FEATURE ARTICLE

Group Active Engagements for Facilitating Principles-Based Learning in Introductory Organismal Biology

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ABSTRACT

Organismal biology (OrgBio) comprises the diversity, structures, and functions of all organisms from bacteria to humans. Arguably, OrgBio is often the most poorly taught and least conceptually rigorous section of the introductory biology sequence offered at most U.S. institutions of higher education. This article reports on the successful implementation of conceptual and pedagogical reforms in an introductory OrgBio course offered at a large public university. Conceptual reforms were based on a theoretical framework consisting of universal physical and chemical laws, deep molecular homologies, and diverse structure-function relationships. Pedagogical reforms involved the development of group active engagements (GAEs) that were designed to encourage students to develop their abilities to engage in principles-based reasoning. A new model for characterizing different approaches toward principles-based reasoning in biology was developed to analyze these GAEs. Two surveys indicated that OrgBio students developed more favorable perceptions about the effectiveness of GAE-based course offerings, as compared to similar lecture-based versions.

Key Words: group active engagement; introductory biology sequence; organismal biology; principles-based reasoning; undergraduate biology major.

\odot Introduction

Introductory biology can be divided into three subdisciplines representing different levels of biological organization: molecular and cell biology (MCB), organismal biology (OrgBio), and ecology and evolutionary biology (EEB). Each subdiscipline has its characteristic core knowledge, research areas, experimental techniques, and student training practices. For several reasons, most of the recent efforts to reform the introductory biology sequence in U.S. colleges and universities have focused on the subdisciplines Both conceptual and pedagogical reforms are necessary to improve principlesbased instruction in an introductory biology course covering the evolution and physiology of organisms.

of MCB and EEB (e.g., Bio, 2010: National Research Council [NRC], 2003; A New Biology for the 21st Century: NRC, 2009; Vision and Change: American Association for the Advancement of Science [AAAS], 2011). First of all, OrgBio comprising the diversity, structures, and functions of life is uncomfortably positioned near the fault line of the dramatic reorganization of biology departments that began in the mid-1960s. This reorganization can seemingly be traced back to the legendary feud between molecular biologist James Watson and evolutionary biologist Edward Wilson when they were young faculty members in the Biology Department at Harvard University (Anonymous, 2009; Wilson, 1994: Chapter 12). Since then, organism-centric departments such as microbiology, zoology, and botany have been reconfigured at many universities to form MCB and EEB departments, with the unfortunate consequence that these reformed departments have generally deemphasized organism-level phenomena in their teaching and research programs.

A second problem lies in how the OrgBio course is traditionally taught in the introductory biology sequence at U.S. universities. This course is presented as a series of diversity classes covering all major groups from bacteria to mammals, with separate units on the

> structures and functions of plants and animals. This organizational framework is supported by the parallel organization of 10-15 chapters devoted to OrgBio in introductory biology textbooks. This approach toward teaching OrgBio is almost universally derided by both instructors and students alike as a "forced march through the phyla." In such courses, the fundamental principles governing diversity, structure, and function do not emerge readily, if at all, from the tsunami of isolated facts about organisms. Judging from contemporary teaching and learning perspectives, this approach is quite unsatisfactory, especially in core introductory courses (AAAS, 2011).

> This article describes the story as it unfolded of how a group of University of Maryland (UMD) faculty set out to save our

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beloved organisms and the discipline of OrgBio from being eliminated from the introductory biology sequence. This article is organized into five main sections that reflect the sequence of our challenges and how we overcame them: (1) the design of a new conceptual framework for teaching introductory OrgBio, (2) the unanticipated limitations of conceptual reform, (3) the development and implementation of new pedagogical innovations involving group active engagements (GAEs) for effectively teaching the OrgBio principles, (4) the development and application of a new model for evaluating principles-based teaching in biology, and (5) the impact of conceptual and pedagogical reforms on students' perceptions of their OrgBio learning.

