MOLECULAR, CELLULAR, AND DEVELOPMENTAL BIOLOGY

Yale Science Building, 203.432.3538
http://mcdb.yale.edu
M.S., Ph.D.

Chair
Scott Holley

Director of Graduate Studies
Joshua Gendron

Professors Ronald Breaker, John Carlson, Lynn Cooley,* Craig Crews, Stephen Dellaporta, Thierry Emonet, Paul Forscher, Valerie Horsley, Mark Hochstrasser,* Scott Holley, Vivian Irish, Farren Isaacs, Akiko Iwasaki,* Douglas Kankel, Paula Kavathas,* Haig Keshishian, Mark Mooseker, Jon Morrow,* Anna Pyle, Hugh Taylor*

Associate Professors Shirin Bahmanyar, Damon Clark, Nadya Dimitrova, Joshua Gendron, Stavroula Hatzios, Yannick Jacob, Megan King,* Kathryn Miller-Jensen,* Weimin Zhong

Assistant Professors David Breslow, Binyam Mogessie, Jacob Musser, Sigrid Nachtergaele, Michael O'Donnell, Josien van Wolfswinkel, Jing Yan

Lecturers Robert Bazell, Edgar Benavides, Francine Carland, Surjit Chandhoke,* Seth Guller,* Richard Harrington, Amaleah Hartman, Ronit Kaufman, Thomas Loreng, Maria Moreno, Kenneth Nelson, Aruna Pawashe,* Joseph Wolenski

* A secondary appointment with primary affiliation in another department or school.

FIELDS OF STUDY

Research in the Department of Molecular, Cellular, and Developmental Biology spans biology from the organismal to the molecular levels. Topics in genetics and molecular biology include studies of non-coding RNAs, genome engineering, genome organization and regulation, gene dosage, bacterial chemotaxis, oncogenes, and systems and synthetic biology. Research topics in cellular and developmental biology include structure and dynamics of the cell cytoskeleton, molecular motors, chemical biology, the nuclear envelope, lncRNAs, regeneration, developmental biomechanics, vertebral column development, stem cell biology, and systems developmental biology. Research in neurobiology focuses on growth cone motility, neural differentiation, synaptogenesis, visual perception, olfaction, and the formation of topographic maps. Research in the plant sciences provides training in the molecular genetics of flowering, meristematic activity, epigenetics, the physiology of hormone action, sex determination, and the circadian clock. Because of the breadth of the department, students are provided with unique training and research opportunities for interdisciplinary studies.

To enter the Ph.D. program, students apply to the Molecular Cell Biology, Genetics, and Development (MCGD) track; the Biochemistry, Quantitative Biology, Biophysics, and Structural Biology (BQBS) track; or the Plant Molecular Biology (PMB) track

within the interdepartmental graduate program in Biological and Biomedical Sciences (BBS), https://medicine.yale.edu/bbs.

INTEGRATED GRADUATE PROGRAM IN PHYSICAL AND ENGINEERING BIOLOGY (PEB)

Students applying to the MCGD or BQBS track of the Biological and Biomedical Sciences program may simultaneously apply to be part of the PEB program. See the description under Non-Degree-Granting Programs, Councils, and Research Institutes for course requirements, and http://peb.yale.edu for more information about the benefits of this program and application instructions.

SPECIAL REQUIREMENTS FOR THE PH.D. DEGREE

Each student is expected to take at least three courses, in addition to MCDB 900/MCDB 901, Research Skills and Ethics I and II. With the help of a faculty committee, each student will plan a specific program that includes appropriate courses, seminars, laboratory rotations, and independent reading fitted to individual needs and career goals. There is no foreign language requirement. At the beginning of the third term of study, the student meets with a faculty committee to decide on a preliminary topic for dissertation work and to define the research areas in which the student is expected to demonstrate competence. By the end of the fall term of the second year, each student prepares a dissertation prospectus outlining the research proposed for the Ph.D. The student is admitted to candidacy for the Ph.D. when (1) the prospectus is accepted by a dissertation committee of faculty members, (2) the committee is satisfied that the student has demonstrated competence in the areas necessary to conduct the proposed work, and (3) the other requirements indicated above are fulfilled. The student should complete the requirements for admission to candidacy by the end of the fall term of the second year and no later than the end of the second year of study. Following admission to candidacy, students are required to meet with their thesis advisory committee at least once a year. The remaining requirements include completion of the dissertation research, presentation and defense of the dissertation, and submission of acceptable copies of the dissertation to the graduate school and to the Marx Science and Social Science Library. All students are required to teach in two one-term courses during their Ph.D. study, but not during the first year of graduate study. Students who require additional support from the graduate school must teach additional terms, if needed, after they have fulfilled the academic teaching requirement. Requirements for M.D.-Ph.D. students are the same as for Ph.D. students, except that a single term of teaching is required. During their first year of study, students must successfully complete MCDB 900/MCDB 901, Research Skills and Ethics I and II, to fulfill the responsible conduct and ethics in research requirement. This requirement must be met prior to registering for a second year of study. Further, in the fourth year of study, all students must successfully complete MCDB 504, RCR Refresher for Senior BBS Students.

