INTRODUCTION

The concept of bacterial growth and substrate utilization is foundational in the field of microbiology, yet the teaching of this concept is often limited to a graph displaying a single ideal growth curve labeled with the four phases of microbial growth: lag, exponential, stationary, and death (Fig. 1). Based on anecdotes from colleagues in microbiology research and education, the microbial dynamics leading to these phases are generally discussed, but the underlying mathematics are often ignored. When the latter are introduced, the Monod equations with Haldane modification are commonly used to describe microbial growth (Eq. 1) and substrate utilization (Eq. 2) (1)

\[
\frac{dX}{dt} = \frac{X \mu_m S}{K_s + S + S^2/K_i} - K_d X \quad \text{Eq. 1}
\]

\[
\frac{dS}{dt} = -\frac{1}{Y} \cdot \frac{X \mu_m S}{K_s + S + S^2/K_i} \quad \text{Eq. 2}
\]

where \(X\) is cell concentration (mass/volume); \(S\), substrate (carbon source) concentration (mass/volume); \(\mu_m\), maximum growth rate (1/time); \(K_s\), half saturation constant (mass/volume); \(K_i\), substrate inhibition constant (mass/volume); \(K_d\), death rate (1/time); and \(Y\), cell yield (mass of cells produced per mass of substrate consumed). When equations were introduced to our colleagues as students, the equations were generally displayed with little expectation for retention or comprehension, i.e., they were presented as “for your information.”

When this pedagogic approach is used, students struggle to understand how the parameters listed above relate to microbial growth. Teaching this concept is not practical in a lab setting either, as experiments require frequent sampling in a time frame of one to two days. Clearly, a different approach is required. Research shows that simulations can be a highly effective tool for improving student performance (2), and examples of effective programs are numerous (3, 4). As a result, we designed a web-based, interactive learning program called Environmental Science Studios (ESS\textsuperscript{tudios}: http://esstudios.arizona.edu/) to model microbial growth and substrate utilization. ESS\textsuperscript{tudios} includes three microbial-growth modules that increase in complexity but that are all based on growth equations described by Equations 1 and 2; the Basic Model is described in this paper.

ESS\textsuperscript{tudios} is intended to support inquiry-based instruction, as it allows for active exploration and manipulation of a model and mimics activities of real-world scientists. Inquiry-based learning can improve student performance and reduce attrition (5). In contrast to passive reception of knowledge associated with conventional science learning, inquiry is active and provides authentic learning tasks (6). The ESS\textsuperscript{tudios}
Microbial Growth and Dynamics (MGD) Modeling Program was developed to promote active, hands-on problem-solving that fosters a deep understanding of growth phenomena (7). The ability to control all of the growth parameters listed in Equations 1 and 2 makes this program adaptable to meet teaching goals for a variety of curricula and education levels. To support the implementation of this tool in classrooms, we have included an introductory lesson for microbial growth in Appendix 1, an explanation of the derivation of Equations 1 and 2 in Appendix 2, instructions for the ESStudios MGD Modeling Program in Appendix 3, and examples of university- and high-school-level assignments in Appendices 4 and 5, respectively.

PROCEDURE

The ESStudios MGD Modeling Program was used as a supplement to traditional lectures in an upper-division undergraduate and graduate environmental microbiology course. The lesson was split across two 75-minute classes. During the first class, students were provided a traditional lecture covering the types of microbial metabolism, factors affecting microbial growth, phases of microbial growth, the mathematics describing growth phases, and differences between microbial growth in the laboratory and microbial growth in the environment.

The second class period began with a 15-minute review of the first lecture and a 5-minute demonstration of the ESStudios MGD Basic Model. Students were given the rest of the period to complete a worksheet on laptops. Students were encouraged to use the think-pair-share process for this assignment. In this process, students first contemplate a question alone, then pair up to discuss the question, and finally share their approaches with surrounding groups. Some questions had multiple possible answers, and students were encouraged to either find multiple solutions or compare and contrast results with other groups.

CONCLUSION

This activity’s purpose was to expose students to real-world experimentation skills that involve a cycle of hypothesis formation about parameter effects, dynamic testing of hypotheses, evaluation of results, and hypothesis revision when necessary (8). Such cycles of hypothesis formation and testing in computer simulations can foster intuitive understandings of complex systems more effectively than experience with formal equations (9). Using the ESStudios MGD Modeling Program, students were able to easily conduct a large number of virtual experiments, make direct on-screen comparisons across experiments, and develop a strong understanding of the effect of growth parameters on microbial growth curves. During the first lecture, students were asked to describe how changing a growth parameter (e.g., growth rate, $\mu_m$) might change the appearance of a growth curve; despite having the equations displayed in front of them, students struggled to predict changes and made little to no connection between growth characteristics and growth parameters. After experimenting with the program, students were able to predict the changes to a growth curve when growth parameters were changed and to identify the parameter responsible for differences when presented with two growth curves.

