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The Mathematics and Mechanics of Biological Growth

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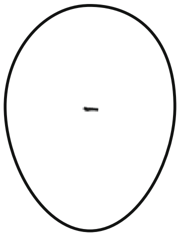
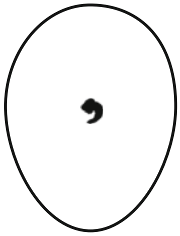


This book is dedicated to the 3Z:
Zébulon, Zakkai, and Zéphyr.
Not as an acknowledgement of their patience or help,
as they have none and gave me little,
but for the daily joy and chaos that they create
and for the fabulous examples of growth processes
that they generated over the last seventeen years.
My interest in growth conveniently coincided
with their birth and childhood.

Preface



To the nature lover, there is a distinct feeling of awe and beauty when observing the gradual development of a child, the slow growth of trees, the fine structure of a seashell, or the opening of a flower. Throughout human cultures and civilizations, philosophers, artists, and scientists have marveled and pondered at the cycle of life, the changes from an embryonic form to a newborn, the maturation of the newborn, and the constant physiological renewal of the adult. All these processes can be summarized by a single concept: growth. Growth provides an organism with the ability to adapt and control its environment through its life and through time. Growth is at the very core definition of life itself.

The problem of growth has been traditionally central to all aspects of biological research but of marginal interest to physicists, engineers, and mathematicians. However, in the last thirty years with the rise of medical bioengineering, biophysics, and mathematical biology, the problematic of describing and understanding growth quantitatively has become a main topic of multidisciplinary research.

Writing a book in an active field, spanning centuries of knowledge and covering multiple disciplines, is a risky proposition. The idea for this monograph came to me more than ten years ago when I realized that the general topics of mathematics of growth was becoming a central theme of research for many scientists in different communities. There was a clear need to bridge different concepts and ideas originating from multiple communities and, in particular, create a common language to describe phenomena appearing in different scientific disciplines. This monograph is an attempt in this direction.

Following my own interests and limited abilities, there is a strong bias in the choice of topics presented in this monograph.

First, most of the descriptions are at the continuum level, essentially from tissues to organs with very little discussion on cellular processes responsible for growth. Whereas much is known at the cellular level, our understanding of transduction mechanisms, linking cellular processes to tissue and organ growth, is still in infancy.

Second, the emphasis is on physical and mechanical aspects of growth at the level of organs and organisms but not at the population level. The mathematics of evolving populations of cells or individuals, and their coupling with chemical fields is well developed. It can be found in classic textbooks of mathematical biology and will not be repeated here.

Third, the theory is developed around modern concepts of solid mechanics and illustrated through the use of reduced simplified models that can be analyzed by the methods of applied mathematics. Unavoidably, the concepts may be advanced but the models are often simple. The hope is that these models provide some insight into the mechanisms governing growth and the interplay between growth, mechanics, and geometry. More realistic models would typically require both an extensive discussion of the underlying biological system and extensive computational analyses. I leave these tasks to the experts in these different fields.

Fourth, the emphasis is on the consequences of growth rather than on its origin. The discussion is mostly restricted to the analysis of tissue and organs made out of a single elastic component rather than the more general theory of mixtures that takes into account the coupling between fluids and various tissue components. These advanced theories for growth and remodeling have been used to develop realistic models but cannot be easily analyzed mathematically. They also require a more general computational framework that is still in development. My general philosophy is that little progress can be made for models with multiple components unless we have a thorough understanding of the simpler problems studied here.

Fifth, whereas I try to provide general introductions to different topics and key references to many authors, most of the topics presented here have come about through my own research projects. I have worked on these with various collaborators over the last twenty years. Therefore, this monograph is not an exhaustive review of the field as much as my personal views on the subject. I do not believe that it is the only approach or even that it is superior to other points of view. I would like to encourage other researchers to provide alternative, complementary, or contradictory approaches as it will only enrich the debate and help develop a general theory of growth. While I have tried to be thorough in citing relevant works in the literature, I have undoubtedly missed important references and, I can only apologize to the colleagues that I have offended in the process.

This book is designed to be at the quadruple interface of mathematics, biology, physics, and mechanics. Life at the interface is particularly rich and exciting as it takes advantage of ideas, concepts, and methods from different fields. It is also particularly dangerous as it is the ideal ecological zone for highly specialized predators. I expect that biologists will find the biological modeling over-simplistic and focussing on questions of little interest to them. I believe that many mathematicians will find the mathematical description too informal and lacking the rigor expected in various well-established disciplines ranging from partial differential equations to differential geometry. Some engineers may lament at the lack of finite-element simulations and detailed mechanical measurements. And, I fully expect that many physicists will view the treatment of mechanics as being too technical and unnecessarily complicated. These criticisms are all valid. It is the curse of interdisciplinarity to always fall short of the expectations required by disciplinary purity. But, it is only when these opprobriums will be bestowed on me that I will know that I have managed to reach different communities and that I may have attained some measure of success.

