

## Research Interests

Alexander P. Petroff

As a mathematical naturalist, I use my explorations through swamps, fields, and forests to guide my explorations of mathematics and *vice versa*. Currently, I am using reaction-diffusion equations and fluid mechanics to understand the ecology of microorganisms that I observe in natural mud. During my graduate work, I showed how the geometries of a channel network in Florida and billion-year-old fossils both arise from growth in a harmonic field. Over the course of my career, I will continue to combine field work, theory, and experiments.

**Current and Future Work** The overwhelming majority of research into biological physics is focused on a few model organisms such as *E. coli*. Despite the great advances made in this field, it is generally impossible to extrapolate these results to the dynamics of ecosystems and the extraordinary diversity of organisms. This is a problem. One of the great challenges of the coming century is to predict how ecosystems will adapt to a warming planet. Moreover, by studying organisms that specialize to unique physical environments, we can discover new phenomena that enrich our understanding of mathematics but are inaccessible to model organisms.

I devise simple models and experiment to explain the dynamics of complex microbial ecosystems in natural sediment. Within this porous medium, bacteria are densely packed ( $10^9$  cells/cm<sup>3</sup>) and extremely diverse ( $10^7$  species/cm<sup>3</sup>). When light shines on mud, photosynthetic organisms on the surface produce oxygen and sugars. As these nutrients diffuse through the sediment, the resulting free-energy gradient is dissipated by a cascade of microbial interactions. Remarkably, evidence of this cascade is visible to the naked eye in the form of millimeter-scale strata. How does this ecosystem come to a steady state and what can destabilize it? Given an environment, can we predict the behaviors of the organisms within it? What new phenomena can we discover by studying the diverse behaviors of these organisms? I answer these questions in two ways. First, I observe and model how the diffusion and consumption of nutrients from a source cause a complex community to organize into strata. Second, I enrich individual microbes to study the strategies they use to cope with life in a nutrient gradient.

I am currently working on two experiments in which we seek to understand an emergent length-scale, the penetration depth of oxygen.[1] Each is a two-dimensional slice of the microbial community. In the first experiment, we take a horizontal slice from the surface to understand how oxygen-consuming bacteria organize around photosynthetic bacteria. We have built an experiment that allows us to measure the concentration of oxygen throughout a thin microbial community. Illuminating a spot on this slice, we localize oxygen production, measure the resulting distribution of oxygen, and infer the distributions of sources and sinks. I have derived the governing equations for the distribution of oxygen. As a professor, I will use this experiment and model to investigate how oxygen is partitioned between the sediment and atmosphere. This partitioning, which is poorly understood, is likely important to the abrupt rises in atmospheric oxygen in the Proterozoic eon that led to the evolution of

complex life. In the second experiment, we take a vertical slice to understand how nutrient exchange at the oxygen penetration depth couple the dynamics of aerobic and anaerobic bacteria. We observe the formation of a front of bacteria that burn the waste products of anaerobic bacteria with oxygen. I have devised the equation of motion for these organisms. We find that competition for nutrients forces diverse organisms together into a coherent front that stabilizes the oxygen penetration depth. As a professor, I will adapt this experiment to include a temperature gradient. This experiment will allow us to observe and model how an ecosystem reorganizes as permafrost melts.

Enriching microbes from sediment also allows us to discover and model new physical phenomena in nature and the lab. We have enriched two microbes that create fluid flows to overcome oxygen diffusion limitation, the sulfur-oxidizing bacteria *Thiovulum majus* and the ciliate *Uronemella*. In their natural environment, these microorganism have both evolved the ability to form communities to stir the surrounding fluid. We have observed these communities in the lab and modeled their behavior. By deriving the equations of motion for the cells, we have identified how they use a hydrodynamic instability to spontaneously generate large-scale flows that transport oxygen forty times faster than diffusion.[2] This project has identified the physical basis for the convergent evolution of two phylogenetically disparate microbes.[3] Moreover, we have discovered a new type of collective motion. *T. majus* cells self organize into hexagonally-packed rotating crystals of quickly-spinning cells.[4] We showed how this behavior arises from the tornado-like flow of water created by each cell. These crystals show beautiful new dynamics. Crystals rotate, display active surface melting, and can “count” the number of cells in a crystal. The discovery of this new state of matter was only possible because we enriched these difficult-to-grow organisms.