HONORS REQUIREMENT

Students must meet the Graduate School's Honors requirement by the end of the fourth term of full-time study. (See Degree Requirements under Policies and Regulations.)

MASTER'S DEGREE

M.S. (en route to the Ph.D.) The minimum requirements for award of the Master of Science degree are (1) two academic years registered and in residence full-time in the graduate program; (2) satisfactory completion of the first two years of study and research leading to the Ph.D.; this requirement may be met either (a) by completing a minimum of five courses with an average grade of High Pass and at least one Honors grade, in addition to satisfactory performance in MCDB 900/MCDB 901, or (b) by (i) successfully completing at least three courses with an average grade of High Pass and at least one Honors grade, (ii) satisfactory performance in MCDB 900/MCDB 901, and (iii) passing the prospectus examination; (3) recommendation by the department for award of the degree, subject to final review and approval by the degree committee. No courses that were taken prior to matriculation in the graduate program, or in Yale College, or in summer programs may be applied toward these requirements.

Prospective applicants are encouraged to visit the BBS website (https://medicine.yale.edu/bbs), MCGD, BQBS, and PMB tracks.

COURSES

MCDB 500a or b / MB&B 500a or b, Biochemistry Staff
An introduction to the biochemistry of animals, plants, and microorganisms, emphasizing the relations of chemical principles and structure to the evolution and regulation of living systems.

MCDB 517b / ENAS 517b / MB&B 517b / PHYS 517b, Methods and Logic in Interdisciplinary Research Corey O'Hern and Emma Carley
This full PEB class is intended to introduce students to integrated approaches to research. Each week, the first of two sessions is student-led, while the second session is led by faculty with complementary expertise and discusses papers that use different approaches to the same topic (for example, physical and biological or experiment and theory).

MCDB 530a / IBIO 530a / MBIO 530a, Biology of the Immune System Grace Chen, Ann Haberman, Carla Rothlin, Kevin O'Connor, Carrie Lucas, Ellen Foxman, Markus Müschen, Andrew Wang, Peter Cresswell, Jordan Pober, Joao Pereira, Craig Roy, Joseph Craft, Paula Kavathas, Noah Palm, Craig Wilen, Jeffrey Ishizuka, Daniel Jane-Wit, and David Schatz
The development of the immune system. Cellular and molecular mechanisms of immune recognition. Effector responses against pathogens. Immunologic memory and vaccines. Human diseases including allergy, autoimmunity, cancer, immunodeficiency, HIV/AIDS.

MCDB 550a / C&MP 550a / ENAS 550a / PHAR 550a / PTB 550a, Physiological Systems W. Mark Saltzman and Stuart Campbell
The course develops a foundation in human physiology by examining the homeostasis of vital parameters within the body, and the biophysical properties of cells, tissues, and organs. Basic concepts in cell and membrane physiology are synthesized through exploring the function of skeletal, smooth, and cardiac muscle. The physical basis of blood flow, mechanisms of vascular exchange, cardiac performance, and regulation of overall circulatory function are discussed. Respiratory physiology explores the mechanics of ventilation, gas diffusion, and acid-base balance. Renal physiology

examines the formation and composition of urine and the regulation of electrolyte, fluid, and acid-base balance. Organs of the digestive system are discussed from the perspective of substrate metabolism and energy balance. Hormonal regulation is applied to metabolic control and to calcium, water, and electrolyte balance. The biology of nerve cells is addressed with emphasis on synaptic transmission and simple neuronal circuits within the central nervous system. The special senses are considered in the framework of sensory transduction. Weekly discussion sections provide a forum for in-depth exploration of topics. Graduate students evaluate research findings through literature review and weekly meetings with the instructor.

