The confluence of mathematics and biology is central to scientific advancement in the 21st century. Challenges as diverse as global climate change, pharmaceutical design, emergent diseases, and genomics-age medicine all require scientists and mathematicians with expertise in both fields. And yet, the development of undergraduate curriculum standards and model programs in mathematical biology has been sporadic and slow. This report, intended to stimulate discussion among mathematical scientists, reviews recent developments in mathematical biology education and proposes foundational courses and mathematical competencies that should be part of any undergraduate program in mathematical biology.

Despite the centrality of mathematical insight for ecology, evolution, neurophysiology, and population genetics, undergraduate mathematics has enjoyed less synergy with the life sciences than with physics, engineering, and economics.

Attempts to connect pedagogy and curricula of the two disciplines go back at least to the Cullowhee Conference on Training in Biomathematics held in 1961 at Western Carolina University, attended by many of the leading mathematical biologists of that time. Many of the issues addressed there remain important: Should there be different mathematics courses or training programs for biology students than for other engineering and science students? Why did biology courses then focus mainly on detailed information about particular aspects of biological systems, with little emphasis on experiential learning? A significant number of textbooks were developed in the 1970s for courses primarily focused on calculus with some biological examples. As a rule, however, these texts made little use of actual data, and sought mainly to motivate mathematical topics through biological examples. Most of these texts were out of print by the early 1990s, and the courses they had served had morphed into surveys of calculus for a mixed population of social and life science students. The few courses that survived were either based in life sciences (not mathematics) departments, or were at a few institutions with a significant group of biology researchers based in mathematics departments.

By the early 1990’s, there were few mathematics courses designed specifically for life science students and many bench biologists remained unconvinced of the need for quantitative education. But several workshops on education in mathematics for biology students led to an appreciation for a broader view of mathematics education for life science students that incorporated the diversity of mathematics, aside from just calculus, and several textbooks (Adler, Brown and Rothery, Neuhauser) arose that re-invigorated the offering of courses in math departments that focused on the needs of life science students. Concurrent with these texts, the
fields of bioinformatics and computational biology were beginning to flower, organismal biology became ever more quantitative with the development of new instrumentation, epidemiology continued its trends towards modeling to provide guidance to public health and the numerous fields converged to create transdisciplinary sciences such as neurobiology. This led to a more integrated view of life science education, heralded in the NRC Bio2010 report, which explicitly argued for incorporation of a diversity of mathematical topics throughout biology courses and not simply isolated in the mathematics and statistics courses undergraduates in the life sciences were being required to take.

Thus, the state of biology education with respect to mathematics is largely settled. The major reports on biology education since the Bio2010 report (including the HHMI/AAMC and the NSF/AAAS Vision and Change in Undergraduate Biology Education) all emphasize the benefits of an integrative, multi-disciplinary view of modern biology with quantitative concepts and skills being a central component. With major support from the NSF for programs such as UBM and CCLI (now TUES), a large number of model programs and curricular modules have been developed to incorporate quantitative methods in biology courses, to utilize modeling approaches to analyze problems across many levels of the biological hierarchy, and to integrate simulation and visualization methods with mathematical analysis to illustrate the power of quantitative approaches to address biology. Guidance is now available from numerous institutions (see the Math and Bio2010 report and the MAA Notes volume) so that examples can be tailored to local needs.

