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Collaborative Understanding of Cyanobacteria in Lake Ecosystems

Meredith L. Greer, Holly A. Ewing, Kathryn L. Cottingham, Kathleen C. Weathers

Understanding the system is central to mathematical modeling. What better way than getting your feet wet (see Figure 1)? We describe here a collaboration in which the mathematicians help collect data, the ecologists synthesize more data from model output than they can produce empirically, and the collaboration produces both mathematical approaches and field work that would not happen if ecologists and mathematicians worked alone.



FIGURE 1. Sampling cyanobacteria

(credit: Kathryn L. Cottingham)

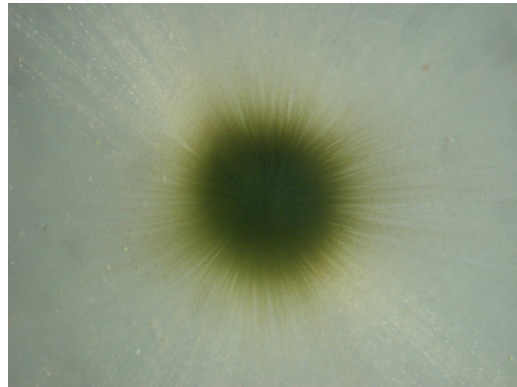


FIGURE 2. *Gloeotrichia echinulata*

(credit: Cayelan C. Carey)

Understanding the complicated systems arising in the mathematics of planet Earth requires the contributions of multiple disciplines. Ecologists are skilled in collecting and interpreting data and thinking about the complex systems involved; mathematicians provide a modeling perspective and a different way to understand large data sets. In fact, mathematicians offer additional perspectives that frequently generate new ideas and identify gaps in ecological knowledge. Collaborations such as ours are needed to understand ecological

systems. We hope more mathematicians, perhaps inspired by our example, will get their feet wet.

Gloeo

Our subject is *Gloeotrichia echinulata* (Gloeo for short, pronounced ‘Glee-o’), a cyanobacterium appearing in many New England lakes (see Figure 2). Gloeo lives in lake water during the summer, sinks to the bottom in late summer and early fall, then winters in sediment in its dormant akinete form until the water warms up in the late spring or summer (see Figure 3). It then germinates in sediment that receives light and moves up into the upper layers of water in a process called recruitment. Colonies in the water may then divide to make more colonies, depending on environmental conditions [9].