MCDB 560b / C&MP 560b / ENAS 570b / PHAR 560b, Cellular and Molecular Physiology: Molecular Machines in Human Disease Emile Boulpaep and Peter Takizawa

The course focuses on understanding the processes that transfer molecules across membranes at the cellular, molecular, biophysical, and physiological levels. Students learn about the different classes of molecular machines that mediate membrane transport, generate electrical currents, or perform mechanical displacement. Emphasis is placed on the relationship between the molecular structures of membrane proteins and their individual functions. The interactions among transport proteins in determining the physiological behaviors of cells and tissues are also stressed. Molecular motors are introduced and their mechanical relationship to cell function is explored. Students read papers from the scientific literature that establish the connections between mutations in genes encoding membrane proteins and a wide variety of human genetic diseases.

MCDB 561a / MB&B 561a / PHYS 561a, Modeling Biological Systems I Thierry Emonet and Kathryn Miller-Jensen

Biological systems make sophisticated decisions at many levels. This course explores the molecular and computational underpinnings of how these decisions are made, with a focus on modeling static and dynamic processes in example biological systems. This course is aimed at biology students and teaches the analytic and computational methods needed to model genetic networks and protein signaling pathways. Students present and discuss original papers in class. They learn to model using MatLab in a series of in-class hackathons that illustrate the biological examples discussed in the lectures. Biological systems and processes that are modeled include: (1) gene expression, including the kinetics of RNA and protein synthesis and degradation; (2) activators and repressors; (3) the lysogeny/lysis switch of lambda phage; (4) network motifs and how they shape response dynamics; (5) cell signaling, MAP kinase networks and cell fate decisions; and (6) noise in gene expression. Prerequisites: MATH 115 or 116, BIOL 101–104, or with permission of instructors. This course also benefits students who have taken more advanced biology courses (e.g. MCDB 200, MCDB 310, MB&B 300/301).

MCDB 562b / AMTH 765b / CB&B 562b / ENAS 561b / INP 562b / MB&B 562b / PHYS 562b, Modeling Biological Systems II Thierry Emonet

This course covers advanced topics in computational biology. How do cells compute, how do they count and tell time, how do they oscillate and generate spatial patterns? Topics include time-dependent dynamics in regulatory, signal-transduction, and neuronal networks; fluctuations, growth, and form; mechanics of cell shape and motion; spatially heterogeneous processes; diffusion. This year, the course spends roughly half its time on mechanical systems at the cellular and tissue level, and half on

models of neurons and neural systems in computational neuroscience. Prerequisite: a 200-level biology course or permission of the instructor.

MCDB 564a, Light Microscopy: Techniques and Image Analysis Joseph Wolenski and Joe Howard

A rigorous study of principles and pertinent modalities involved in modern light microscopy. The overall course learning objective is to develop competencies involving advanced light microscopy applications common to multidisciplinary research. Laboratory modules coupled with critical analysis of pertinent research papers cover all major light microscope methods—from the basics (principles of optics, image contrast, detector types, fluorescence, 1P and 2P excitation, widefield, confocal principle, TIRF), to more recent advances, including super-resolution, light sheet, FLIM/FRET, motion analysis and force measurements. Enrollment is capped at eight to promote interactions and ensure a favorable hands-on experience. Priority is given to students who are planning on using these techniques in their independent research.

MCDB 570b, Biotechnology Craig Crews, Yannick Jacob, Joseph Wolenski, and F Kenneth Nelson

The principles and applications of cellular, molecular, and chemical techniques that advance biotechnology. Topics include the most recent tools and strategies used by government agencies, industrial labs, and academic research to adapt biological and chemical compounds as medical treatments, as industrial agents, or for the further study of biological systems.

MCDB 585a or b, Research in MCDB for B.S./M.S. Candidates Douglas Kankel

A two-credit course taken in the third-to-last term (typically the second term of the junior year). At the start of this course, each student forms a committee composed of the student's adviser and two faculty members that meets to discuss the research project. At the end of this course, students complete a detailed prospectus describing their thesis project and the work completed thus far. The committee evaluates an oral and written presentation of this prospectus; the evaluation determines whether the student may continue in the combined program. Required of students in the joint B.S./M.S. program with Yale College. 2 Course cr

MCDB 591a / ENAS 991a / MB&B 591a / PHYS 991a, Integrated Workshop Yimin Luo

This required course for students in the PEB graduate program involves a series of modules, co-taught by faculty, in which students from different academic backgrounds and research skills collaborate on projects at the interface of physics, engineering, and biology. The modules cover a broad range of PEB research areas and skills. The course starts with an introduction to MATLAB, which is used throughout the course for analysis, simulations, and modeling.

