

Undergraduate Lecture Notes in Physics

Fabrizio Cleri

# The Physics of Living Systems



Springer

# **Undergraduate Lecture Notes in Physics**

Undergraduate Lecture Notes in Physics (ULNP) publishes authoritative texts covering topics throughout pure and applied physics. Each title in the series is suitable as a basis for undergraduate instruction, typically containing practice problems, worked examples, chapter summaries, and suggestions for further reading.

ULNP titles must provide at least one of the following:

- An exceptionally clear and concise treatment of a standard undergraduate subject.
- A solid undergraduate-level introduction to a graduate, advanced, or non-standard subject.
- A novel perspective or an unusual approach to teaching a subject.

ULNP especially encourages new, original, and idiosyncratic approaches to physics teaching at the undergraduate level.

The purpose of ULNP is to provide intriguing, absorbing books that will continue to be the reader's preferred reference throughout their academic career.

## **Series editors**

**Neil Ashby**  
University of Colorado, Boulder, CO, USA

**William Brantley**  
Department of Physics, Furman University, Greenville, SC, USA

**Matthew Deady**  
Physics Program, Bard College, Annandale-on-Hudson, NY, USA

**Michael Fowler**  
Department of Physics, University of Virginia, Charlottesville, VA, USA

**Morten Hjorth-Jensen**  
Department of Physics, University of Oslo, Oslo, Norway

**Michael Inglis**  
SUNY Suffolk County Community College, Long Island, NY, USA

**Heinz Klose**  
Humboldt University, Oldenburg, Niedersachsen, Germany

**Helmy Sherif**  
Department of Physics, University of Alberta, Edmonton, AB, Canada

More information about this series at <http://www.springer.com/series/8917>

Fabrizio Cleri

# The Physics of Living Systems



Springer

Fabrizio Cleri  
IEMN, CNRS UMR8520  
Université de Lille I Sciences et  
Technologies  
Villeneuve d'Ascq  
France

ISSN 2192-4791                    ISSN 2192-4805 (electronic)  
Undergraduate Lecture Notes in Physics  
ISBN 978-3-319-30645-2        ISBN 978-3-319-30647-6 (eBook)  
DOI 10.1007/978-3-319-30647-6

Library of Congress Control Number: 2016948100

© Springer International Publishing Switzerland 2016

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, express or implied, with respect to the material contained herein or for any errors or omissions that may have been made.

Printed on acid-free paper

This Springer imprint is published by Springer Nature  
The registered company is Springer International Publishing AG Switzerland

*A mio padre e mia madre,  
che mi hanno lasciato in eredità  
la dolcezza di un mondo antico.*



*You'll get mixed up  
with many strange birds as you go.  
So be sure when you step.  
Step with care and great tact  
and remember that*

***Life's a Great Balancing Act.***

*Just never forget to be dexterous and deft,  
and never mix up your right foot with your left.*

Dr. Seuss, Oh, the places you'll go! Random House, 1990

# Preface

Before diving head to feet into the subject matter, a few words are in order to provide the moral excuse for writing this book and to give me the opportunity to tell a story that goes back to the year 2006.

When I arrived as a full professor in the Department of Physics of the University of Lille, the Director of that time, Michel Foulon, wanted the newly hired professor (it would be great if I could add “young” here, but I was already 45 at that time) to break some walls and open some original routes in research and teaching. I will always express my warmest thanks and deepest gratitude to Michel, for the wide freedom he allowed me in the choice and organisation of the new enterprise.

A quick look around Lille, a medium-sized, very lively city in the upper north of France, right next to the border with Belgium, gave me the obvious answer. With its about seventy institutes and laboratories revolving around biology, genetics, biotechnology, medical and clinical R&D, especially (but not exclusively) focussed on cancer research and therapy, *biophysics* was the way to go. It would have been a somewhat new field for me, but not far from my scientific interests at that time.