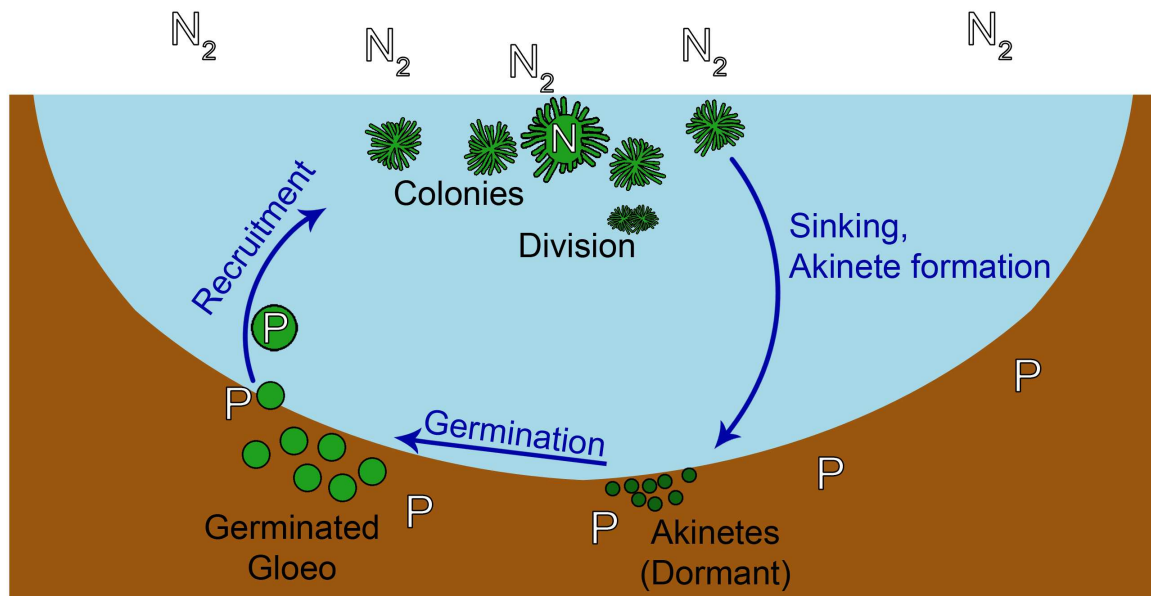


FIGURE 3. The Gloeo life cycle.

Gloeo is a particularly compelling subject because it brings to the water nitrogen (N) and phosphorus (P), two nutrients that commonly limit the growth of phytoplankton (algae and cyanobacteria that photosynthesize while floating in lake water). Thus Gloeo may give other

species a more nourishing home [4]. When germinating on the bottom of a lake, Gloeo takes up P that has been ‘locked’ into the sediment by chemical reactions. During recruitment, Gloeo brings ‘back’ some of this P [1, 8]. Similarly, Gloeo colonies convert dissolved N_2 from the atmosphere into forms usable by other phytoplankton (see Figure 3).

This ability to add nutrients to the lake is especially important since the lakes with which we are most concerned are *oligotrophic*: the water is clear, oxygen levels are high, coldwater fish can thrive at depth, N and P concentrations are low, and few cyanobacteria live in the lake. Some of these lakes are used for drinking water and most are important for recreation. Managers and home owners alike are concerned that these lakes do not, over time, become *eutrophic*: with murkier, greener water, lower levels of oxygen, no coldwater fish in bottom waters, higher N and P concentrations, more cyanobacteria, and eventually unsuitable for drinking [11]. Increased nutrient concentrations are the major cause of the switch from oligotrophic to eutrophic conditions and are often driven by human activities such as fertilizer use and land development in the surrounding watershed [11]. However, since the N and P taken up by Gloeo may become available to other organisms, a thriving Gloeo population may help push a lake toward the eutrophic state [4].

Our long-term goal is to study the interplay of Gloeo with N and P, from both external inputs (e.g., fertilizer) and internal sources (like the P in the sediment), in order to understand how Gloeo blooms might affect lake eutrophication. This is a complex question that depends on many factors, so we start with a smaller, but essential, question: What controls Gloeo population dynamics? The answer may allow us to discover when and where Gloeo might become abundant, and hence which subsystems we might want to monitor and perhaps even try to manage better.

Enter Mathematical Modeling

In summer 2010, mathematical modelers Meredith Greer and Audrey Lustig began to work with a group of ecologists — Kathy Cottingham, Holly Ewing, Kathleen Weathers, and many more — studying Gloeo in Lake Sunapee, an oligotrophic lake in New Hampshire. We read extensively about Gloeo, discussed its life cycle, and then developed a compartmental model (see Figure 4) focusing on akinetes, germinated Gloeo, and colonies in the water for a single field season (late spring through early fall). Once we understood the dynamics of a single season, we hoped to piece together consecutive years. This is still our goal, but after listing the data needed to estimate the parameters, we saw that the model was too far-reaching to be a starting point.

