Gallery of Fluid Motion

Rocket yeast

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Fluid flows play a vital role in the transport and organization of living systems [1]. Across all scales, microbial populations are mixed, shaped and reorganized by flows. In laboratory experiments, microbial growth on agar plates has been used as a model system to investigate how spatial population structure impacts evolution [2]. In these experiments, a thin layer of cells at the colony front divides and generates genetically similar daughters who are not pushed very far away before they themselves divide, mimicking range expansions on land. Because the underlying substrate is a solid, the microbial population cannot be advected, and the interplay between transport and spatial population dynamics has scarcely been investigated with such laboratory systems. The video highlights a novel experimental system to grow microorganisms on the *surface* of a liquid. To our surprise, we discovered that *S. cerevisiae* (baker's yeast) growing on a viscous liquid behaves similarly to "active matter". They metabolically generate fluid flows many times larger than their unperturbed colony expansion speed, and those flows, in turn, can dramatically impact the population morphology and genetic segregation patterns.

We grew microbial populations on the surface of a nutrient-rich fluid 10^4–10^5 times more viscous than water. The viscosity of the fluid is controlled by adding 2-hydroxyethyl cellulose, a long chain polymer, to yeast extract, peptone, and dextrose (glucose) microbial growth medium. The extreme but finite viscosity inhibits undesired thermal convection and allows microorganisms to effectively live at the air-liquid interface due to capillary forces. We followed the segregation of two selectively neutral *S. cerevisiae* strains, genetically identical except for constitutively expressing different fluorescent proteins. The resulting colony expansion is then monitored from the top over several days with an incubated Zeiss Lumar.V12 stereoscope. In parallel, the fluid flow velocity field is extracted near the substrate's surface with particle image velocimetry by tracking (10–20)-μm fluorescent, neutrally buoyant, polyethylene beads seeded with a dilute concentration in the medium [3]. Figure 1 shows successive snapshots of a yeast colony growing on top of the liquid media at

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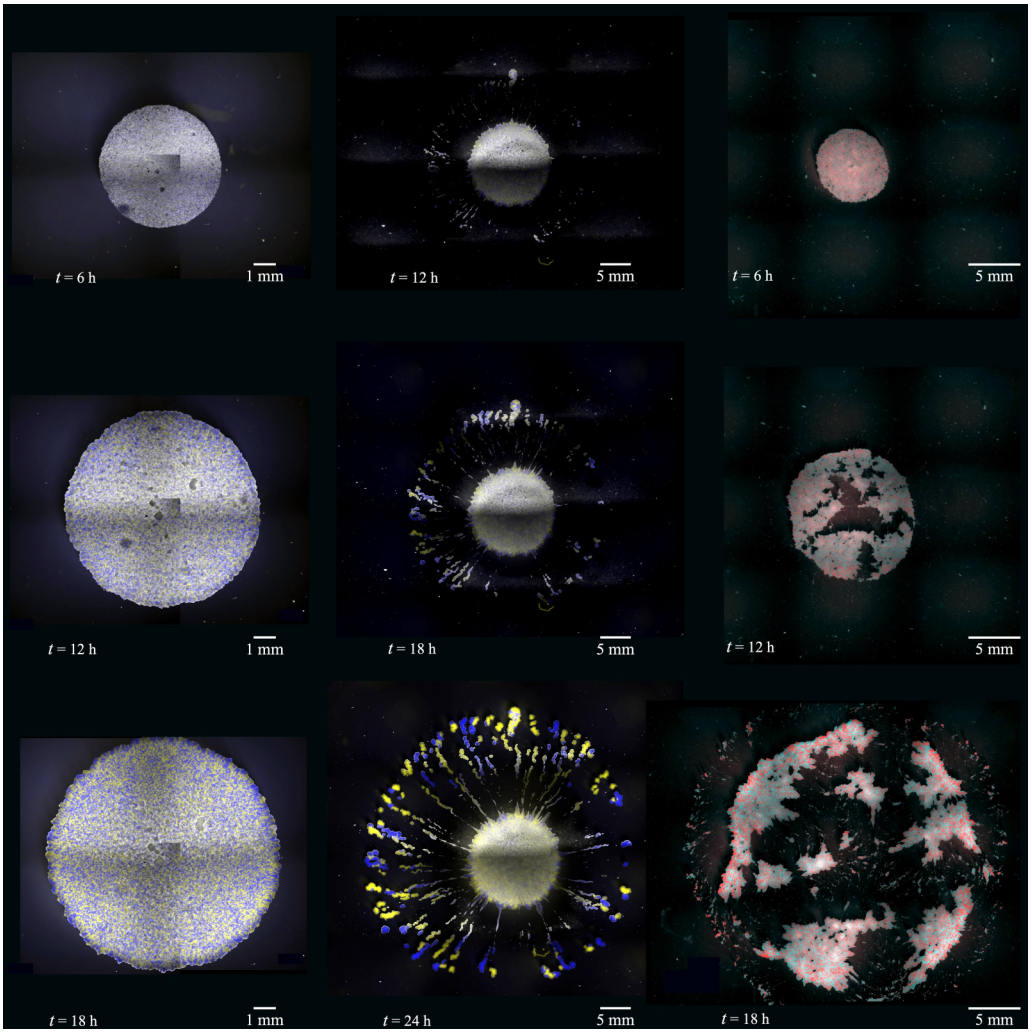