The Development of a New Conceptual Framework for Teaching Introductory OrgBio

Starting in the early 1980s at the UMD, undergraduate majors in the biological sciences totaling around 2000 students were required to complete a four-semester introductory biology sequence consisting of MCB, EEB, Genetics, and one of four diversity courses focused on microbes, animals, plants, or insects. Physiology was typically not presented at the introductory level, but instead students could enroll in an upper level physiology course devoted to one of the same four groups. The obvious result was that our students received fragmentary knowledge of OrgBio, which resulted in incomplete perspectives of many important topics. Just to cite several of many possible examples, those students interested in host–pathogen interactions learned about the hosts or the pathogens, but not both; those students interested pollination biology had to make a similar decision choosing between pollinators and plants.

In 2005, the biological sciences program at UMD organized an OrgBio teaching committee composed of all the faculty offering either diversity or physiology courses focusing on one of the four main organism groups listed above. The charge given to this committee was to design a principles-based course in introductory OrgBio comparable to the successful courses in MCB and EEB principles courses already being offered in our introductory sequence. It turned out that this assignment was more challenging that one might expect looking in from the outside, because almost all OrgBio faculty had received their graduate training on a single organism or a specific group of organisms. Thus, we found it really difficult to identify broad OrgBio principles that transcended individual groups. Eventually, we were able to agree on three overarching themes that became the conceptual framework for designing the new OrgBio course:

- 1. **Universal physical and chemical principles**: All life is governed by universal physical and chemical principles that are often expressed in mathematical terms.
- 2. **Deep molecular homology**: All living organisms are descended from a common ancestor (or common ancestral community). Thus, they share a common genomic toolkit encoding for homologous molecules that utilize physicochemical principles for regulating the molecular activities of life.
- Diverse structure-function relationships: Major lineages of living organisms exploit universal physicochemical principles and the common genomic toolkit in order to evolve diverse structure-function relationships for carrying out life's physiological processes.

It was humbling to realize a little while later that these themes were little more than contemporary restatements of Charles Darwin's eloquent concluding sentence from the first edition of *On the Origin of Species* (1859):

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one (*i.e., deep molecular homology*); and that, whilst this planet has gone cycling on according to the fixed law of gravity (*i.e., universal physical and chemical principles*), from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved (*i.e., diverse structure-function relationships*).

Moreover, the new OrgBio course was positioned as the third course in the introductory sequence following the MCB and EEB courses. We designers agreed that our course should therefore attempt to integrate key concepts learned from the previous two biology courses as appropriate in order to provide a more complete understanding of how organisms function, develop, and have evolved over time. The target student population was second-year biology majors, although the OrgBio enrollment would also include large numbers of first-year students who had waived the first two biology courses due to high scores on Biology Advanced Placement Exam or another college-level examination as well as third-year students who had graduated from local community colleges and then transferred to UMD. Because these students had previously taken several introductory courses in math, chemistry, and physics in order to satisfy their general science requirements, we were also committed to incorporating more quantitative reasoning into this course than is usually presented in an introductory biology sequence (Thompson et al., 2013).

The development of the new syllabus for OrgBio involved both faculty input and student feedback (see Supplemental Material Table 1 available with the online version of this article). The broad integrated coverage of course topics extended beyond any individual faculty member's expertise. Although subject material for teaching from our new conceptual framework was usually presented in popular introductory textbooks, that material was organized into the problematic arrangement described in the Introduction. In addition, those textbooks did not support the quantitative reasoning emphasized in the syllabus, so we worked very closely with physics colleagues who were simultaneously reforming the introductory physics sequence for life-science students (Redish et al., 2014). The biological sciences program at the UMD helped compensate for the narrow backgrounds of certain OrgBio faculty coming from specialized research backgrounds by assigning two instructors with complementary backgrounds to each course offering and by paying several campus specialists to help guide research-oriented OrgBio instructors to design the initial lectures for a few classes. Our students were routinely asked during office hours and semi-structured interviews what was working and not working for them. We present a model syllabus in Table 1 of the Supplemental Material for any instructor who would like to replicate our conceptual organization.

It followed from the conceptual framework described above that the first part of the new OrgBio course focused on the major evolutionary events and characteristic phenomena occurring in different groups of organisms, as opposed to the taxonomic characteristics defining those groups. As an example, the three classes on prokaryotic diversity emphasized molecular, evolutionary, and functional aspects of the prokaryotes (Table 1). The second part placed particular emphasis on the physical and chemical principles, homologous molecular **Table 1.** Major topics covered in three classes on prokaryotic diversity and two classes on gas exchange from organismal biology course.