The state of mathematics education with respect to biology however, is harder to pin down. Many individuals have developed successful courses on their own, but few fully developed programs in biomathematics have arisen, especially at smaller institutions. We note that there have been many professional initiatives. These include the formation of BioSIGMAA, the special interest group of the MAA focusing on computational and mathematical biology; the (now defunct) NSF funded UBM program, textbooks (e.g., those of Adler, Neuhauser, Robeva et al., Allman and Rhodes) as well as conferences and workshops (e.g., MAA-PREP workshops). Professional organizations, such as the Society for Mathematical Biology and curriculum committees of the MAA have also weighed in. The views of the latter can be found in The CRAFTY Report of 2000 (www.maa.org/cupm/crafty/cf_project.html) as well as the 2004 CUPM Curriculum Guide (http://www.maa.org/cupm/part1.pdf -- see Recommendations 3 and 4). The first of these reports, however, addresses the needs of biology students (rather than mathematical biology or biomathematics students), and the second simply encourages collaboration between mathematicians and biologists, without any specifics. The Mathematical Biosciences Institute (MBI) and the National Institute for Mathematical and Biological Synthesis (NIMBioS) have taken strong leadership roles to promote research and professional development in biomathematics, and each has run an occasional education workshop. However, neither institute has undergraduate education as a major focus of its mission. The bottom line is that while many are interested, no centralized leadership has emerged.

The barriers are legion: David Bressoud remarks on some of the challenges in his 2005 “Launchings” column: (http://www.maa.org/columns/launchings/launchings_06_05.html)

Biology programs will not require additional mathematics for its own sake. In fact, none of the traditional mathematics courses, as currently constituted really meet the needs of most biology majors…. The other piece of the challenge is to put in place faculty who can foster and support
such an interdisciplinary approach. Too often, programs that span mathematics and biology are the exclusive preserve of one biologist and one mathematician who have each made a stretch to establish a connection that will break as soon as either tires. The problem is not just a shortage of scholars with suitable training. We must also overcome institutional obstacles to the accommodation of those individuals who bridge the disciplines.

In the view of this committee, these challenges remain. This committee is especially cognizant of the need to present recommendations that respect departmental autonomy, so as to accommodate a variety of institutional attitudes toward interdisciplinary curricula as well as departmental (and interdepartmental) staffing challenges. To that end, we outline two foundational courses, indicate some directions for more advanced undergraduate study, and present a list of fundamental mathematical competencies. We conclude with some recommendations regarding biological competencies.

Throughout, we have in mind as our audience departments of mathematics at liberal arts colleges, research and comprehensive universities, and community colleges. Such departments may wish to construct a new major or minor, a concentration within an existing major or an interdisciplinary concentration attached to an existing major. Our hope is that by presenting competencies rather than prescribed mathematical content, we will provide the flexibility needed for multiple routes to success, based on local capabilities. This is especially important given the enormous breadth of biology as a discipline.

**Foundational Courses and Competencies**

Much of what is fundamental for mathematics students who are interested in modern quantitative biology would fit into two basic courses – one that focuses on the practice of modeling, and the other on the analysis and exploration of data. Below we describe some suggested content. Though basic, these courses would likely have some mathematical and perhaps also life sciences prerequisites, but they need not take this exact form, as long as the students have some significant exposure to these topics and ideas over the course of the program.

Following our description of the courses, we have listed the mathematical competencies that such students should acquire. These are divided into two groups – one at the level of linear algebra or lower and the other comprising some more advanced topics. We note and endorse the additional and complementary competencies recommended by *Scientific Foundations for Future Physicians*, a report prepared jointly by AAMC and HHMI: [http://www.hhmi.org/grants/pdf/08-209_AAMC-HHMI_report.pdf](http://www.hhmi.org/grants/pdf/08-209_AAMC-HHMI_report.pdf). (See pp. 19 – 24.)

There are several types of programs that might be designed to meet the interests of students interested in mathematical biology, ranging from a full-blown major in mathematical or computational biology to a track within a more standard mathematics major or some sort of interdisciplinary minor. In any case, we view the material and point of view in the foundational courses as essential to all programs. The choice of more advanced topics could be individualized based on students’ interests and institutional resources.