Feedback on the activity was positive (Table 1), and during the activity, we noted that students asked questions indicative of a higher level of understanding. For example, we asked students to decrease the time between the lag and stationary phases of growth and describe how this could be accomplished in the laboratory. Students realized that changing the growth rate was required, and it could be accomplished by changing the environment (e.g., temperature) or changing the organism. Presented with these two options, students debated the validity of changing the organism and whether doing so would also lead to changes in other growth parameters that would preempt the stated goal. We have not previously observed such demonstrations of content mastery in this subject when teaching microbial growth in upper-division courses. This activity demonstrates the potential of ESStudios to shift pedagogy from teaching a mathematical concept using generalizations and dry oration to teaching the concept with visuals, case studies, and interactions which allow direct relation of the underlying mathematics with the physical manifestations of microbial growth.

SUPPLEMENTAL MATERIALS

Appendix 1: Introduction to microbial growth
Appendix 2: Model equations and derivation
Appendix 3: Model program instructions
Appendix 4: Undergraduate activity
Appendix 5: High school activity

ACKNOWLEDGMENTS

Development of the ESStudios MGD Modeling Program was funded by the University of Arizona Water, Environmental and Energy Solutions initiative which is supported by the Arizona Technology and Research Initiative Fund. The authors declare that there are no conflicts of interest.

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Juniors in Environmental Science
I felt like having a real-time visual of how even a small change to one of the variables in the equation affected the curve helped me understand the important role each variable plays in the culturing of microbes and in interpreting growth curves. The program itself was very straightforward, and I did not have any difficulties creating my growth curves.

ESSTUDIOS is an excellent tool for educators and students studying microbiology. The software is user-friendly and straightforward, and really helped me understand the function of each growth parameter and visualize how they affect a microbial growth curve.

Masters Student in Environmental Science
I really enjoyed changing the parameters to see their effect on the microbial growth curve. This visual tool helped me to grasp the concepts related to microbial growth.

PhD Student in Environmental Science
I found the ESSTUDIOS software to be very beneficial for my microbial education. It allowed me to visualize how different parameters affect microbial growth.

Teaching Assistant and Masters Student in Environmental Science
I have covered this material as both a student without using ESSTUDIOS and as a teaching assistant utilizing ESSTUDIOS, and I can see clearly the benefit of hands-on student modeling. Understanding concepts such as physiological lag or substrate utilization is greatly assisted when the student themselves can modify factors and see what has changed as a result. Overall, I found that the students who worked through the module using ESSTUDIOS had a much faster and stronger understanding of the dynamics of microbial growth than those learning in a purely lecture-based context.

Professor of Microbiology
Having ESSTUDIOS as an active learning tool in the classroom was very helpful. It helped to engage students to understand the myriad of factors that affect microbial growth in an active manner. Coupled with the sample questions provided, I felt that ESSTUDIOS was an invaluable tool for understanding microbial growth curve dynamics.

TABLE 1.
Feedback following ESSTUDIOS activity.

| Feedback |
|----------|
| **Juniors in Environmental Science** |
| I felt like having a real-time visual of how even a small change to one of the variables in the equation affected the curve helped me understand the important role each variable plays in the culturing of microbes and in interpreting growth curves. The program itself was very straightforward, and I did not have any difficulties creating my growth curves. ESSTUDIOS is an excellent tool for educators and students studying microbiology. The software is user-friendly and straightforward, and really helped me understand the function of each growth parameter and visualize how they affect a microbial growth curve. |

| **Masters Student in Environmental Science** |
| I really enjoyed changing the parameters to see their effect on the microbial growth curve. This visual tool helped me to grasp the concepts related to microbial growth. |

| **PhD Student in Environmental Science** |
| I found the ESSTUDIOS software to be very beneficial for my microbial education. It allowed me to visualize how different parameters affect microbial growth. |

| **Teaching Assistant and Masters Student in Environmental Science** |
| I have covered this material as both a student without using ESSTUDIOS and as a teaching assistant utilizing ESSTUDIOS, and I can see clearly the benefit of hands-on student modeling. Understanding concepts such as physiological lag or substrate utilization is greatly assisted when the student themselves can modify factors and see what has changed as a result. Overall, I found that the students who worked through the module using ESSTUDIOS had a much faster and stronger understanding of the dynamics of microbial growth than those learning in a purely lecture-based context. |

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| Having ESSTUDIOS as an active learning tool in the classroom was very helpful. It helped to engage students to understand the myriad of factors that affect microbial growth in an active manner. Coupled with the sample questions provided, I felt that ESSTUDIOS was an invaluable tool for understanding microbial growth curve dynamics. |

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