Prokaryotic Diversity Classes	Gas Exchange (GE) Classes
 I. What wonderful life! Prokaryotic cell structure Ecological roles Woese's simple tree of life Major characteristics of three domains Universal tree of life Models of two vs. three domains of life Genetic recombination Horizontal gene transfer Last common ancestral community 	I. Moving moleculesUnifying principles – physics equationsDiversity – different organsHigh permeability of gas moleculesBiological version of Fick's Law (FL): $J_A = -DA \frac{\Delta P_p}{\Delta x}$ Natural selection manipulates FL parametersUnicellular organisms – no GE specializationsPlants – Leaf structure and stomatal functionGE adaptations in basal animalsConvergent GE organs in complex animalsGE in aquatic animals – gill structureGE in terrestrial insects – tracheal systems
 II. What wonderful life: operons and pathogens Operon model of gene expression Gram strain and bacterial cell walls Bacterial pathogens and pathogenesis Antibiotic resistance III. What wonderful life in extreme environments Microbiome Oxygen evolution and its biological and geological consequences Hyperthermophiles Monolayer vs. bilayer membranes Deep-sea hydrothermal vents Other extremophiles Bacteriorhodopsin 	II. Clever tricks Water – challenging ventilatory medium GE exchange in cephalochordates Evolution of "fish" gills Two-phase unidirectional pump Gill design – countercurrent flows Swim bladders/simple lungs in bony fishes Most terrestrial animals – bidirectional flow Negative pressure breathing (NPB) in amniotes Human ventilatory system NPB and pneumothorax treatment

Table 2. Unifying principles and evolutionary diversity in the classes devoted to life's fundamental physiological processes.

Fundamental Process	Unifying Principles	Evolutionary Diversity	
Scaling	Area/volume ratios, log–log plots	Different allometric solutions	
Animal development	Homeobox genes, other regulatory genes	Developmental cascades, different body plans	
Gas exchange	Fick's Law, Einstein–Smoluchowski equation (time-to-diffuse equation)	Different organs – leaves, gills, tracheae, lungs	
Circulation/intercellular transport	Hagen–Poiseuille equation	Different animal and plant systems, vertebrate evolution	
Nutrient uptake	Cation electrochemical gradients, homologous transport proteins	Different organs – fungal hyphae, plant roots, small intestines	
Osmoregulation/excretion	Same as nutrient uptake, plus osmosis (van't Hoff equation)	Different organs, aquatic vs. terrestrial environments	
Electrical signaling	Same as nutrient uptake, plus common neuron structure, Ohm's law, Nernst equation	Different sensory organs, different neural systems, different signal processing	
Motility	Homologous actin–myosin or tubulin–dynein/ kinesin systems	Different processes – binary fission, ciliary beating, ameboid movement, muscular contraction, and so on	
Animal locomotion	Lever biomechanics	Different movements	

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mechanisms, and evolutionary diversity operating to carry out life's primary physiological processes in all organisms (Table 1). The physical constraints operating in some systems (e.g., gas exchange and circulatory systems) exert profound effects on the design, function, and pathology of these systems in different organisms (Tables 1 and 2). By contrast, due to the deep molecular homologies operating in other systems (e.g., nutrient uptake and osmoregulatory systems), these processes depend on common molecular mechanisms in all microbes, plants, and animals. Thus, our OrgBio course presented unique perspectives on the diversity, structure, and function of all organisms, emphasizing the unifying physical, chemical, phylogenetic, and evolutionary principles governing life. Furthermore, the major concepts emphasized in our OrgBio course turned out to be closely aligned with the core concepts presented in the Vision and Change report (AAAS, 2011) and the organismal-level principles elaborated in the BioCore Guide (Brownell et al., 2014).

The Unanticipated Limitations of Conceptual Reforms

During periodic OrgBio faculty discussions, we expressed considerable satisfaction with the new course, in large part because it was certainly more engaging to teach than the OrgBio courses we had experienced in our undergraduate years. However, much to our surprise, student comments from official teacher evaluations, periodic formative assessments, and frequent informal discussions provided what could be charitably characterized as a more nuanced view. Some high-achieving students did talk quite enthusiastically about how the OrgBio course transformed their approach to learning biology, but many students expressed negative opinions ranging from "much too hard," "too much physics and math," "impossible to study for exams," "not coordinated with the textbook," and "needs discussion sections," to "the worst class ever."