We conclude with some suggestions regarding topics and competencies in the life sciences that would best inform mathematics students for further work in biomathematics. That said, we also believe that the conversation needs to go both ways. Departments engaged in setting up a program in biomathematics will also need to do the difficult and sometimes politically sensitive
work of persuading colleagues in the life sciences to incorporate and reinforce mathematical concepts in their own coursework. Ideas such as equilibria, stability, growth and rate of change are not unfamiliar to biologists, but mathematical formulations of these ideas may be. Just as mathematicians need to become more fluent in language of biology, biology educators will also need to maintain a level of comfort with the basic mathematical tools and ideas that inform their work in order to reinforce those concepts for their students.

FOUNDATIONAL COURSES

Modeling

Modeling is the process of abstracting certain aspects of reality to include in the simplifications of reality we call models. What is included in the model depends on the questions addressed, and different questions arise on different temporal and spatial scales and at different levels of the biological hierarchy (e.g., molecular, cellular, organismal, ecological). Of course, there are trade-offs in modeling—no one model can address all questions. These trade-offs involve generality, precision, and realism.

The modeling course should include dynamical multivariable models in discrete and continuous time, as well as an introduction to processes of growth and diffusion. Construction of a model should pay attention to structural considerations – how are the various components of the system grouped and how do they interact? Are there symmetries that might reduce the complexity of the problem? Different aggregations (e.g., by sex, size, physiological state) can lead to different types of questions to investigate. And, whether discrete or continuous, analysis of a model should include discussion of equilibria and stability – that is, qualitative analysis as well as quantitative. Keep in mind that “The purpose of models is not to fit the data but to sharpen the questions.” (Samuel Karlin, 11th R.A. Fisher Memorial Lecture, The Royal Society of London, 20 April, 1983.)

The modeling course should also include stochastic approaches, because nothing is certain, especially in biology! Students who have become accustomed to the “certainty” of mathematics may find stochasticity unnerving. However, learning how to manage stochasticity mathematically gives us tools to identify and estimate risk and to determine whether or not an experimental result is significant. It also enhances our ability to construct more sophisticated models. Finally, the modeling process also requires validation. Evaluating models depends in part on the purpose for which the model was constructed. Models oriented toward prediction of specific phenomena may require formal statistical validation methods, while models designed to elucidate general patterns of system response may require corroboration with the available observed patterns. Predictions made in silico should be validated in vitro or in vivo as is appropriate to the situation.

Data analysis

Students should have plenty of opportunities to hone their ability to manipulate and visualize real data, including using nonlinear transformations to gain new insights. Whenever possible, use real
data sets, and at least occasionally, use real data sets gathered by students. In the process, students should practice critical examination of how data is gathered and presented.

A variety of statistical methods exist to characterize single data sets and to make comparisons between data sets. We recognize that using such methods with discernment takes practice. Rather than giving a list of statistical tests with which students should be familiar, we emphasize instead that students be comfortable with the considerations involved in statistical inference in general, including the power of a statistical test. That said, among the concepts ordinarily covered in an introductory course, we recommend in particular that students have experience with regression analysis. Throughout, we recommend that courses emphasize the assumptions and conditions under which a particular analysis is valid, not just performing calculations. Though we do not recommend that students develop fluency in any particular programming language, we do think that students need programming in some language as well as experience with a variety of data structures (and their management). This will prepare students for more advanced topics in statistics and optimization, as well as for the bioinformatics tools now used in most every subfield in biology. This course would also naturally provide an opportunity for exposure to a variety of widely used databases, including those available from NCBI.

General remarks on courses

By design, preparation in biomathematics requires taking a broad view. We have explicitly recommended that continuous, discrete, algebraic, geometric, multivariate, deterministic, stochastic, and statistical themes be included, and that applications be integral to the foundational courses. Acquiring the competencies reflected in both of the courses described above naturally involves analytical and critical thinking and problem solving, and there may be substantial conceptual overlap as well. For example, the task of fitting data to models could go in either (or both!) of the courses described above. The modeling course could introduce the basics of least squares fit, with the subtleties explored in the data analysis course. Encouraging creativity and curiosity will follow from effective pedagogy, and every course should provide ample opportunities for practicing communication skills. Use of technology is also expected and naturally built into both courses.

