trapping mechanism and could instead stem from the differences between pushers and pullers, the deformation of flagella by shear, or from an active, behavioral response to shear. Only circumstantial evidence exists to date for such a behavioral response [22,23], which remains an intriguing possibility that would open the door to a broad range of questions regarding the physiological mechanism of flow-sensing among microorganisms and the ecological consequences of microorganisms being able to control their position in environmental flows.

An immediate ecological consequence of the effect of shear on the swimming direction of microorganisms is a reduction in their chemotactic performance [24], because chemotaxis presupposes the ability to freely move in the most favorable direction. This phenomenon has been observed in the case of aerotaxis in experiments in which *B. subtilis* cells were simultaneously exposed to shear and to an oxygen gradient transverse to the flow direction [17••]. These experiments illustrate the versatility of microfluidics in creating environments with both controlled flow and controlled chemical conditions, in this case an oxygen gradient created by exploiting the gas permeability of the microchannel material (polydimethylsiloxane). It was found that increasing shear increasingly deteriorates aerotaxis, with shear rates above $20\ s^{-1}$ resulting in an abatement of >60% in the aerotactic performance. It is an interesting possibility that microorganisms frequently exposed to strong flows may have evolved motility patterns that minimize this negative impact of shear [25]. For example, the 'run-and-reverse' swimming pattern characteristic of marine bacteria [9] has been proposed to be advantageous for performing chemotaxis in the presence of shear [24,25], a prediction that remains to be experimentally validated. More broadly, chemotaxis in moving fluids is a rich topic, relevant to many natural processes but lacking observations to date.

Gyrotaxis in phytoplankton

Shear can also strongly affect phytoplankton. Many species of phytoplankton move upwards in the water column to optimize light exposure for photosynthesis during the day and dive back down at night for shelter from predators and supply of nutrients [26]. These migrations are often achieved through gravitaxis, the ability to orient along or against the direction of gravity. Gravitaxis can result from passive torques that align cells vertically, though active sensing of gravity cannot be ruled out for some species [27]. For example, the green alga *Chlamydomonas* swims against gravity due to its bottom-heaviness, whereby posteriorly located heavy organelles cause a torque that rights the cell up. The interaction between this gravitational torque and the hydrodynamic torque due to shear results in gyrotaxis, the tendency of cells to swim and accumulate into downwelling regions of the flow [28]. In the presence of vertical gradients in horizontal flow velocity, such as those generated by tidal currents or wind stress, when the shear is too intense and the associated torque overwhelms the gravitational torque, vertical migration stalls and cells are trapped at that depth

Figure 2



Fluid flow affects the swimming patterns and spatial distribution of bacteria and phytoplankton. **(a)** Trajectories and spatial distribution of smooth-swimming *B. subtilis* cells in a laminar parabolic flow (red) in a microfluidic channel. Bacterial trajectories, acquired by moving the microscope stage in synchrony with the mean flow speed, reveal shear-induced loops. Live cells, initially randomly distributed, quickly depleted from the central region of the channel (purple); in contrast, dead cells showed no spatial depletion under the same flow (grey). Modified with permission from [17••] **(b)** Thin layer of the phytoplankton *H. akashiwo*, which formed by gyrotactic trapping in a 1-cm-deep chamber with a vertically varying shear (red). Modified with permission from [29]. **(c)** Trajectories of the phytoplankton *C. reinhardtii* exposed to a laminar flow in a 1 mm × 1 mm square channel. With no light, the cells were homogeneously distributed over the width of the channel (top panel). When a light source on the right of the flow was switched on, cells oriented upstream and migrated towards the center of the channel (bottom panel). Modified with permission from Ref. [30•].

(Figure 2b). This 'gyrotactic trapping' mechanism has been proposed and demonstrated in laboratory experiments and mathematical models with *Chlamydomonas nivalis* and *Heterosigma akashiwo* [29] and might be one of the mechanisms responsible for the formation of the intense thin layers of phytoplankton frequently observed in the coastal ocean [26]. A related process occurs when cells are exposed to a light gradient in flow, where phototaxis (motility towards a light source) causes reversible cell accumulations along the centerline of a pipe flow [30•] (Figure 2c).