Of particular concern was that students tended to "revert to wild-type" behavior in that they proceeded to memorize the principles and the organism examples, but they were generally unable on exam questions to apply those principles to other organisms and/ or different biological circumstances. Even our dean received angry complaints from OrgBio students who felt that such questions were unfair because we had not explicitly covered that information in our lectures. This outcome was particularly distressing to OrgBio faculty because the original rationale for developing this new course was to encourage the ability of OrgBio students to carry out principles-based reasoning.

What Does Principles-Based Reasoning Look Like in Biology Courses?

We had naively assumed that an effective pedagogy for teaching a principles-based OrgBio course would simply require that we changed our lectures from identifying the major characteristics that differentiate major taxonomic groups to highlighting the broad concepts that unify life. This switch might have been a necessary first step, but it was insufficient to reinforce, elaborate, and provide practice for helping the students to learn how to organize their knowledge according to those concepts and apply that knowledge to new contexts. In epistemological terms, the students persisted in thinking of themselves as passive memorizers of OrgBio concepts as opposed to active learners who would engage with the knowledge presented in class to develop their own deeper understanding of those concepts (Hall et al., 2011; Hall, 2013). We were not even certain what principles-based reasoning would operationally look like in an introductory biology course.

A biology colleague suggested that we should use Bloom's taxonomy (Bloom et al., 1956) to determine whether our classroom activities might involve principles-based reasoning. In brief, Bloom's taxonomy is a hierarchical classification of thinking skills, with remember and understand being considered as lower-order skills, and other skills such as apply, analyze, and evaluate representing higher-order skills (Krathwohl, 2002; Persaud, 2021). Bloom's taxonomy is certainly useful for evaluating learning objectives, classroom activities, and examination questions in order to determine the different types of thinking skills required of the students in biology courses (e.g., Crowe et al., 2008; Momsen et al., 2010). Although Bloom's taxonomy can be interpreted as devaluing the process of knowledge acquisition, we believe that the ability to memorize critical knowledge is foundational for learning biological principles.

Another theoretical framework for considering our pedagogical goals is what our physics education colleagues call reasoning from principles, which involves the application of core physics concepts and related equations toward solving physics problems. In physics pedagogy, a sophisticated form of principles-based reasoning is referred to as modeling instruction, which involves the developing and testing of conceptual models as the basis for building toward quantitative descriptions of those models (Hestenes, 1987; Brewe, 2008; Brewe et al., 2010). Reasoning from principles can thus be seen as a type of deductive reasoning in that general models are being used to generate the equations needed to understand and interpret specific cases. The reverse inductive process of reasoning to principles is not typically employed in physics, because new equations are rarely assembled from experimental observations, but instead are routinely mathematically derived from existing equations. By contrast, Darwin's and Alfred Russel Wallace's theory of natural selection exemplifies the process of reasoning to a new biological principle: they independently assembled the available evidence supporting inheritance, variation, overproduction, and differential survival to argue that the organisms best adapted to the environment are the most likely to produce the next generation (Darwin & Wallace, 1858).

When we reflected back on our initial efforts to develop the new active-engagement pedagogy discussed in the next section, it became clear that we were implicitly working from the idea that biological reasoning processes involve the interplay between knowledge and principle, which can be depicted as a figure-eight model (Figure 1). In this figure, the top half (#1 and #3) illustrates two types of reasoning from principles (or their models) to knowledge, the latter of which consists of facts, results, and observations. The bottom half (#2 and #4) illustrates two types of the reverse reasoning from knowledge to principles. The left side (#1 and #2) identifies specific classroom activities involved in the process of reasoning with biological knowledge already known to the students. Some OrgBio activities are designed either to encourage students to use a broad principle to organize and interpret their existing knowledge or to explain or integrate their knowledge to formulate a broad principle. The right side (#3 and #4) identifies specific classroom activities involved in the process of principles-based reasoning with new knowledge that is discovered by OrgBio students during their

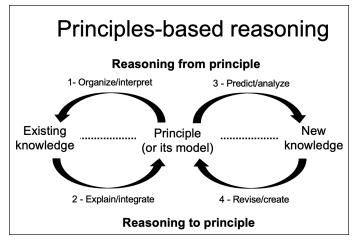


Figure 1. A figure-eight model of biological principlesbased reasoning used to identify the types of student reasoning skills that are encouraged by the group active engagements (GAEs) in Table 3. The top half of the model illustrates the process of reasoning from principle, and the bottom half shows the opposite process of reasoning to principle.

classroom activities, although it is generally already known by practicing biologists.