We expect that both of these courses could be taught at an introductory level, assuming one semester of calculus and modest familiarity with computing. Or they could be taught at a more advanced level, assuming two semesters of calculus and linear algebra, together with a semester long introduction to computing. Although the initial choice will depend on departmental resources and staffing, we expect that with some experience, courses will be revised in significant ways.

FUNDAMENTAL MATHEMATICAL COMPETENCIES

The basic skills listed below will follow naturally from existing courses (e.g., calculus, linear algebra, introduction to computer science). Alternatively, a department may devise a new course
that covers these topics together. Such a course might for example, have some biological question as a context.

- Computation and algorithmic thinking
- Rate of change
- Matrix algebra
- Computation and interpretation of eigenvalues and eigenvectors

MORE ADVANCED TOPICS

These could be introduced as special topics in one of the foundational courses or be considered for independent study for appropriate students.

- Fluids and PDEs
  Although the mathematics is more advanced, students need to see that the basic ideas, such as the use of conservation laws and the power of stochastic simulation, apply in more complex situations.

- Theory of Probability
  Such a course will support students’ further explorations in statistics, as well as deeper understanding of stochasticity and bioinformatics programming.

- Biomechanics and the role of physics in biology
  The modern sciences are converging (usually on biology) and students need to see that basic physical principles, including Newtonian analysis of forces and electromagnetism, remain true and useful in biology even though the applications are far more complicated than in introductory physics. This study provides a link to bioengineering and other more applied fields.

- Chemical kinetics
  The cell is a big bag of chemicals, and as with physics, students need to see mathematical methods at work uniting chemistry and biology through fundamental concepts like reaction rates, mass action, and diffusion.

- More advanced topics in data analysis
  A more advanced course could include an introduction to various bioinformatics algorithms as well as topics such as machine learning (hidden Markov models, support vector machines, neural networks) or other approaches such as maximum likelihood or MCMC, that are broadly used in biomathematics.
We recognize that the directions in which a department will expand biomathematics opportunities will depend on departmental interests and resources, and the list above need not be considered comprehensive. However, in our view, it is essential that students be provided with an undergraduate research opportunity or other capstone experience. All students should have the chance to put their knowledge to work and to see the huge jump from well-posed classroom problems to the challenges of asking questions and groping for methods in open-ended research. Mentors should also seize this opportunity to help students develop scientific communication skills, both oral and written.

**BIOLOGICAL COMPETENCIES**

One of the curricular problems that we confront at the interface of biology and mathematics is trying to put together "packages" of biological content areas and mathematical skills in such a way that they make sense. However, the mathematical skills (and biological content) needed for bioinformatics may be quite different from those needed for biogeochemistry, for example. So for mathematically oriented undergraduates, we believe it would be more appropriate to take an introductory biology course, equivalent to that required for biology majors, then some upper level course in a particular biological subdiscipline. Which upper division courses and how many will depend on the interests of the student and availability of courses and faculty. Some topics that are particularly relevant include:

- Genetics and evolution: DNA, RNA, and the four "forces" of evolution (selection, mutation, migration, and drift).
- Cell biology: cell cycle, central dogma, gene regulation, how cell membranes regulate communication via electrochemical gradients.
- Biological systems and networks: the immune system, the brain, the circulatory and respiratory systems, gene regulatory networks, ecosystems, foodwebs. Systems biology takes a “holistic” approach to study interactions among the components of a biological system and the impact of those interactions on the overall function and behavior of the system.
- Population biology: How populations grow and the main forms of interaction (competition, predation/parasitism, mutualism).
- Biomedical science: Cancer biology as a link between cell biology and evolutionary biology; drug design and testing; epidemiology as an application of population biology

Ultimately, the goal is not just knowledge of content, but also an introduction to biology as a discipline. What constitutes an “interesting” question in biology? How do biologists think about those questions? What are the “standard” approaches, if any? To be successful as mathematical biologists, students must be able to have productive conversations with biologists and biological texts. One of those texts (or contexts) is the laboratory, so we further recommend that students
have some biology laboratory experience. Such an experience will also increase student understanding of the challenges involved in designing experiments and collecting data to validate a model.