When the flow is turbulent, strong patchiness in the distribution of phytoplankton can arise as a result of the coupling between turbulent shear and gyrotactic swimming [31•,32]. These predictions, obtained with mathematical models of turbulence, have been tested experimentally only for the simplified case of phytoplankton swimming in steady vortices, where a strong accumulation of cells in the vortex cores was observed [31•], in line with predictions [33]. The effects of actual turbulence — a collection of unsteady vortices at different scales — on phytoplankton motility represents both a challenge for the experimentalist due to the difficulty of visualizing individual microorganisms within three-dimensional turbulent flows, and an opportunity for the marine microbiologist to find stronger mechanistic bases for the long-recognized importance of turbulence for phytoplankton [34], making this a promising field for further investigation.

The effects of flow on microbial interactions with surfaces

Near surfaces, both microbial ecology and fluid mechanics take on substantially different forms to their counterparts in bulk fluid. Microorganisms near surfaces can change their flagellation, induce virulence, and secrete

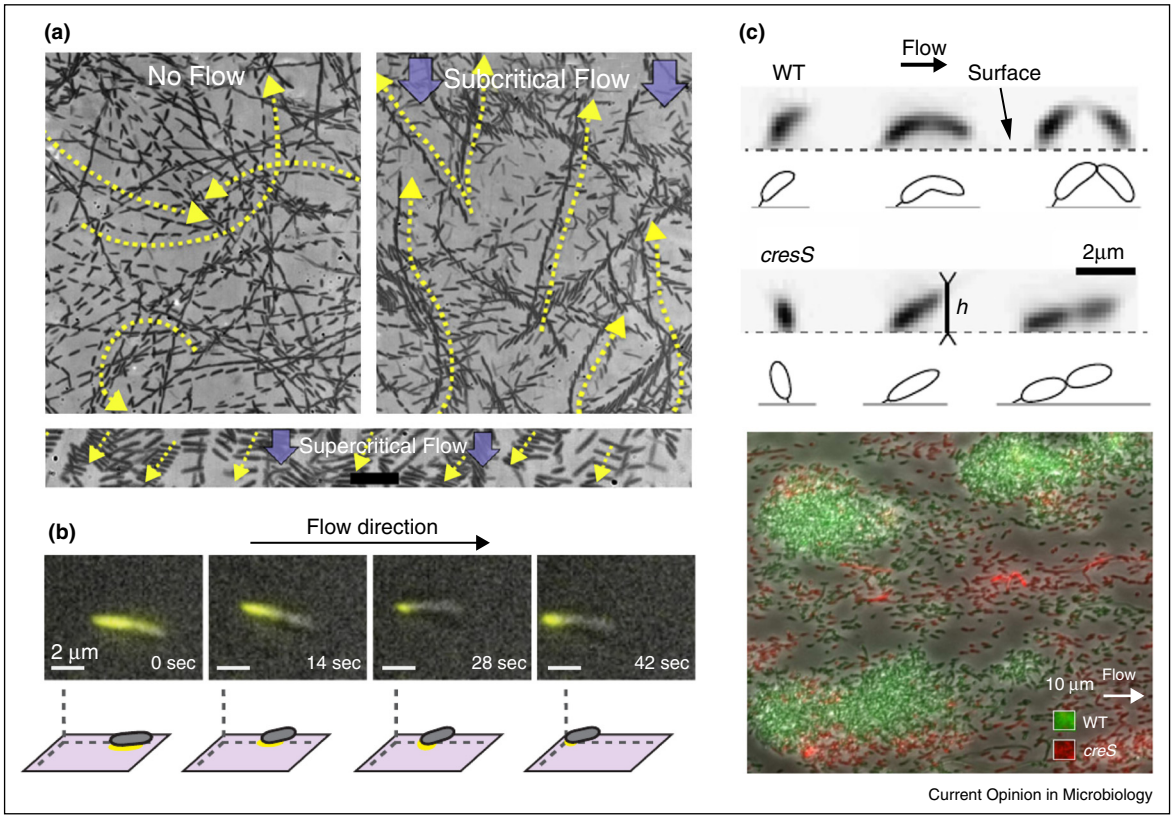
polymers that anchor them to the substrate and protect them against chemical insults. Meanwhile, flows near surfaces are often characterized by large values of shear and can produce attractive or repulsive forces as well as torques on microorganisms swimming within tens of micrometers from the surface. As a result, hydrodynamic microbial processes near surfaces are very distinct from those in bulk fluids.