It is worth noting that research biologists engage in the types of principles-based reasoning illustrated in the right side of Figure 1 whenever they take knowledge that had never before applied to that particular problem, or that was newly discovered, to create a model of a new major principle. A classic example of both types of this biological principles-based reasoning is Watson and Crick's (1953) elucidation of molecular structure of DNA. First they used the knowledge obtained from nucleic acid biochemistry and X-ray crystallography to assemble a ball-and-stick model of DNA structure. Then they used that model to reason how a DNA molecule could be replicated to make two copies: "It has not escaped our attention that the specific pairing we have postulated immediately suggests a possible copying mechanism for the genetic material" (Watson & Crick, 1953). In summary, we designed the GAE activities to promote all aspects of principles-based reasoning that are central to learning and understanding biology.

The Development of an Active-Engagement Pedagogy for Teaching Principles-Based OrgBio

We identified several learning objectives to guide our development of a new active-engagement pedagogy for our OrgBio course. This pedagogy was designed to help students:

- distinguish passive vs. active participation in their learning activities, and improve from being passive recipients toward becoming more active participants;
- 2. understand their roles in collaborative learning, and develop into more effective participants in collaborative learning;
- 3. evaluate and cultivate their skills for doing different types of principles-based reasoning (Figure 1); and

 integrate OrgBio knowledge into a coherent conceptual framework emphasizing universal physical and chemical laws, deep molecular homologies, and diverse structure– function relationships.

In our initial efforts, we supplemented conventional lectures with simple active-learning activities such as clicker questions and thinkpair-share activities. However, we soon became convinced that these supplemented lectures by themselves were not sufficient to encourage students to engage in principles-based reasoning. It was obvious from office-hour discussions and examination answers that students needed more practice to develop their reasoning skills. Thus, several OrgBio instructors proceeded to develop a set of what we called GAEs, which are devoted to teaching major principles that are not readily learned in typical classroom settings. The GAEs are composed of model-building activities, small-group discussions, and whole-class check-ins that are designed after activeengagement exercises described in scientific teaching literature (e.g., Ebert-May et al., 1997; Ebert-May & Hodder, 2008; Handelsman et al., 2007) following the pedagogical recommendations of Wood (2009). In essence, students are encouraged to use their prior experience and new knowledge obtained from classroom activities to construct physical, conceptual, and/or quantitative models of fundamental principles and to apply those models toward solving new problems. In its final form, the active-engagement version of our OrgBio course devoted one-third of its class sessions to GAEs that took most or all of their designated class periods. The remaining two-thirds of the sessions were more lecture-based, but included several interspersed small-group activities each lasting 3-5 min that are largely devoted to facilitating knowledge acquisition instead of developing reasoning skills.

Table 3 summarizes the major topics and classroom activities involved in the GAEs and the types of principles-based reasoning needed to complete them. For example, in the diffusion GAE, students use their measurements from random walk simulations to construct the equations needed to characterize diffusion in biological systems (Figure 2); this GAE is then followed by homework problems that apply those equations toward understanding the functioning and evolution of different organisms. In the endosymbiosis GAE, students construct pipe-cleaner models of different organisms in order to evaluate the feasibility of different scenarios for the evolution and ultrastructure of primary and secondary plastids. Jardine et al. (2017b) reported that the GAEs in this OrgBio course were effective at helping our students learn the core concepts and scientific competencies that are specified in the Vision and Change report (AAAS, 2011). Readers are encouraged to examine, download, and use the resources for teaching the GAEs listed in Table 3 that are available at an open-access website http://hdl. handle.net/1903/29435 (Cooke & Jensen, 2022). All GAEs require minimal, if any, supplies and no specialized laboratory equipment. Other GAEs from a different version of the OrgBio course are presented elsewhere (Carleton et al., 2016; Haag & Marbach-Ad, 2016; Marbach-Ad et al., 2016).