MCDB 595a and MCDB 596b, Intensive Research in MCDB for B.S./M.S. Candidates Douglas Kankel

A four-credit, yearlong course (two credits each term) that is similar to MCDB 495/496 and is taken during the senior year. During this course, students give an oral presentation describing their work. At the end of the course, students are expected to present their work to the department in the form of a poster presentation. In addition, students are expected to give an oral thesis defense, followed by a comprehensive examination of the thesis conducted by the thesis committee. Upon successful

completion of this examination, as well as other requirements, the student is awarded the combined B.S./M.S. degree. Required of students in the joint B.S./M.S. program with Yale College. 2 Course cr per term

MCDB 602a / CBIO 602a / MB&B 602a / MBIO TBD-2, Molecular Cell Biology Thomas Melia and Patrick Lusk
A comprehensive introduction to the molecular and mechanistic aspects of cell biology for graduate students in all programs. Emphasizes fundamental issues of cellular organization, regulation, biogenesis, and function at the molecular level. Graduate Prerequisites: Some knowledge of basic cell biology and biochemistry is assumed. Students who have not taken courses in these areas can prepare by reading relevant sections in basic molecular cell biology texts. We recommend Pollard et al., *Cell Biology* (3rd ed., 2016), Alberts et al., *Molecular Biology of the Cell* (6th ed., 2014), or Lodish et al., *Molecular Cell Biology* (8th edition, 2016). Undergraduate Prerequisites: This is a graduate-level cell biology class. Any undergraduates wishing to enroll must have already taken MCDB 205. In addition, undergraduates are strongly encouraged to reach out to the course directors prior to enrollment.

MCDB 603a / CBIO 603a, Seminar in Molecular Cell Biology Megan King
A graduate-level seminar in modern cell biology. The class is devoted to the reading and critical evaluation of classical and current papers. The topics are coordinated with the CBIO 602 lecture schedule. Thus, concurrent enrollment in CBIO 602 is required. Prerequisites: Any undergraduates wishing to enroll must have already taken MCDB 205. In addition, undergraduates are strongly encouraged to reach out to the course directors prior to enrollment.

MCDB 625a / GENE 625a / MB&B 625a, Basic Concepts of Genetic Analysis Jun Lu
The universal principles of genetic analysis in eukaryotes are discussed in lectures. Students also read a small selection of primary papers illustrating the very best of genetic analysis and dissect them in detail in the discussion sections. While other Yale graduate molecular genetics courses emphasize molecular biology, this course focuses on the concepts and logic underlying modern genetic analysis.

MCDB 630b / MB&B 630b, Biochemical and Biophysical Approaches in Molecular and Cellular Biology Sigrid Nachtergaele and Jing Yan
In this course, we provide an overall of various biochemical and biophysical approaches used in modern research in molecular and cellular biology, ranging from spectroscopic tools, microscopy, to X-ray crystallography. The goal of the course is to make students familiar with these techniques so that they can find relevant materials in their future research. Does not count for graduate course credit for BQBS graduate students.

MCDB 650a, Epigenetics Yannick Jacob and Nadya Dimitrova
Study of epigenetic states and the various mechanisms of epigenetic regulation, including histone modification, DNA methylation, nuclear organization, and regulation by noncoding RNAs. A detailed critique of papers from primary literature and discussion of novel technologies, with specific attention to the role of epigenetics in development and its impact on human health.

MCDB 677b / GENE 777b, Mechanisms of Development Kaelyn Sumigray and Zachary Smith
An advanced graduate seminar on animal development focusing on conserved mechanisms that govern germline development, embryogenesis, and somatic

differentiation in molecular detail. The course runs in parallel to the Spring session of the Department of Genetics Seminar Series and is divided into two components: six Yale faculty-led lectures on core concepts in development and six combined journal club/student-led discussions with outside developmental biology speakers on their cutting-edge research. Over the course of the term, small student groups are responsible for presenting one journal club-formatted discussion on two papers selected from the outside speaker's lab, as well as emceeing a dedicated question and answer session between the class and the speaker. This course provides a rare opportunity for students to actively engage with world leaders on their work in developmental genetics, epigenetics, and cell biology, as well as learn essential skills in experimental thinking and scientific communication. The course grade is based on forty percent take-home problems, forty percent class participation and twenty percent student-led journal club / distinguished speaker question and answer session. There are no official prerequisites. However, some familiarity with concepts and techniques of modern biology is necessary to get the most out of the course.