Thus, I started assembling an undergraduate school (“master”, according to European nomenclature) with some colleagues from the Institut Pasteur, the Institut de Biologie and the Interdisciplinary Research Institute from CNRS, of course the Department of Physics, and my own CNRS Institut de Microélectronique et Nanotechnologie. The key idea was to shake up a cocktail of fundamental research in biophysics and applications in medical physics. The latter had its stronghold in the Oscar Lambret Cancer Therapy Center, just at the opposite end of the subway from the university. It was there that I met the brilliant Thierry Sarrazin, soon to become my best partner in crime, with whom I could put together a master programme in medical physics to be coupled with the programme in biophysics. Since its opening in 2010, this has been a successful story. Our new master in Biological and Medical Physics has attained a stable number of students, improving both the teaching throughput of the Department and the research potential of the laboratories, which now have a privileged route to attract some of our best students to the enormously exciting area of biophysical research.

Then, what is the place of this book? Already before the formal creation of the master course, I had started teaching biophysics units at various levels. As a theorist, I had chosen this way to learn about the basics, while increasingly redirecting my own research interests towards two main subjects: molecular mechanics of cell constituents, and microscopic radiation effects on the nucleic acids DNA and RNA. However, since the very beginning I realised that it was the very youngest students, second- or third-year undergraduate, who had to be exposed to introductory subjects of biophysics as early as possible. Without such an early exposure, there would be no ‘feeding’ for the students towards the more advanced subjects, and the master courses of the 4th and 5th years would have fallen from the sky, onto the shoulders of completely unprepared students. For that reason, I created from scratch a course of Introduction to the Physics of Living Systems for the physics sophomore. The idea was not to introduce much new physics for these students, but rather use their already acquired, albeit still elementary, knowledge about thermodynamics, mechanics, fluid physics, and electricity, to start *seeing* the physics behind the biology. Second-year students are still enough close to the high school to have some basic biology in their backpack, and that’s all that was needed. The course was original in its layout, trying not to follow the much abused path of ‘unveiling hidden physical principles underlying biological facts’. Rather, in the footsteps of D’Arcy Thompson, J.S.B. Haldane, Archibald Hill, and the more modern Knut Schmidt-Nielsen, Steven Vogel, J.C. Pennycuick and few others, I wanted to *start from physics* and show how living organisms *must conform* to the inevitable bounds imposed by gravity, light, temperature, atmosphere, oceans of the Earth, and by the more general constraints deriving from such life-setting variables as the water phase diagram, oxygen diffusivity, molecular elasticity, to name just a few.

This book evidently stems from the lecture notes for that course. Clearly, this is not a book for the research scientist in biophysics: the level is too elementary, the maths goes little beyond high school basics (at least for the *franco-français* students), and the subjects are well assessed and could not truly represent the last cry in biophysics research. It is primarily intended as a biophysics primer for young students, and, by just skipping a few pages too dense in formal math developments, it should be a pleasurable reading also for educated professionals working in the area of life sciences.

The physics inherent to living systems is immense and challenging. Where a physicist seeks mathematical rigour and experimental repeatability under extremely well-controlled conditions, the biologist rather seeks inductive proof, statistical correlations and performs hugely complex experiments with a whole bunch of competing (and often ill-known) free parameters. Biophysics is sometimes considered with a bit of a raised eyebrow by ‘purist’ colleagues: it may be felt that it requires sometimes too simple experiments, and too little theory, to keep the pace with ‘big-time’ physics such as superstring theory, tokamak magnetohydrodynamics, or the quest for the Higgs boson. However, the more I delve into the subject, the more interesting questions and puzzling connections I discover. To me, the fact that a simple experiment assembled in the backyard of the laboratory, or a

crystal clear piece of non-quantum, non-relativistic theory, or even a back-of-the-envelope calculation of a dimensionless number, could reveal a crucial information about the living, represents instead a great advantage and a fascinating opportunity.

Experienced readers will notice that the subject matter treated in this book is partly covered, and often with much deeper scope, in several other texts, such as (to cite just a few prominent ones) *Physics of life* by Clas Blomberg, *Biological physics* by Philip Nelson, *How animals work* by Knut Schmidt-Nielsen, *Comparative biomechanics, or Life's physical world* by Steven Vogel, *Physical biology of the cell* by Phillips, Kondev & Theriot, *Newton rules biology* by C.J. Pennycuick.

