New and Notable

If Life Keeps Throwing Curveballs, You've Probably Reached a Wall

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Almost all organisms live surrounded by fluid, and in all of them core biochemical processes take place in a liquid medium. Hydrodynamics thus plays a major role in all living processes, and even more so for swimmers, i.e., organisms that mostly depend upon hydrodynamic forces to propel themselves during normal life. An enormous number of species meet this criterion, ranging from microbes to both fish and birds. In an elegant article, Jashnsaz et al. (1) show that hydrodynamics may be playing a very important role in the life history of another swimmer, the fascinating and relatively less known bacterial predator with the Carrollian name of _Bdellovibrio bacteriovorus_ (BV).

BV is a bacterial predator that preys on Gram-negative bacteria like _Escherichia coli_ (2). It attaches itself to the prey using a type-4 pili-dependent process, and enters the periplasmic region, forming a structure called a _bdelloplast_ out of the host organism, and slowly consuming and digesting its host. It grows filamentously in the bdelloplast, dividing by septation along its length, often producing an odd number of progeny from each invasion (2), and then escapes into the environment after lysing the bdelloplast (Fig. 1).

Because of its predatory lifestyle, BV has been touted as a possible "living antibiotic" (3), leading to a revival of interest in its somewhat unique evolutionary history and metabolism. However, one of the mysteries in BV's lifecycle has been the question of how it locates its prey. No evidence has been discovered that suggests it does chemotax toward single prey, although there is some evidence of weak chemotaxis toward colonies of prey, believed to arise from prey lysate (1).

If BV does not chemotax, how does it locate its prey? Previous work suggested that BV collides randomly with its prey, but perceptive biologists have noted how rare it is for bacteria to collide (4). This observation of course echoes a familiar result from the theory of random walks (5). Assuming that in the absence of chemotaxis both microbes perform a random walk, the probability of BV colliding with _E. coli_ is similar to the probability that two random walkers will meet at the same point. While living in Zurich in the early 1900s, the Hungarian mathematician George Polya kept running into the same people again and again, inspiring him to calculate what the odds of that were (5). Polya proved that in three dimensions there is a significant probability that the walkers will never meet even in infinite time! Thus, the chances of our humble predator finding enough sustenance to survive and reproduce appear bleak by the laws of probability.

However, in two dimensions two random walkers will meet each other with a probability of one. BV's chances would be therefore much higher if there was a way of contriving that its prey and itself stay effectively in two dimensions. Enter hydrodynamics. It is well known that swimming microorganisms at low Reynolds numbers are attracted to solid surfaces (6). This effect leads to the accumulation of microswimmers close to walls, something that has been observed previously for both spermatozoa and microbes (6). Jashnsaz et al. (1) show that this effect concentrates both _E. coli_ and its predator near the walls of the experimental apparatus. They can demonstrate that this is due to hydrodynamic forces because both BV and _E. coli_ also move in circles close to the walls, another effect of surfaces on the motion of a low Reynolds number swimmer (6). By showing that the helicity of the motion changes whether the wall is above or below the swimmer, they convincingly demonstrate that wall-induced hydrodynamic forces influence the bacterial trajectories.

They hypothesize and then demonstrate that because of the same effect, BV and _E. coli_ also tends to get trapped by large beads. The combination of the hydrodynamic effects leads to a circular motion of both predator and prey around such defects, effectively increasing the colocalization of the microbes by confining them to smaller volumes or to effectively one-dimensional trajectories. This effect is
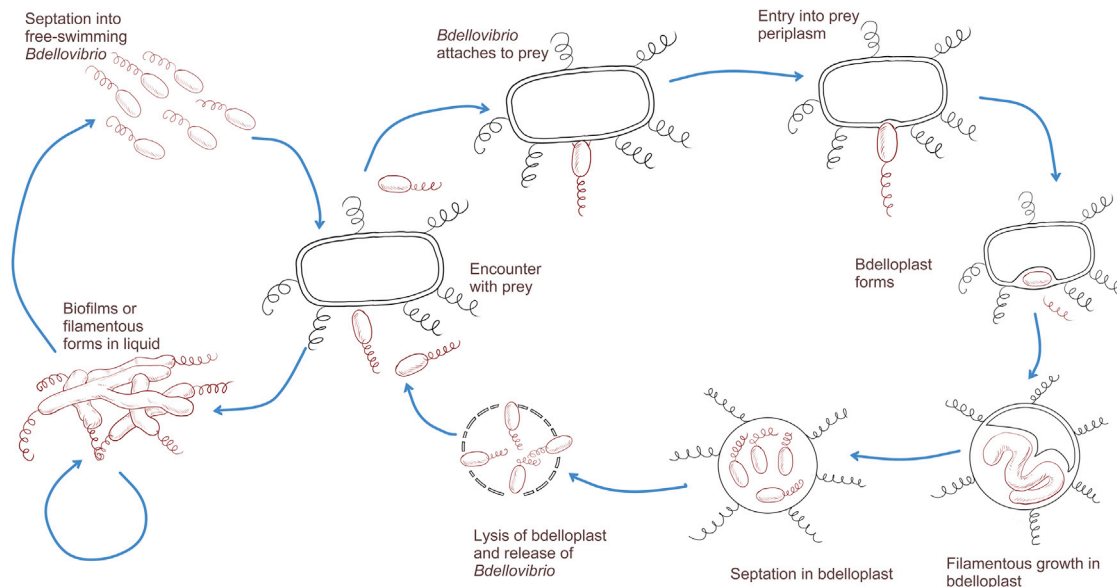
FIGURE 1 A cartoon of the life cycle of the bacterium BV based upon Sockett (2). The article by Jashnsaz et al. (1) in this issue helps solve the question of how BV captures its prey using random collisions. To see this figure in color, go online.