Students who have completed a program that includes the foundational course material, and who possess the fundamental competencies should be well poised to embark on graduate work in this field. The names and types of programs vary enormously. Here are some examples: Bioinformatics; Bioengineering; Mathematical Biology; Biostatistics; Computational Biology, GBCB (Genetics, Bioinformatics, and Computational Biology). Some programs are interdisciplinary in the sense that the students are officially in a mathematics graduate program, but their research is located in another department. Moreover, graduate programs in many biology subdisciplines may welcome students with the kind of preparation we have described.

IMPLEMENTING CHANGE

As already noted, our committee agrees that trying to design an “ideal” program (on a course-by-course basis) in mathematical biology is probably hopeless. The "field" such as it is, is simply too broad and multifaceted (and local institutional expertise too varied) to be embodied in a single curriculum. We emphasize that there are many paths to success, largely for the same reasons: biology is producing such a wealth of mathematical, computational, and statistical problems, that mathematically savvy students with some background in biology have very broad horizons open to them. Therefore, we have taken an approach recommending "competencies" rather than particular existing courses. Familiarity with algorithmic thinking, computation, model construction, and data analysis (in any number of courses or biological contexts) will be more important for future success than whether a student has taken partial differential equations or probability theory, specifically.

That said, having a variety of exemplars can be a good way to jumpstart a department’s conversation. We know that no department would opt to uncritically adopt some other school’s program. More likely is that in discussion of such a model program, the department would try on other ideas for size – does this idea fit our faculty, our students, our resources, our departmental and institutional missions? Furthermore, having multiple models can help establish credibility for a new program as well as assist with assessment. In what follows we provide a selection of sample programs and a list of resources.

Many departments of mathematics have introduced mathematical and computational biology into their curricula. Implementations range from modules for use in existing courses to full degree programs. Outside of Research I institutions, however, there are few examples of programs leading to a bachelor’s degree in mathematical or computational biology. Why?

1. Curriculum development requires expenditure of faculty time and flexibility in staffing – scarce commodities especially in smaller institutions.
2. Successful implementation may require hiring new faculty with expertise in mathematical biology.
3. Unless there are many mathematics majors, it may not be prudent to split an existing major into several new majors. Alternatively, if the mathematical biology major is
conceived as a concentration within the existing major, there may be reluctance to incur additional administrative or advising costs.

4. Resistance to change is widespread in academic institutions – irrespective of size or Carnegie classification.

There are no magic bullets, but we do have some suggestions:

1. Start small. Develop a module or unit for an existing course; then grow. Especially helpful ideas may be found in the MAA publication, Undergraduate Mathematics for the Life Sciences: Models, Processes, and Directions edited by Glenn Ledder, Jenna Carpenter, and Timothy Comar. (http://www.maa.org/ebooks/notes/NTE81.html).

2. Educate your department (and yourself, if necessary) about this field:

   i. Look for and share articles in mathematical biology journals, such as the Bulletin of Mathematical Biology (http://www.springer.com/new+%26+forthcoming+titles+%28default%29/journal/11538) which describes problems that are of both mathematical and biological interest.

   ii. Attend contributed paper sessions in this area at national meetings. The MAA’s special interest groups in mathematical and computational biology (BioSIGMAA -- http://sigmaa.maa.org/bio/) and in environmental mathematics (SIGMAA EM-- http://sigmaa.maa.org/em/) have frequent sessions and speakers both at JMM and at Mathfest. The American Mathematical Society has regular special sessions in this area. The Society for Mathematical Biology (http://smb.org/index.shtml) has education resources, education sessions at its annual meeting, and awards for travel by educators and students.

   iii. Give a presentation at a departmental seminar, invite a mathematical biologist to visit, or both.