However, both the breadth of subjects touched upon and the pedagogical approach followed here should be unlike any of the above, highly commendable and respected works. The keywords behind the present effort can be summarised in the following three concepts:

1. use the least possible amount of mathematics and molecular chemistry, and provide a minimum necessary knowledge of cell and structural biology;
2. propose a wide subject coverage, with a macro → micro → macro logical path: start from the macroscopic world, namely the thermodynamics of the Universe and the Solar system, and, via such subjects as the greenhouse effect and energetics of metabolism, step down to the microscopic world (physics of bacteria and unicellular life, cells and tissues, biomolecules); hence, move again upwards in length- and timescales to the physics of organs and whole organisms, and end up with subjects in zoology (e.g. simplified aerodynamics of insect flight, energy budget for the survival and reproduction of a flock of animals), and planetary ecology (species competition in the Biosphere, limits of ecosystems);
3. exploit as much as possible the physics knowledge base of second-year undergraduate students (elementary thermodynamics, classical mechanics and electrokinetics, elementary fluid mechanics), without need to introduce more complex notions, unless strictly necessary.

The book can be approached at least at two different levels, by different groups of readers, namely: as an undergraduate textbook in introductory biophysics and as a “case of curiosities” for professionals working in the vast life sciences and biomedical domains. For the first approach, each chapter contains the necessary background and tools, including exercises and Appendices, to form a progressive course. In this case, the chapters can be used in the order proposed by the index, eventually split over two semesters (Chaps. 5–9 covering somewhat more advanced subjects, susceptible of further developments). For the second approach, the curious but less physics-oriented reader might skip the first chapter (if school memories of thermodynamics are still haunting his/her dreams), as well as all the grey boxes containing the more formal developments, and create his/her own menu of chapters *à la carte* (with the only author’s suggestions of reading Chap. 8 before Chap. 9, and Chap. 10 before Chap. 11). Also, note that the bibliographical references at the end of each chapter are not intended to provide a fully detailed support for all the

subjects treated, as it would be the case for a scientific paper, but rather to merely propose some possible directions of development.

No book will ever be complete and definitive, and this one can be no exception. In particular this one, I should say. The material has been expanding over the years, some subjects leaving the place to newer ones according to my own curiosity, or to the discovery of interesting scientific papers amenable to an easily accessible level. Had I kept going with including any new items that came to my attention as a teacher, I would have never written this book. However, one has to stop somewhere, to give account of the state of the house at a given point. Hopefully, others will continue this effort and provide it with more motivation, better writing, deeper substance, nicer examples and smarter problems. Hopefully, among these there could be one of my former students or one of the readers of this book. In any case, it is my hope that in reading this book, be it for an introductory course as a student, or for a curiosity refresher as a practicing life scientist, your interest and attention towards biophysics could only increase.

Todi, Italy  
April 2016

Fabrizio Cleri

This work has been possible also thanks to the many colleagues and students with whom I have been interacting, during all these years. Whereas discussing with colleagues is (almost) always a pleasure and a good occasion for funny jokes, the daily exchange with students is definitely the most refreshing and challenging moment. I am grateful to all those people who had the patience of listening to me, advising and correcting my mistakes, and helping me to find better and better ways to transmit the message. And I know it is not over yet.

Special thanks are in order for those colleagues and friends who took the burden of reading early versions of the various chapters and could bring their precious comments, criticisms, enlightenments to my ongoing, often immature work. In alphabetical order: Angela Bartolo, Bruno Bastide, Ralf Blossey and Jean Cosleou (Lille), Enrico Carlon (Leuven), Dominique Collard (Tokyo), Luciano Colombo (Cagliari), Antonio Di Carlo (Rome), Bahram Djafari-Rouhani, Alessandro Faccinetto, Stefano Giordano and Frank Lafont (Lille), Rob Phillips (Pasadena), Felix Ritort (Barcelona), Paola Salvetti (Dubai). However, for any error, imprecision or misprint still lurking in the text, the responsibility must be fully charged to the author.

I am grateful to the people at Springer who invested their energies and resources to propose this book to the public, especially to Maria Bellantone, who constantly encouraged and guided me in the pursuit of this project, and to the editorial assistants Annelies Kersbergen and Mieke van der Fluit.