probably likely to be very important in BV's real habitat, in the soil and in natural water bodies. Hydrodynamics here performs the function of achieving dimensionality reduction for increasing the efficiency of random search. Dimensionality reduction for efficient searching is a general strategy that is found at many scales in biology.

BV's predatory lifestyle thus numbers it among those organisms that utilize hydrodynamic interactions to help it survive and reproduce. Of course, the causality is really the other way around. Surface effects lead to concentrations of microswimmers near walls, creating an ecological niche for a predator that is now able to rely on mere chance to encounter its prey. In evolution, as in quantum mechanics, if something is possible, it will probably happen! In fact, there is scope for thinking about this as a unifying principle for a lot of interesting biology. Fluid flow creates reproducible and repeatable patterns and structures that create hydrodynamic niches that evolution then fills.

Two other examples that fit this definition of hydrodynamic niches come to mind. The first are the broadcast spawners, such as sea urchins, sea anemones, and corals (7), that

reproduce by releasing both their sperm and their eggs into the sea. The eggs release chemoattractant plumes and the sperms chemotax along the plumes toward the eggs, but given the wide open seas where these organisms live, it would appear to be a rather risky or expensive reproductive strategy. However, reproduction appears remarkably efficient, with average rates that can exceed 90%. Hydrodynamics is believed to be playing a role here in two ways. Structures that form due to turbulence often lead to coalescence of eggs and sperm together, much as some kinds of turbulent flow appear to lead to coalescence of debris. Secondly chemoattractants released by the eggs are transported larger distances by fluid flows in the coral reefs and on the seabed. Thus, the structure of turbulence in this case appears important for the creation of physical conditions that make it possible for broadcast spawners to survive (7).

A second example of a strange hydrodynamic niche is one occupied by filamentous suspended bacterial biofilms or biofilm streamers. These are biofilms that are attached to the surface at one end but have a long filamentous tail that freely oscillates in the fluid,

and are commonly seen in rivers and hot springs as well as in biomedical devices where they pose a significant health hazard (8). Experiments in microfluidic channels showed that the streamers always began from the internal wall just following a corner and were freely suspended in the middle of the flow. Numerical analysis of the flow fields indicated that the place where the streamers adhered to the wall was associated with secondary flow fields in the shape of counterrotating vortices. While the mechanistic details are still somewhat unclear, there is little doubt that the structure of the internal flow fields again provide a hydrodynamic niche that allow the formation of these streamer structures (8).

Hydrodynamic niches at different scales must exist in our oceans, river waters, and even in the atmosphere. There is almost no doubt that much remains unexplored, especially in the air but also in stable turbulent structures in flowing water.

For BV itself, the physical complexity of its real habitat may increase the importance of other kinds of flow patterns at longer length scales. Wall-induced hydrodynamic forces are important a few bacterial lengths away from the wall, but flow-induced

vortices or turbulent patterns may play a role at longer length scales. It would be interesting to study the effect of fractal-like surface architecture on microorganism motility, especially in moving water because interactions between stable flow patterns and surface effects are likely to have significant effects here.

Jashnsaz et al. (1) therefore help us place the life cycle of BV at the intersection of two major themes in biological physics. The first is that of the properties of random walks and of the benefits of dimensionality reduction for search strategies. The other is that of the hydrodynamic niche, in particular the one formed by hydrodynamic interactions of swimming microorganisms with surfaces. There is no doubt that both of these themes will continue to throw up new surprises and wonders in future years, as we begin to explore nonmodel organisms in their habitat with the tools of physics-inspired quantitative biology.

Finally, adapting Monod, because whatever is found true for *E. coli* is often true for us, we can let BV draw out one last moral from its story. If life keeps handing you curveballs, it's probably a sign that you've reached a wall!

ACKNOWLEDGMENTS

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