MCDB 700b, Molecular and Biochemical Principles of Gene Function Anna Marie Pyle and Farren Isaacs

Although many graduate students in the physical sciences begin conducting their thesis work on problems in the biological sciences, many of them lack preparation in the molecular foundations of the discipline. MCDB200 provides these students with a strong foundational and practical knowledge of the contemporary field of molecular biology and genetic manipulation, greatly facilitating their thesis research. Prerequisites: CHEM 161 or 163, and BIOL 101 (or placement out of BIOL 101 via BIOL 101 placement exam, or via AP5 or IB7HL with permission of core course instructor). o Course cr

MCDB 720a / INP 720a, Neurobiology Haig Keshishian and Paul Forscher

Examination of the excitability of the nerve cell membrane as a starting point for the study of molecular, cellular, and intracellular mechanisms underlying the generation and control of behavior.

MCDB 743b / GENE 743b / MB&B 743b, Advanced Eukaryotic Molecular Biology Mark Hochstrasser, Matthew Simon, and Franziska Bleichert

Selected topics in transcriptional control, regulation of chromatin structure, mRNA processing including spliceosomal splicing, mRNA turnover, RNA interference, translational regulation, protein modification, and protein degradation. Emphasis is placed on how these processes are regulated and the experiments that led to their discovery and understanding. Prerequisite: biochemistry or permission of the instructor.

MCDB 752b / CB&B 752b / CPSC 752b / MB&B 752b and MB&B 753b and MB&B 754b / MB&B 753b and MB&B 754b / MB&B 754b, Biomedical Data Science: Mining and Modeling Mark Gerstein and Matthew Simon

Biomedical data science encompasses the analysis of gene sequences, macromolecular structures, and functional genomics data on a large scale. It represents a major practical application for modern techniques in data mining and simulation. Specific topics to be covered include sequence alignment, large-scale processing, next-generation sequencing data, comparative genomics, phylogenetics, biological database design, geometric analysis of protein structure, molecular-dynamics simulation, biological networks, normalization of microarray data, mining of functional genomics data sets,

and machine-learning approaches to data integration. Prerequisites: biochemistry and calculus, or permission of the instructor.

MCDB 900a / CBIO 900a / GENE 900a, Research Skills and Ethics I Patrick Lusk
This course consists of a weekly seminar that covers ethics, writing, and research methods in cellular and molecular biology as well as student presentations ("rotation talks") of work completed in the first and second laboratory rotations.

MCDB 901b / CBIO 901b / GENE 901b, Research Skills and Ethics II Chenxiang Lin
This course consists of a weekly seminar that covers ethics, writing, and research methods in cellular and molecular biology as well as student presentations ("rotation talks") of work completed in the third laboratory rotation.

MCDB 902a and MCDB 903b, Advanced Graduate Seminar Staff
The course allows students to hone their presentation skills through yearly presentation of their dissertation work. Two students each give thirty-minute presentations in each class session. Students are required to present every year beginning in their third year in the MCDB program. Each MCDB graduate student is expected to attend at least 80 percent of the class sessions. Two faculty members co-direct the course, attend the seminars, and provide feedback to the students.

MCDB 911a / CBIO 911a / GENE 911a, First Laboratory Rotation Patrick Lusk
First laboratory rotation for Molecular Cell Biology, Genetics, and Development (MCGD) and Plant Molecular Biology (PMB) track students.

MCDB 912a / CBIO 912a / GENE 912a, Second Laboratory Rotation Patrick Lusk
Second laboratory rotation for Molecular Cell Biology, Genetics, and Development (MCGD) and Plant Molecular Biology (PMB) track students.

MCDB 913b / CBIO 913b / GENE 913b, Third Laboratory Rotation Patrick Lusk
Third laboratory rotation for Molecular Cell Biology, Genetics, and Development (MCGD) and Plant Molecular Biology (PMB) track students.

MCDB 940a, Developing and Writing a Scientific Research Proposal Farren Isaacs
Through lectures, discussions, writing activities, and revisions, students become familiar with the principles of scientific grant writing, including language, style, content, and how to formulate a hypothesis and specific aims. Students effectively articulate their overall research plan and the significance of their research in writing and in oral presentations, and they learn to critique and review grant proposals by engaging in peer-review activities with fellow classmates. By the end of the term, students review, revise, and complete the research strategy for an NRSA F31 or NSF and/or the foundation for their qualifying proposal.

MCDB 950a and MCDB 951b, Second-Year Research Josh Gendron
By arrangement with faculty.