As professor, I will continue my research into the organizations and dynamics of complex microbial ecosystems to understand the coevolution of life and the environment. This challenge is at the heart of cataclysmic changes in the past, such as rise of oxygen, and present, such as modern rise of carbon dioxide in the atmosphere.

**Graduate Work** Rivers networks are among the most visually striking features on the Earth surface. How water flows into different parts of the network is one of the principal processes that determines network geometry. In general, because water flows down hill, the competition between different branches of a network is strongly coupled to the shape of the surrounding landscape. To simplify this problem, we studied the geometry of stream networks that grow in response to groundwater. We showed that the competition for groundwater around a seepage network in the Florida panhandle is determined entirely by the geometry of the network. Moreover, competition is mathematically simple, the groundwater flow is determined by a solution of the Poisson equation. Using these results, we showed that the geometry of bifurcations[5, 6], the equilibrium profile of a stream[7], and the topography around a growing spring[8] can all be understood from first principals. To test these predictions, we made frequent field trips to a natural kilometer-scale seepage network, used observations of enigmatic networks on Mars, and conducted table-top experiments. We found that the predictions of simple models are in good agreement with the observed forms of channels on Earth and Mars and experiments and thus offer fundamental insight into the growth of

networks.

The second aspect of my thesis considered the growth of microbial communities and their relationship to ancient fossils. To understand and date the evolution of early metabolisms, including photosynthesis, one must recognize and interpret microbial fossils. This goal is challenging because many of the oldest putative fossils are only identified as biotic by a peculiar shape. One particularly enigmatic class of fossils are millimeter to meter scale laminated structures called *stromatolites* that are widely thought to be fossilized microbial mats. In an effort to develop a biological interpretation for these structures, we combined physical insight with observations of modern cyanobacterial mats from laboratory cultures and the field. We showed that growth of a bacterium in some modern stromatolites is limited by the rate at which diffusion transports nutrients from the surrounding water, through the microbial mat, and to the bacterium. Through a combination of physical reasoning, laboratory experiments, and field observations, we have found that one class of stromatolites arises from the diffusion of ions through a thin microbial mat[9, 10] and the spacing between neighboring stromatolites can record the competition for nutrients[11].

- [1] Petroff A, Tejera F, Libchaber A (2016) Mud, microbes, and oxygen, a three-body problem. *J. Stat. Phys. in review*.
- [2] Petroff A, Libchaber A (2014) Hydrodynamics and collective behavior of the tethered bacterium *Thiovulum majus*. *PNAS* 111:E537–E545.
- [3] Petroff, A, Pasulka A, Soplol N, Wu XL, Libchaber A. (2015) Biophysical basis for convergent evolution of two veil-forming microbes. *Royal Society Open Science* 2:150437.
- [4] Petroff A, Wu XL, Libchaber A (2015) Fast-moving bacteria self organize into active two-dimensional crystals of rotating cells. *PRL* 114:158102.
- [5] Devauchelle O, Petroff A, Seybold H, Rothman D (2012) Ramification of stream networks. *PNAS* 109:20832–20836.
- [6] Petroff A, Devauchelle O, Seybold H, Rothman D (2013) Bifurcation dynamics of natural drainage networks. *Proc. R. Soc. A* 371:20120365.
- [7] Devauchelle O, Petroff A, Lobkovsky A, Rothman D (2011) Longitudinal profile of channels cut by springs. *JFM* 667:38–47.
- [8] Petroff A, Devauchelle O, Abrams D, Lobkovsky A, Kudrolli A, Rothman D (2011) Geometry of valley growth. *JFM* 673:245–254.
- [9] Petroff A, Beukes N, Rothman D, Bosak T (2013) Biofilm growth and fossil form. *PRX* 3:041012.
- [10] Bosak T, Knoll A, Petroff A (2013) The meaning of stromatolites. *Annu. Rev. Earth Planet. Sci.* 41:21–44.
- [11] Petroff A, Sim MS, Maslov A, Krupenin M, Rothman D, Bosak T (2010) Biophysical basis for the geometry of conical stromatolites. *PNAS* 107:9956–9961.