   iv. Attend a seminar or workshop at the Mathematical BioSciences Institute (MBI-- http://mbi.osu.edu/) or The National Institute for Mathematical and Biological Synthesis (NIMBioS--http://nimbios.org/) or BioQUEST (http://bioquest.org/)

3. Befriend a biologist! Begin a conversation with your colleagues in the biology and health sciences areas about mathematical biology. If you have a separate department in Environmental Science or Environmental Studies, those colleagues will also have a rich assortment of ideas. If there is a nearby or affiliated medical school, research physicians often have relatively simple quantitative problems that can be inspiring to students. Biologists in particular may be considering ways to make their curriculum more quantitative – if so, you have an opportunity for collaboration as well as a stronger base for funding requests. Audit a biology course (especially if it’s been a while since you’ve been in a biology classroom), Invite your biology colleagues to audit a math class.
4. Enlist your academic administration as stakeholders. Explain that this field is at the cutting edge by making them aware of important problems that mathematicians and biologists are working together to address. The most compelling are easy to relate to human life: cancer biology, environmental issues, antibiotic resistant organisms, the human genome project, protein (mis)folding conditions such as Alzheimer’s disease. Invoke national reports such as the HHMI report (http://www.hhmi.org/grants/pdf/08-209_AAMC-HHMI_report.pdf) which makes the case that familiarity and experience with mathematical reasoning is the new norm in biology and health sciences education.

5. Consult papers and monographs related to pedagogy or curriculum development; many are listed among the Resources below.

PRINT AND WEB RESOURCES

A. Professional organizations and institutes

Most of these have links to information about mathematical biology curriculum development.

SMB http://smb.org/index.shtml

BioSIGMAA http://sigmaa.maa.org/bio/

MBI http://mbi.osu.edu/

NIMBioS http://nimbios.org/

ESA Theory http://www.esa.org/theory/

BioQUEST http://bioquest.org/


B. Textbooks

Calculus


James L. Cornette and Ralph A. Ackerman, *Calculus for the Life Sciences: A Modeling Approach* (Available online only at http://cornette.public.iastate.edu/CLS.html)

Data Analysis

M.C. Whitlock and D. Schluter, The Analysis of Biological Data, Roberts and Co, 2008

Modeling

H. Kokko, Modelling for Field Biologists and Other Interesting People, Cambridge 2007.
S. Railsback and V. Grimm Agent-Based and Individual Based Modeling, Princeton 2012

Bioinformatics

P. Higgs and T. Attwood Bioinformatics and Molecular Evolution, Wiley 2005.
N. Jones and P. Pevzner, An Introduction to Bioinformatics Algorithms, MIT 2004

Other
See also the lists of textbook suggestions compiled by these mathematical biology educators:

Louis Gross (Mathematical Modeling)
http://www.tiem.utk.edu/~gross/math.modeling.books.txt.fmt
Michael Knorrenschild (Environmental Modeling)

C: Technology

Polynomial Dynamical Systems: ADAM
http://dvd.vbi.vt.edu/adam.html

Cell modeling: VCell http://vcell.org/

Copasi http://copasi.org/tiki-view_articles.php

Agent based modeling: NetLogo http://ccl.northwestern.edu/netlogo/

Statistics: R: http://www.rstudio.com/

D. Undergraduate research opportunities
MBI http://mbi.osu.edu/

NIMBioS http://nimbios.org/

E. Other resources
These include links to publications or organizations especially concerned with mathematical biology curriculum development.


Undergraduate Mathematics for the Life Sciences: Models Processes and Directions edited by Glenn Ledder, Jenna Carpenter, and Timothy Comar
http://www.maa.org/ebooks/notes/NTE81.html

Vision and Change in Undergraduate Biology Education
http://visionandchange.org/

BioQUEST http://bioquest.org/
### F. Institutional contacts

This table provides contact information regarding curricular innovation in mathematical biology at a variety of institutions.

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