# Contents

<b>1</b>	<b>Introduction</b>	1
<b>2</b>	<b>Thermodynamics for Living Systems</b>	9
2.1	Macroscopic and Microscopic	9
2.1.1	Isolated System	12
2.1.2	Energy	13
2.1.3	Heat	13
2.2	Perfect Gas	14
2.2.1	Counting Microstates	15
2.3	Entropy and Disorder	17
2.3.1	Irreversibility and Probability	19
2.4	Closed Systems	20
2.4.1	Temperature	22
2.4.2	Caloric Definition of the Entropy	23
2.5	Free Energy	25
2.5.1	Exchanges of Energy at Constant Volume	26
2.5.2	Exchanges of Energy at Constant Pressure	27
2.6	Open Systems	27
2.6.1	Entropy of a Mixture	29
2.7	The Biosphere as a Thermal Engine	30
2.7.1	A Synthesis of Photosynthesis	35
2.8	Energy from the Sun	38
2.8.1	The “Greenhouse” Effect	39
2.8.2	The Temperature of the Earth’s Surface	41
Appendix A:	Some Useful Mathematical Tools	45
Problems		54
References		58
<b>3</b>	<b>Energy, Information, and The Origins of Life</b>	61
3.1	Thermodynamics, Statistics and the Microscopic	61
3.1.1	A Probability Interlude	64

3.2	Life and the Second Principle . . . . .	68
3.3	Impossibility of Spontaneous Aggregation . . . . .	72
3.4	Complexity and Information . . . . .	73
3.4.1	Free energy for the Synthesis of Biomolecules . . . . .	78
3.5	Against All Odds . . . . .	80
3.6	Modern Theories About the Origins of Life on Earth . . . . .	83
3.6.1	Not just a Bag of Molecules . . . . .	86
3.6.2	The RNA World . . . . .	87
3.6.3	Abiotic Hypotheses . . . . .	89
3.6.4	Between Quiet and Thunder . . . . .	89
3.6.5	And Still Thinking . . . . .	96
	Appendix B: From DNA to Proteins (and Back) . . . . .	97
	Problems . . . . .	109
	References . . . . .	110
<b>4</b>	<b>Energy Production and Storage for Life . . . . .</b>	<b>113</b>
4.1	From Food to ATP . . . . .	113
4.2	Storage of Energy in the Cell . . . . .	115
4.3	Energy-Converting Membranes . . . . .	117
4.4	Krebs' Cycle and the Production of ATP . . . . .	121
4.4.1	The Role of the Enzymes . . . . .	124
4.5	Electrons and Protons Flowing . . . . .	128
4.6	Energy Yield in the Cycle . . . . .	134
4.7	Temperature and Heat in the Animal Body . . . . .	136
4.7.1	Temperature Monitoring . . . . .	138
4.8	Heat from the Cells . . . . .	140
4.8.1	Fever and Hyperthermia . . . . .	144
4.8.2	Metabolic Rate and Thermogenesis . . . . .	145
4.8.3	Of Brown Fat, Alternative Respiration, and Thermogenic Plants . . . . .	147
	Appendix C: The Molecules of Life . . . . .	149
	Problems . . . . .	155
	References . . . . .	158
<b>5</b>	<b>Entropic Forces in the Cell . . . . .</b>	<b>159</b>
5.1	Thermodynamic Forces . . . . .	159
5.2	The Strange Case of Osmosis . . . . .	161
5.2.1	Microscopic Model . . . . .	163
5.2.2	Thermodynamic Model . . . . .	164
5.2.3	Osmolarity and the Healthy Cell . . . . .	165
5.3	Hydrophobicity, Depletion and Other Entropic Forces . . . . .	167
5.3.1	The Depletion Force Between Large Objects in Solution . . . . .	169
5.3.2	Steric Forces and Excluded Volume . . . . .	172