Upstream swimming

It has long been known that many motile microorganisms accumulate near solid surfaces [35–37], where they can reach concentrations up to tenfold higher than in the bulk. Recently, it has been recognized that for *Escherichia coli* and *Caulobacter crescentus* this accumulation stems from an attractive hydrodynamic force resulting from the flow field created by the swimming bacterium and the presence of the surface [36,38]. Surface-induced forces are also responsible for the characteristic 'swimming in circles' of many bacteria near a surface [39]. As the flagellum (or flagellar bundle) of a bacterium rotates, the cell body counter-rotates to ensure that the net torque on the organism is zero, as required by the absence of external forces. This differential rotation, coupled with the different distance of the flagellum and the cell body from the surface, causes a torque that continuously reorients the cell's swimming direction, producing a circular trajectory that contributes to trap the cell near the surface [39]. Collisions with the surface (a steric effect) and suppression of tumbles by surface-induced forces (a hydrodynamic effect) further enhance the near-surface trapping [37,40].

Strikingly, in the presence of ambient flow, these interactions with surfaces result in the migration of bacteria against the flow (Figure 1). Microfluidic experiments

Figure 3



Fluid flow affects microbe–surface interactions. **(a)** Trajectories of *E. coli* swimming near a surface in the presence of different flow rates. Under quiescent conditions, *E. coli* swam preferentially in circular trajectories (top left panel). For low values of shear ($<6.4\ s^{-1}$), bacteria frequently swam upstream (top right panel), whereas at higher shear rates they were dragged downstream (bottom panel). Modified with permission from Ref. [42]. **(b)** Upstream twitching of fluorescently-labelled *P. aeruginosa* in the presence of a shear rate of $\sim 500\ s^{-1}$ at the surface (top) and associated schematic (bottom). Images are composites of DIC and TIRF microscopy. Cells adhered to the surface using the pili on their upstream-facing pole. Modified with permission from Ref. [47]. **(c)** Flow-induced bending of *C. crescentus* bacteria towards the surface. Schematics (top) show the effect of the mother cell's flow-induced bending on the attachment of the daughter cell. This mechanism is present in the naturally curved wild-type cells (WT) but absent in straight mutants (*creS*). As a result, WT cells (green) are considerably better at colonizing surfaces compared to *creS* mutants (red), as shown by an overlay of phase contrast and fluorescent images after 32 hours of simultaneous growth in flow (bottom). Modified with permission from Ref. [52••].

have shown that *E. coli* tends to swim upstream along one sidewall of a conduit, as a consequence of the balance between the bacterium's propensity to swim in a circular trajectory and the shear-induced torque [41]. For up to moderate shear rates ($<6.4\ s^{-1}$), upstream swimming was also observed in the proximity of open surfaces [42] (Figure 3a). Upstream swimming can have important consequences for the transport of bacteria within small channels, such as catheters or blood vessels, where flow may induce upstream migration in the absence of any chemical signals. Upstream swimming has also been reported for mammalian [43] and human [44•] sperm cells, where it likely evolved as a guidance mechanism through the female reproductive tract. For both spermatozoa and bacteria, it is currently believed that upstream swimming results from a purely passive, flow-induced reorientation process, rather than from the ability to actively sense shear or the flow direction.