Usually, the classrooms used for presenting GAEs had small tables with three chairs, which allowed us to design GAEs that emphasized collaborative learning activities (e.g., Goodsell et al., 1992; Wood, 2009; Nokes-Malach et al., 2015). In less convenient classrooms, we used blue masking tape at the beginning of the semester to subdivide the classroom into defined working spaces for three to four students each. (Surprisingly, the tape persisted long enough into the semester for students to become accustomed



to always sitting at the same places with their groups.) During the GAEs, the instructor and undergraduate learning and teaching assistants (ULTAs) circulated among student groups to support productive activities, encourage collaborative interactions, and engage them in brief discussions to make sure they understood the purpose of the GAE (Jardine et al., 2020). The ULTAs were most effective if they were permanently assigned to interact with no more than six student groups each. If enough ULTAs were available to maintain that ULTA-to-group ratio, then it became feasible to scale up this GAE-based pedagogy to large classrooms holding 150 students or more. The longer 50-min GAEs were typically followed by homework assignments consisting of conceptual questions and

quantitative problems to ensure that the students understood the principle modeled in that particular GAE class and could apply it to other biological systems. Students were encouraged to discuss the questions with other students in their group as well as other classmates, but they were expected to write up the answers on their own. Thus, they gained the advantages of working together without being dependent on other students for their homework grades. This approach helped students to overcome their distaste for group projects that was acquired in high school, where the grades assigned to individual students often depended on the work submitted from the entire group. Even though this policy of sharing knowledge did occasionally lead to academic misconduct, we felt that the goal of

Table 3. Group active engagements (GAEs) in OrgBioB and C courses. The numbers in the reasoning column refer to the types of principles-based reasoning identified in Figure 2. Each GAE marked with an asterisk includes two sets of group homework assignments. The resources for teaching the GAEs listed below are available at an open-access website (Cooke & Jensen, 2022).

GAE Topics	Main Activities/Model Building	Reasoning	Time (min)
Introduction – the OrgBio adventure	Small-group discussions about active learning	n/a	20
Thermodynamics of life – universal laws*	Building energy flow diagrams to identify the rules operating in bioenergetics and metabolism	2, 3	50–60
Phylogenetic reasoning – the trees of life*	Interpreting the phylogenetic tree of vertebrate evolution	1, 2	50
Origins of life – life emerging from nonliving environments*	Comparing Darwin's warm little pond vs. deep-sea hydrothermal vent models for the origins of Earth's and extraterrestrial life	3, 4	50
Endosymbiosis – a civil union of unequal partners*	Using pipe-cleaner cell models to visualize alterative scenarios for structural and molecular events in plastid endosymbiosis	3	50
Plants – flower development	Applying the ABC model to interpret the genetics of flower development	1	15
Diffusion – physical opportunity and biological constraint*	Using computer simulations of random molecular movement to generate the quantitative relationships expressed in diffusion equations	3, 4	50
Evolutionary developmental biology – homeobox stories	Interpreting the roles of homeobox genes in animal development and evolution	1, 2	15
Natural history museum field trip*	Visiting a natural history museum to understand the evolution of all life, especially animals	1	90–120
The scaling of size and shape – Oh my, look at how much those animals have grown!*	Using several physical models to visualize how the mathematics of geometric scaling affects organismal structure and function	2, 3, 4	50
Gas exchange – clever tricks for solving environmental challenges	Using existing knowledge and diffusion equations to make predictions about how gas exchange works in different situations	2, 3	15
Circulation – sharing the wealth*	Comparing plant and animal systems to generate Hagen–Poiseuille (H-P) equation and to illustrate how H-P equation operates in those systems	2, 3	50
Osmoregulation – homologous mechanisms operating in different environments*	Applying osmotic-flow models to understand the physiology of osmoregulation in aquatic animals	2, 3	50
Biomechanics – if I had a lever*	Manipulating wooden models of lever systems to understand animal locomotion	2, 3, 4	60–70

