The Fluid Dynamics of Cell Motility

Fluid dynamics plays a crucial role in many cellular processes, including the locomotion of cells such as bacteria and spermatozoa. These organisms possess flagella, slender organelles whose time-periodic motion in a fluid environment gives rise to motility. Sitting at the intersection of applied mathematics, physics and biology, the fluid dynamics of cell motility is one of the most successful applications of mathematical tools to the understanding of the biological world.

Based on courses taught over several years, this book details the mathematical modelling necessary to understand cell motility in fluids, covering phenomena ranging from single-cell motion to instabilities in cell populations. Each chapter introduces mathematical models to rationalise experiments, uses physical intuition to interpret mathematical results, highlights the history of the field and discusses notable current research questions. All mathematical derivations are included for students new to the field, and end-of-chapter exercises help to consolidate understanding and practise applying the concepts.

ERIC LAUGA is Professor of Applied Mathematics at the University of Cambridge and a Fellow of Trinity College, Cambridge. He is the author or co-author of over 170 publications in the field of fluid mechanics, biophysics and soft matter. He is a recipient of a CAREER Award from the US National Science Foundation (2008), and of three awards from the American Physical Society: the Andreas Acrivos Dissertation Award in Fluid Dynamics (2006), the François Frenkiel Award for Fluid Mechanics (2015) and the Early Career Award for Soft Matter Research (2018). Eric Lauga is a Fellow of the American Physical Society.

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ERIC LAUGA
University of Cambridge

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To Dominique, Alexis, William and Raphaël

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Preface

Fluid dynamics plays a crucial role in numerous biological processes, from the largest animals to the smallest cells, and research activity at the intersection of fluid dynamics and biology has been steadily growing since the pioneering work of Taylor in the 1950s. Over the last 20 years, fluid mechanics conferences and journals have seen a stark increase in research relevant to, or inspired by, biology. An area of particular interest is the role of low Reynolds number flows in cellular life. Enabled by advances in microscopy and micromanipulation, experimental data have been used to inspire new models and enable hydrodynamic discoveries, while in turn quantitative theories using fluid mechanics have been precisely tested.

One area where this back and forth between theory and experiments has been very successful is the study of cell motility. Exemplified by the swimming of microorganisms such as bacteria and spermatozoa, this is an area where fluid dynamics has not only helped explain many natural phenomena but also one where biology has led to a new understanding of hydrodynamics. Several comprehensive review papers have been written on the subject but often they (including the ones I wrote) do not have all the space required to be fully pedagogical. In this book, I therefore chose to focus on the basic mathematical modelling tools and emphasise the key physical ideas behind active biological fluids.

This book develops, from first principles, the mathematical framework necessary to model and quantify the motion of active microorganisms in viscous fluids and applies these methods to understand a range of phenomena in cellular biophysics, from single-cell motion to instabilities in cell populations. Ideally, this book should be viewed as a case study in biological fluid dynamics, demonstrating how the tools of applied mathematics and continuum mechanics may be harnessed to provide quantitative and physical insights into the biological world. It is my hope that the methodology outlined here will be applicable to many other problems from nature and will inspire students to develop their own approach.

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The target audience for this book includes graduate or advanced undergraduate students in either fluid mechanics, applied mathematics or physics who are interested in problems at the intersection of physical and natural sciences. The reader of this book should be familiar with basic hydrodynamics at the undergraduate level, including the derivation of the mass and momentum conservation equations, the Navier–Stokes equations and their boundary conditions and the energy equation. Undergraduate knowledge of mathematical methods, as well as vector and tensor calculus, is also assumed.

Most of the chapters in this book evolved from a set of notes for a course in Part III of the Mathematical Tripos at the University of Cambridge, which had itself developed from lectures given at the University of California, San Diego and at various summer schools. Along with the lecture notes, I have also gathered over 90 relevant mathematical problems, so each chapter includes mathematical exercises to be used for further study or to be assigned as homework or exam questions. It was my goal for the final product to be sufficiently self-contained to be useable as a textbook.

This book has 15 chapters and is organised along three parts, with the roadmap on the next page showing how knowledge from a chapter is essential for a subsequent one. Part I (4 chapters) covers the fundamental biological, mathematical and physical background and presents idealised models of active locomotion; Part II (5 chapters) reviews the mathematical modelling of single-cell locomotion powered by flagella; Part III (6 chapters) is devoted to situations in which cells interact with their environment, either via a background flow, a complex or fluctuating fluid, other cells or boundaries.

The total sum of the work I carried out with many collaborators, postdocs and students has helped me gain a better understanding of the subject, and I am grateful for it. Thank you to P. Katsamba, L. Koens, M. Lisicki, E. Riley, T. Spelman, M. Tătulea-Codrean and K. Wan for giving me feedback on some chapters. Special thanks to A. Chamolly and W. Liao for going through the entire book with a fine and rigorous comb and M. Tătulea-Codrean for her help with the exercises. I am grateful to my colleague R. Goldstein for his feedback and advice and I also thank T. Montenegro-Johnson, D. Das and D. Brumley for their help with some of the figures. Finally, let me express my gratitude to my father, for lending his immense drawing skills to my book, and to my wife, for spending too many hours proofreading it.

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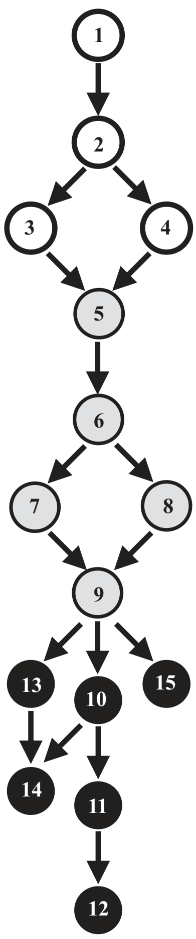

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