Upstream twitching

A separate mechanism of upstream locomotion induced by flow is related to twitching motility (Figure 1), a form of surface-attached bacterial movement mediated by type IV pili [45]. This process was first discovered in *Xylella fastidiosa* [46] and also reported in *Pseudomonas aeruginosa* [47]. These bacteria attach to the surface by pili located predominantly at one pole and the pili's periodic extension and retraction pulls the cell in the direction of that pole. It was found that the torque induced by the shear at the surface flips the bacteria around this 'pivoting' pole, resulting in the cell pointing and thus slowly migrating upstream [47] (Figure 3b). The uncoiling and recoiling of type I pili have been similarly shown to promote surface motility against moderate flows in *E. coli* [48]. Because the shear rates used in these experiments fall in the range typical of catheter tubes and plant vascular systems, these observations may have important implications for microbial dispersal in both natural and medical settings.

Shear-enhanced surface colonization

Shear can also enhance bacterial colonization of surfaces via shear-trapping, which drives the accumulation of bacteria in the immediate vicinity of a surface and thus fosters bacteria-surface encounters. This was demonstrated through observations of the attachment rate of *P. aeruginosa* to the glass bottom of a microfluidic channel in the presence of flow [17••], which revealed an increase in the surface colonization with increasing shear rate. A related phenomenon of shear-enhanced adhesion was previously reported for *E. coli* [49], in this case resulting from a surface-specific catch-bond interaction between *E. coli*'s fimbriae and mannose-coated surfaces. In contrast, the shear-enhanced surface colonization [17••] and reversible adhesion [50] of *P. aeruginosa* were observed on untreated glass surfaces and appear to be non-specific. Physiological levels of shear have also been observed to increase the adhesion and gliding motility of the parasite *Toxoplasma gondii* on the human vascular endothelium [51].

The effect of shear can be particularly pronounced when attachment does not occur via the cell body, but through a stalk, as in the case of *C. crescentus*. Observations of this bacterium in microfluidic devices [52••] revealed that shear at a surface causes attached stalked cells to bend towards the surface, in the direction of the flow, as expected for a flexible sessile structure (Figure 3c). The natural curvature of *C. crescentus*'s cell body then aids in orienting the adhesive pili located at the cell pole towards the surface, thereby promoting the surface attachment of the daughter cell upon cell division and enhancing surface colonization. The absence of this mechanism in straight mutant cells, suggests that the cell's natural curvature could be an evolutionary adaptation to surface colonization in the presence of flow.

Conclusions

The research we have highlighted illustrates the profound effects that fluid flow can have on the migration abilities and spatial distribution of microorganisms, ranging from bacteria to phytoplankton and probably beyond. Because the spatial distribution of microorganisms affects a host of microbial processes, including resource competition, encounter rates with viruses, predators and conspecifics, as well as chemical signaling including quorum sensing and allelopathy, hydrodynamic processes are an important feature in the ecology of microorganisms and can have far-reaching and hitherto largely unrecognized consequences both in natural ecosystems such as oceans and lakes, and in industrial settings such as biofuel reactors and wastewater treatment plants.

The recent handshake between microbial ecology and fluid mechanics, typified in the studies reviewed here, has brought about an appreciation of the intensity and diversity of the effects of flow on microorganisms. We believe that this body of work represents only the incipit of the range of microbial processes that, in different habitats and for different microorganisms, are influenced by fluid mechanical forces, torques and transport. Many physically interesting and ecologically important questions remain to be addressed. How can different types of flows — laminar versus turbulent, bulk versus near surfaces, steady versus unsteady — affect the spatial distribution of a given microbial population? How do the biological differences in cell morphology and motility — prokaryotic versus eukaryotic, pushers versus pullers — change the interaction between cells and flow? Are microorganisms such as bacteria and phytoplankton able to sense and actively respond to fluid flow and shear stresses, a phenotype that would altogether transform the current view of microbial processes in flow? To answer these questions we would need even more sophisticated and cutting-edge experimental methods, such as the ability to visualize the

dynamics of submicrometer propulsion appendages in flow. These challenging questions have only begun to be addressed, representing ample opportunities for further research, and we foresee that answers will have profound consequences in ecology, industry, and health.

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