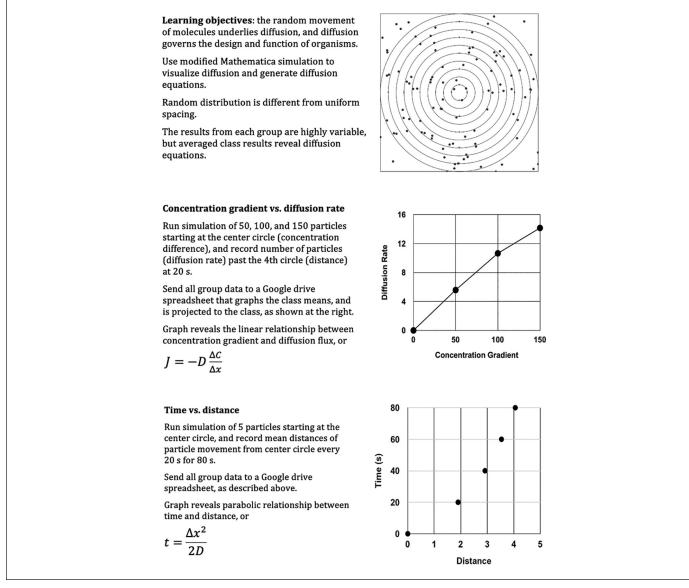


Figure 2. An overview of the diffusion group active engagement (GAE) that is designed to guide students to use a random movement simulation to generate two physics equations for characterizing diffusion. The graphs shown were taken from an organismal biology course taught in Fall 2016. Initially, student groups ran the simulation in order to visualize the random movement of particles. Then the groups positioned 50, 100, and 150 particles (= concentration differences) in the center of the concentric circles, ran the simulation for 20 and counted the number of particles (= diffusion rate) that have moved past four circles (= distance). After averaging the data from all the groups, the resulting graph displayed the linear relationship between diffusion rate and concentration difference that is the basis of Fick's First Law. Lastly, the groups positioned five particles in the center and measured the distance they traveled in successive 20-second intervals. Once again averaging all the data from student groups, the resulting graph displayed the parabolic relationship between time and distance that is the basis of the Einstein–Smoluchowski relation also called the time-to-diffuse equation. The group homework assignment involved multiple problems to illustrate how these equations provide opportunities and constraints for the evolution and functions of multicellular organisms. Random walk simulation from Mathematica was modified by Todd Cooke and Patrick Shipman (Colorado State University, Fort Collins).

encouraging collaborative learning was worth the risk. Besides, it was fairly easy to identify copied answers to conceptual questions, albeit admittedly harder for quantitative problems. Four in-class examinations were composed of short-essay and quantitative problems that were similar to those assigned in the group homework but that also covered subject material presented in the lecture-based classes. Considerable effort was devoted to undergraduate learning and teaching assistant (ULTA) training. All ULTAs participated in weekly preparation meetings lasting an hour or more that covered course content, GAE presentations, and specific class issues for the upcoming week. In addition, first-time ULTAs attended a second weekly discussion that focused on the theory, practice, and evaluation of active learning.

We cannot emphasize enough how central the ULTAs were to the successful implementation of the GAEs, as is detailed in Jardine et al. (2017a, 2020). In essence, they formed conceptual, pedagogical, and sociocultural bridges between instructors and students. We instructors found that ULTAs were quite adept at replying to student questions with thought-provoking questions and at promoting discussions between group members. The ULTAs who had previously taken the OrgBio course were able to attest to reluctant students about the effectiveness and enjoyment of engaging with the GAEs, which helped to encourage students to stay on task. The office hours of the ULTAs were held in student spaces during the evenings before homework due dates to further encourage productive conversations about the GAEs and related homework problems. Lastly, during their weekly prep meetings, the ULTAs would often provide informative feedback about those evening conversations that allowed instructors to understand what was unclear to the students and how to improve the GAE for the next semester.

O Does This GAE-Based Pedagogy Work?

We lack objective measures such as those developed for the GenBio-MAPS assessment (Couch et al., 2019) for determining if students develop a greater understanding of OrgBio principles and how to reason with them in our active-engagement courses. Nevertheless, according to the results from two intersecting subjective surveys, students perceived that the GAE-based pedagogy was a much more effective strategy for learning OrgBio. Table 4 presents student responses to course evaluation questions for a senior instructor who offered three different versions of OrgBio over a 15-year period. OrgBioA used conventional lectures from 2005 to 2008 to teach OrgBio to 125–150 mixed regular and honors students at UMD. OrgBioB used GAE activities from 2008 to 2014 to teach the same material to comparable student groups. OrgBioC used the same pedagogy as OrgBioB, but this version was taught from 2010 to 2019 to 50–96 honors students.