FIG. 1. Image sequence of a microbial range expansion on the surface of a liquid substrate with three different viscosities in decreasing order from left to right. The snapshots are shown at regularly spaced time intervals. https://doi.org/10.1103/APS.DFD.2020.GFM.V0020.

three different viscosities. At the highest viscosity, cell proliferation and movement on the liquid interface produce compact circular colonies with a more stretched aspect than when they are grown on agar gel. Direct hydrodynamic flow measurements in the substrate revealed that nonmotile yeast colonies generate a fluid flow in the shape of a vortex ring below the colony's edge. The origin of the flow is attributed to a local reduction of the substrate density due to nutrient depletion. As the microbial population grows, the substrate density decreases, leading to a misalignment between the fluid pressure and the density contours in the vicinity of the colony and drives a flow similar to geophysical flows generated by a baroclinic instability.

As the viscosity of the substrate is lowered, the self-induced flow intensifies, and novel colony morphologies were observed. Intermediate viscosities led to remarkable fingerlike protrusions at the colony frontier. As can be seen from the video, after an initial compact colony formation, mostly monoclonal "fingers" start growing from the edge of the colony and then break into smaller cell clusters. This surprizing morphology resembles dendritic crystal growth in the presence of a

solute-driven buoyant flow and could be attributed to a liquidlike behavior at the colony perimeter due to the lubricating effect of cellular division. Thin streams of cells are pulled and ripped away from the colony by the self-induced flow while actively growing. At the lowest viscosity, the expanding colony is entirely fragmented into many genetically diverse and mutually repelling islandlike clusters that can colonize an entire 94-mm-diameter Petri dish within 36 h, many times faster than their expansion speed in the absence of a flow. For a complete description of the observed morphologies and details on flow generation mechanism, see Ref. [3].

The musical track accompanying the video lends a sense of humor to the dramatic and transient lives that microbes live. Invisible to researchers, the microscopic world can feel static when observed from a human's quickened pace. In this video, range expansion is presented as an exploration, and the chosen musical track helps personify these miniature protagonists as organisms far from stasis.

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[1] T. Tél, A. de Moura, C. Grebogi, and G. Károlyi, Chemical and biological activity in open flows: A dynamical system approach, Phys. Rep. **413**, 91 (2005).

[2] O. Hallatschek, P. Hersen, S. Ramanathan, and D. R. Nelson, Genetic drift at expanding frontiers promotes gene segregation, Proc. Natl. Acad. Sci. U.S.A. **104**, 19926 (2007).

[3] S. Atis, B. T. Weinstein, A. W. Murray, and D. R. Nelson, Microbial Range Expansions on Liquid Substrates, Phys. Rev. X **9**, 021058 (2019).