5.4	Diffusion Across a Membrane . . . . .	174
5.4.1	Permeability and the Partition Coefficient . . . . .	181
5.5	Forced Flow in a Channel . . . . .	182
5.6	Moving Around in a Fluid World. . . . .	188
5.6.1	Brownian Swimmers . . . . .	191
5.7	Squeezing Blood Cells in a Capillary . . . . .	193
	Appendix D: Membranes, Micelles and Liposomes . . . . .	195
	Problems . . . . .	200
	References . . . . .	202
<b>6</b>	<b>Molecular Motors in the Cell . . . . .</b>	<b>205</b>
6.1	Molecular Motors . . . . .	205
6.2	The Mechanics of Cyclic Motor Proteins . . . . .	207
6.2.1	Two-State Model of a Machine . . . . .	211
6.2.2	Continuous Energy Surfaces . . . . .	213
6.3	The Thermal Ratchet Model . . . . .	216
6.4	Symmetry-Breaking Transformations . . . . .	221
6.4.1	The Tubulin Code . . . . .	224
6.5	Cell Shape and Cytoskeleton Polymerisation . . . . .	226
6.5.1	Polymerisation Dynamics and the Treadmill Effect . . . . .	227
6.6	Variations on a Theme of Polymers . . . . .	229
6.6.1	Enzymatic Reactions and Kinetics . . . . .	233
6.7	The Movement of Unicellular Organisms . . . . .	236
6.7.1	Linear Translation with Drag . . . . .	238
6.7.2	Rotatory Translation with Drag . . . . .	240
6.7.3	Swimming Without Paddling . . . . .	242
	Appendix E: The Cytoskeleton . . . . .	244
	Problems . . . . .	249
	References . . . . .	251
<b>7</b>	<b>Bioelectricity, Hearts and Brains . . . . .</b>	<b>253</b>
7.1	Cells Processing Electromagnetic Information . . . . .	253
7.1.1	The Eyes of a Plant . . . . .	255
7.1.2	Birds and Flies Can See a Magnetic Field . . . . .	256
7.1.3	The Neuron . . . . .	257
7.1.4	The Neuromuscular Junction . . . . .	260
7.2	The Electric Potential of the Membrane . . . . .	262
7.2.1	Passive and Active Diffusion . . . . .	262
7.2.2	The Nernst Equation . . . . .	265
7.2.3	Polarisation of the Membrane . . . . .	267
7.3	The Membrane as a Cable . . . . .	271
7.4	Excitation of the Neurons . . . . .	275
7.5	The Action Potential . . . . .	278
7.5.1	The Hodgkin-Huxley Model of the Membrane . . . . .	278

7.6	Transmission of the Nerve Impulse . . . . .	282
7.6.1	Wave-Like Propagation of the Impulse . . . . .	283
7.6.2	The Refractory Period and Orthodromic Conduction . . . . .	285
7.7	Brain, Synapses, Information . . . . .	288
7.7.1	Electrical Model of the Synapse . . . . .	290
7.7.2	Treatment of the Neuronal Information . . . . .	293
7.8	Cells in the Heart . . . . .	296
7.8.1	The Rhythm and the Beat . . . . .	300
7.9	Electricity in Plants? . . . . .	303
Appendix F:	The G-H-K equations . . . . .	306
Appendix G:	Electric Currents for Dummies . . . . .	307
Problems . . . . .		313
References . . . . .		315
<b>8</b>	<b>Molecular Mechanics of the Cell . . . . .</b>	<b>317</b>
8.1	Elastic Models of Polymers . . . . .	317
8.1.1	The Freely-Jointed Chain . . . . .	319
8.1.2	The Worm-Like Chain . . . . .	326
8.2	Biological Polymers . . . . .	328
8.2.1	Bending Fluctuations and the Persistence Length . . . . .	328
8.2.2	Elasticity From Entropy . . . . .	331
8.2.3	Pulling Nanometers with Piconewtons . . . . .	334
8.3	Mechanics of the Cell Membrane . . . . .	337
8.3.1	The Minimal Free Energy Model . . . . .	340
8.3.2	A More Refined Curvature Model . . . . .	342
8.3.3	Temperature and Entropy Fluctuations . . . . .	345
8.4	Deformation Energy . . . . .	347
8.4.1	Membrane Protrusions and Cell Crawling . . . . .	348
8.4.2	The Shape of a Bacterium . . . . .	351
8.5	How a Cell Splits in Two . . . . .	354
8.5.1	Chromosome Condensation . . . . .	356
8.5.2	Assembly of the Mitotic Spindle . . . . .	357
8.5.3	Assembly of the Contractile Ring . . . . .	361
Problems . . . . .		364
References . . . . .		365
<b>9</b>	<b>The Materials of the Living . . . . .</b>	<b>367</b>
9.1	Stress and Deformation . . . . .	367
9.1.1	The Biologist and the Engineer . . . . .	371
9.1.2	Brittle and Ductile . . . . .	373
9.2	The Viscoelastic Nature of Biological Materials . . . . .	376
9.3	Soft Tissues . . . . .	381
9.3.1	Where Soft Turns Hard . . . . .	385