## Teaching Statement

Alexander P. Petroff

In addition to my position as a Researcher at Rockefeller, I am part-time Visiting Professor of Biology at Bard College. Every year, Bard invites proposals from post-docs and researchers from Rockefeller to design and teach their 400-level biology seminar. This year, my proposal was chosen. My seminar is titled Modeling Biological Complexity. As a graduate student, I was given my departments teaching award for my work as the TA of a similar course.

The goal of this class is to show students how the same mathematics elucidate diverse biological systems. We cover four broadly applicable methods for analyzing complex systems: scaling analysis, random processes, network theory, and information theory. For each of these topics, I first present the theory, show how it can be applied to a few biological problems (e.g., why bacteria cannot use fins), and illustrate it with a demo (e.g., reversible stokes flow in an annulus). In the following several classes, the students present different papers I selected about how this model is applied to qualitatively different biological problems. For example, in the section on randomness, I present random walks, the normal distribution, and the Poisson distribution. In the following two classes, students present papers on how bacteria use biased random walks to navigate chemical gradients and how random genetic variation within a population drives natural selection. I have also written several problem sets that walk students through the analysis of a biological phenomenon. In the problem set on scaling analysis, the students show that organisms below a critical size can survive a terminal velocity fall and they explore how different organisms exploit this phenomenon.

As a professor, I will adapt this course into a series of lectures. In this version, I will include problems that require greater comfort with mathematics. For example, we will show how memories are stored in a neural network and how gauge fields allow one to predict the motion of swimming microbes. In the coming decades biology and mathematics will become ever more intertwined. This course will familiarize mathematicians with biological systems and identify examples that exemplify universal concepts from elementary mathematics.

In addition to this class, I am excited to fluid mechanics from the perspective of applied math. Nowhere, in my experience, is the recognition of mathematics in the world made more visceral than in motion of fluids. I am excited about teaching this course as an avenue to strengthen students' current mathematical abilities and introduce them to new phenomena, all the while keeping problems rooted in our everyday experience with faucets and streams. Because flowing water is everywhere, it is simple to recognize both the richness of motion it displays and the practical importance. Because the equations of fluid motion are non-linear, their analysis introduces students to a wide variety of new mathematical techniques. At an introductory level, I would be interested in taking problems from fluid mechanics and natural systems and showing how insight can be gained from physical reasoning and scaling analysis. In a class of advanced undergraduates and new grad students, I would enjoy introducing the equations of fluid mechanics with applications to subjects including bacterial motion and stream flow. In a more advanced course, I would enjoy introducing hydrodynamic stability and pattern formation.

My time at Rockefeller has also prepared me to advise graduate students. As a post-doc with Prof. Libchaber, I have had two graduate students do rotations on my project. Over the course of several months, I have worked closely with these students to introduce microbial ecosystems and build new experiments. I look forward to working with a group of people with similar interests who periodically introduce me to new problems and discoveries.

In the coming years, how I structure my classes and lab will be informed by my past experience as a teacher and supervisor, conversations with professors, and suggestions from members of my department. My motivation to teach grows from conversations I have had for as long as I can remember. My parents are a poet and an engineer. My friends are artists, carpenters, scientists, farmers, and lawyers. Talking about ideas with smart people with disparate interests has led me again and again to a wonderful moment in a conversation. In this moment, the listener is brought to understand how rational thought shines through in some never-before-considered detail of the world. With this thought, there is the suspicion that the natural world is slightly more wonderful and intricate than we ever fully appreciated. This is the feeling that has motivated me to talk about science for years and will continue to guide me.