It is clear from Table 4 that the students believed that the active engagement version (OrgBioB) was more intellectually challenging, helped them to learn more OrgBio content, and kept them more engaged than the lecture-only version (OrgBioA). These perceptions are noteworthy, because OrgBioB "sacrificed" considerable class time to work on developing reasoning skills as opposed to conveying more facts. Honors students in somewhat smaller classes (Org-BioC) had even more favorable impressions about the effectiveness of the GAEs than did the mixed students in larger classes (OrgBioB).

Additional evidence supporting these interpretations was obtained from a pre vs. post epistemological survey called the Maryland Biology Expectations Survey that was given to students enrolled in these three OrgBio versions offered by multiple instructors within the narrow period of five semesters (Hall, 2013). Students taking the active-engagement OrgBioB and OrgBioC exhibited significant gains in developing more favorable attitudes toward viewing biology as a coherent discipline constructed of broad overarching principles instead of isolated facts and as a multidisciplinary subject incorporating physics, chemistry, and math. Students taking the conventional lecture OrgBioA often showed significant declines in their attitudes.

In conclusion, our GAE-based pedagogy does undeniably require greater effort from the instructor to teach active classroom activities than conventional lectures. However, it offers significant benefits for encouraging the students to engage with and learn the OrgBio subject material and to develop their skills in biological principles-based reasoning. Although we lack objective measures of assessing learning gains resulting from different pedagogies in our OrgBio course, there is compelling evidence across multiple scientific disciplines that students exhibit much stronger learning gains in active-learning courses than conventional lectures (e.g., Freeman et al., 2014). Moreover, a considerable literature argues that how students think about a scientific discipline and its knowledge (= student epistemology) is critically important to the process of knowledge acquisition (e.g., Elby, 2001; Sandoval, 2005; Hall et al., 2011; Gouvea et al., 2019), as is effectively done with the OrgBio GAEs (Table 4; Hall, 2013). Therefore, we would strongly encourage OrgBio instructors at other institutions to consider using the conceptual and pedagogical reforms offered in this article.

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Table 4. Student responses to instructor evaluation surveys for several versions of the organismal biology (OrgBio) course having different pedagogies and classroom contexts that are described in the text. All surveys evaluated the same instructor. Survey responses were based on a standard Likert scale with 1 = strongly disagree, 2 = agree, 3 = neutral, 4 = agree, and 5 = strongly agree. Data are presented as the means of all student responses to each of the four evaluation statements for each semester that particular version was offered \pm the standard deviations among those means for each course version. Replicate number (*n*) corresponds to the number of semesters each version was offered by the same instructor. *t*-Tests showed that all differences between OrgBioA and OrgBioB were significant at the *P* < 0.05 level, and that all differences between OrgBioB and OrgBioC were significant at the *P* < 0.01 level.

Instructor Evaluation Statements	OrgBioA (<i>n</i> = 5)	OrgBioB (<i>n</i> = 6)	OrgBioC (<i>n</i> = 10)
The course was intellectually challenging	4.10 ± 0.11	4.47 ± 0.10	4.68 ± 0.10
I learned a lot from this course	3.82 ± 0.07	4.07 ± 0.12	4.53 ± 0.23
The instructor helped create an atmosphere that kept me engaged in the course content	3.66 ± 0.30	4.26 ± 0.14	4.60 ± 0.09
Overall, this instructor was an effective teacher	3.96 ± 0.27	4.35 ± 0.11	4.63 ± 0.07

evaluation of the OrgBio course. The authors appreciate the support, guidance, and collegiality from the biology education research and teaching communities at UMD, including Daniel Levin, Gili Marbach-Ad, Joelle Presson, B. Booth Quimby, and Katrina Thompson. This article was markedly improved by the suggestions of the editorial staff and anonymous reviewers. The header photograph was generously provided by Kate Monzo for our non-exclusive use in this article. This project was supported in part by NSF grants DUE 0919816 to Todd Cooke and Edward Redish and DUE 1625670 to Katrina Thompson and Gili Marbach-Ad in the CMNS Teaching & Learning Center.

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