A Reader's Map

This book was conceived to be read at different levels, depending on the reader's interests and background. The difficulty is that a mathematical and mechanical theory of growth naturally combines aspects of biology, mathematics, and mechanics. The bio-mechanician with a good grip of solid mechanics may not always be familiar with some methods of applied mathematics. Similarly, many applied mathematicians and physicists, while often well trained in fluid mechanics, are not typically exposed to advanced concepts of solid mechanics. For the biologically trained but mathematically inclined readers, mathematics and mechanics may be appealing but may present technical difficulties. Accordingly, topics are presented in order of conceptual and mathematical difficulties.

Inspired by the structure of the excellent textbook "Nonlinear Dynamics and Chaos" by Steven Strogatz, I organized this monograph according to the dimensionality of the problem, starting in dimension one before considering problems in dimension two and only then presenting the general theory in three dimensions. Indeed, the coupling of growth and mechanics can be illustrated in simplified geometries where the fundamental concepts can be easily understood. Once these concepts are understood, they are progressively generalized.

Part I presents a general introduction to growth, hopefully accessible to all readers. It presents basic aspects and classification of growth processes and, more or less, use historical developments and abundant examples from biology and physiology to introduce key concepts relating biological growth to physical cues.

Part II was specifically developed for this monograph, both to introduce basic mechanical ideas such as elasticity, viscoelasticity, and plasticity; but also to illustrate the interplay between growth processes and mechanics. In the first chapter, I discuss the simplest instances of growth by restricting deformations along a line. In the process of writing this book, I realized that there was no general theory of growth for filamentary structures. With Derek Moulton and Thomas Lessinnes, we filled this gap and showed how to generalize the theory of elastic rods to include the effects of growth and remodeling. These ideas are used to model many interesting systems, mostly taken from the world of plants.

Part III further generalizes these concepts in simple two-dimensional geometries with applications to accretive growth problems such as seashells and microbial systems exhibiting tip growth. Most of the discussion of two-dimensional elastic surfaces is restricted to axisymmetric membranes and shells. The general problem of deriving a general theory of morphoelastic shells would require a few more chapters and only a short introduction to the general problem is given.

Part IV presents a general theory of growth for three-dimensional bodies based on the twin concept of evolving reference configuration and the multiplicative decomposition of the deformation gradient. This part starts with a brief description of the classic theory of nonlinear elasticity so that readers not versed in the language of large deformations mechanics can learn the basic tools. An extensive discussion on the kinematics of growth viewed as evolving configurations is presented. It is followed by a general discussion on growth laws, dynamics, and stability. The two last chapters are devoted to detailed examples and applications in spherical and cylindrical geometries.

Rather than providing a final conclusion to a field that is still blooming, I conclude, in Part V, with a list of ten challenges. It is my hope that these challenges will motivate other researchers and help move the field forward.

Oxford, UK Alain Goriely
2016

Acknowledgements

I am deeply indebted to a number of friends and collaborators. First, it is with great pleasure that I acknowledge the influence of Michael Tabor on both my professional and intellectual life. Twenty years ago, tired of playing with problems in the theory of integrability, Michael and I decided to look at problems related to growth and mechanics. At that time, we knew next to nothing about rods, membranes, nonlinear elasticity or growth. All we had were a few questions that we thought deserved to be investigated and a few methods from applied mathematics that people did not seem to be using in mechanics. We taught each other the basics and tried to model simple systems, inching our way to a better understanding. Many of the basic ideas and applications presented in this book were born out of these discussions.

Another major influence on this work was my collaboration with Martine Ben Amar. During a sabbatical in Paris, we learned the foundations of rational mechanics and developed together the theory of growth-induced instabilities for nonlinear elastic systems. It was an exciting time of scientific discovery and it remains one of the best academic years of my life.

I would also like to acknowledge the many striking contributions of Derek Moulton through our years of collaboration. In his own work, Derek has been exploring the consequences of growth in many different settings and, doing so, has systematically propelled the field forward. We have been partners in crime for many years, shared the meager rewards of our malfeasance, and paid the price for our idiosyncratic interests. I hope that his punishment will be lighter than mine.

Many of the ideas discussed in this monograph are also the product of many years of work, discussions, reflection, and meetings with my collaborators. In particular, I have tremendously benefited from my interactions with Jon Chapman, Régis Chirat, Michel Destrade, Marcelo Epstein, Krishna Garikipati, Ray Goldstein, Andrew Hausrath, Ellen Kuhl, Thomas Lessinnes, John Maddocks, Angela Mihai, Sébastien Neukirch, Giuseppe Saccomandi, Dominic Vella, Sarah Waters, John Wettlaufer, and Arash Yavari. I take this opportunity to let them know that their intellect and friendship are precious to me.

Central to all academic endeavors is the training and interactions with students. I have been very lucky to be able to supervise several bright students whose hard work features prominently here: Alexandre Erlich, Georgina Lang, Tyler McMillen, Andrey Melnik, Joe McMahon, and Rebecca Vandiver.

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