9.4	Tissues That Are Neither Solid nor Liquid . . . . .	386
9.4.1	Cartilage . . . . .	387
9.4.2	Tendons . . . . .	391
9.5	Rigid as Bone . . . . .	393
9.6	Strong as Wood . . . . .	397
9.6.1	Tension and Compression . . . . .	400
9.6.2	Bending and Twisting . . . . .	402
	Appendix H: Materials Elasticity Theory for Dummies . . . . .	407
	Problems . . . . .	417
	References . . . . .	420
<b>10</b>	<b>Of Limbs, Wings and Fins . . . . .</b>	<b>423</b>
10.1	Force and Movement Produced by a Muscle . . . . .	423
10.2	Dynamics of Muscle Contraction . . . . .	429
10.3	Mechanical Efficiency and Cyclic Contraction . . . . .	430
10.3.1	Cyclic Contraction . . . . .	432
10.4	Optimised Muscles . . . . .	433
10.4.1	Aerobic and Anaerobic Muscles . . . . .	435
10.5	The Flight of an Insect . . . . .	438
10.5.1	Synchronous and Asynchronous Muscles . . . . .	440
10.5.2	The Power Output of an Insect's Muscle . . . . .	442
10.5.3	Simplified Aerodynamics of Flapping Wings . . . . .	444
10.6	How to Choose Right Variables and Units . . . . .	448
10.6.1	Observables, Their Dimensions, and Their Measurement . . . . .	451
10.7	Dimensional Analysis: Animals that Walk and Run . . . . .	453
10.7.1	More Variables and The Buckingham $\pi$ -Theorem . . . . .	456
10.8	Flying Animals and Wingbeat Frequency . . . . .	459
10.8.1	From Birds to Insects . . . . .	463
10.9	Dimensional Analysis: Animals Who Live in Water . . . . .	466
	Problems . . . . .	470
	References . . . . .	472
<b>11</b>	<b>Shapes of the Living . . . . .</b>	<b>475</b>
11.1	Surface Forces and Volume Forces . . . . .	475
11.2	Capillarity, Growing Trees and Water-Walkers . . . . .	478
11.2.1	Insects Who Can Walk on the Water . . . . .	479
11.2.2	The Branching of Trees . . . . .	481
11.3	Curved Surfaces and Minimal Surfaces . . . . .	484
11.3.1	How the Space Can Be Filled . . . . .	487
11.3.2	Limiting Shapes, Stability and Instability . . . . .	491

11.4	Surfaces of Revolution, Seashells and Gastropods . . . . .	493
11.5	Conformal Mapping and the Evolution of Species . . . . .	499
11.6	The Emergence of a Body Plan . . . . .	503
11.6.1	Reaction-Diffusion and Pattern Formation . . . . .	507
11.6.2	Pattern Formation and Gene Expression . . . . .	510
11.7	Phyllotaxis, The Spacing of Leaves . . . . .	515
11.7.1	Getting Away from Fractions . . . . .	518
	Problems . . . . .	523
	References . . . . .	525
<b>12</b>	<b>The Hidden Mathematics of Living Systems . . . . .</b>	<b>527</b>
12.1	Changing Size Without Changing Shape . . . . .	527
12.1.1	Allometry and Scaling . . . . .	529
12.2	Scaling Laws for Animal Locomotion . . . . .	531
12.2.1	Scaling Law for the Characteristic Frequencies . . . . .	533
12.2.2	Walkin' the Dog . . . . .	534
12.3	Paleontology, Or When Animals Were Huge . . . . .	536
12.4	Scaling Laws for Energy Consumption . . . . .	540
12.4.1	Choosing a Mode of Transport . . . . .	541
12.5	Energy Stocks for the Offspring . . . . .	543
12.6	Analytical Models of Population Growth . . . . .	544
12.6.1	Preys and Predators . . . . .	549
12.6.2	Competition and Cooperation Between Species . . . . .	552
12.7	Dynamical Models in Ecology . . . . .	554
12.8	The Limits of the Ecosystems . . . . .	560
12.8.1	Trophic and Non-trophic Interactions . . . . .	563
12.8.2	Linear Models of Structured Population . . . . .	566
	Problems . . . . .	569
	References . . . . .	571
<b>13</b>	<b>Solutions to the Problems . . . . .</b>	<b>573</b>
	<b>Physical Units, Constants and Conversion Factors . . . . .</b>	<b>609</b>
	<b>Index . . . . .</b>	<b>613</b>

# List of Appendices

Since this book is intended as an introduction to biophysics for a public of undergraduate students, as well as for the physics-curious professional in life and health sciences, the continuity of the main text was privileged. Therefore, background notions are relegated in ample and illustrated Appendices, including the minimum mathematical toolbox (Appendix A, and F–H), and some essential notions in molecular and cell biology (Appendix B–E).

In particular the latter could appear excessively superficial and stripped-down versions of the immense amount of knowledge embodied by modern biology. I am including here such a very synthetic account for the sake of completeness, with the aim of providing the uneducated readers with just some basic vocabulary. Those who have a more substantial knowledge of biology will hopefully spare a benevolent look at my humble effort.

A. Some Useful Mathematical Tools.....	45
The Gamma Function	
Dirac's Delta Function	
Gauss and Euler Integrals	
The Stirling Approximation	
Vector Calculus and Analysis	
Simple Tensor Algebra	
Simple Fourier Analysis	
B. From DNA to Proteins (and Back).....	97
DNA Chromatin and Chromosomes	
DNA Transcription and Translation	
A few Words on Epigenetics	
C. The Molecules of Life .....	149
D. Membranes, Micelles, Liposomes.....	195
E. The Cytoskeleton .....	244
F. The G-H-K Equations.....	306

G. Electric Currents for Dummies . . . . .	307
Current and Resistance	
Capacitor	
Kirchhoff's Laws	
Maxwell's Equations	
H. Materials Elasticity Theory for Dummies . . . . .	407
Stres	
Strain	
Elastic Constants and Strain Compliances	
Elastic Moduli for Solid Materials	
Bulk Modulus	
Shear Modulus	
Young's Modulus	
Elastic Deformation Energy	

# List of Greyboxes

Greyboxes are special sections of a chapter, in which mathematical treatments and/or more advanced concepts are developed. They are marked with a grey background and may be skipped by the reader less interested in the formal developments, without compromising the readability of the main text.

Mechanical equilibrium of a perfect gas under pressure . . . . .	24
The Gibbs–Duhem equation . . . . .	28
Transformation of free energy into mechanical work. . . . .	31
The energy stored in a tree . . . . .	37
The method of Lagrange multipliers . . . . .	65
What’s in a bacterium . . . . .	71
Radiochemical dating of the ancient earth. . . . .	91
Beta-oxidation and the degradation of lipids . . . . .	118
The thermodynamic function of enzymes and the $\Delta G$ of chemical reactions . . . . .	126
Electron transfer and REDOX equilibrium . . . . .	131
Heat equation for macroscopic bodies . . . . .	141
Osmotic pressure and surface tension in the cell . . . . .	166
Electrostatics of colloidal particles in ionic solutions . . . . .	175
Random walks and the Brownian motion . . . . .	178
The forced viscous flow equation . . . . .	185
The rectified Brownian motion . . . . .	218
Michaelis–Menten kinetics . . . . .	234
Ohm’s law and the diffusion of ionic charges . . . . .	268
The cable equation . . . . .	272
Maxwell’s equations and extracellular potentials . . . . .	281
Synchronisation of random oscillators . . . . .	299
Bending of rods and membranes . . . . .	322
The force-extension curve of a free polymer . . . . .	333