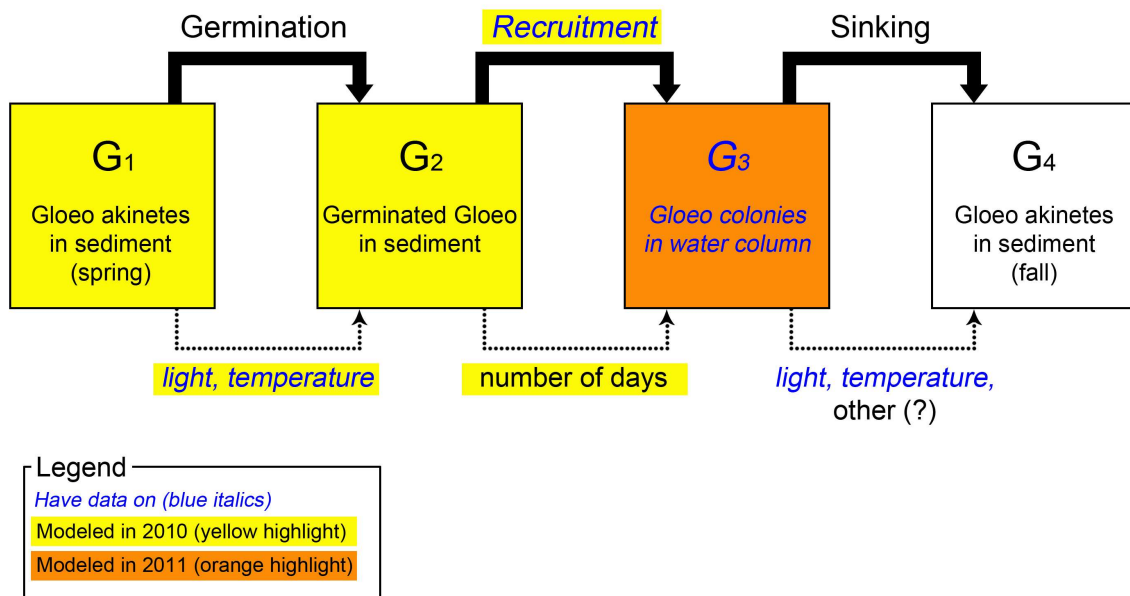


FIGURE 4. Initial compartmental diagram for Gloeo.

Insight #1. We needed to focus on a smaller portion of the Gloeo life cycle.

The literature on Gloeo and other cyanobacteria proposes that germination and recruitment are affected by factors such as temperature and light (see, e.g., [9]). These effects are hard to quantify experimentally, however. It is challenging to germinate Gloeo in a lab, and difficult-to-impossible to design controlled experiments on light and temperature in a lake. But our group did have data on recruitment, light, and temperature for multiple sites at Lake Sunapee. Could mathematical modeling help us identify specific triggers for germination and recruitment? Does light matter most, or temperature — or a combination?

We chose to consider three potential environmental drivers of germination: same-day photosynthetically active radiation (PAR, a measure of light), same-day temperature, and growing degree days (GDD), a measure of cumulative warmth from the start of the season until the day of germination. Based on our compartmental model, we constructed a simple system of differential equations:

$$(1) \quad \frac{dG_1}{dt} = -k \cdot E \cdot G_1,$$

$$(2) \quad \frac{dG_2}{dt} = k \cdot E \cdot G_1 - \gamma G_2.$$

These equations represent changes in G_1 and G_2 within a single field season. Akinetes in compartment G_1 germinate as determined by (1). The E factor encompasses the environmental drivers, daily temperature, daily PAR, and GDD. Germinated Gloeo appears in compartment G_2 , and after an average time $1/\gamma$ spent in sediment, moves into the water, at which point this model stops.

Each of our three environmental drivers, temperature, PAR, and GDD, can be modeled multiple ways. With temperature for example, we can write:

$$(3) \quad E_T(t) = p \cdot T(t),$$

where $T(t)$ is real, recorded temperature, p is a scaling parameter, and $E_T(t)$ is the temperature part of the E factor. Equation (3) assumes that recruitment increases linearly with temperature without limit.

Some literature, however (e.g., [6]), suggests there is an optimal temperature for germination and at temperatures higher or lower than optimal, germination falls off. To account for this, we can model temperature by using:

$$(4) \quad E_T(t) = e^{-\left(\frac{T(t)-T_0}{q}\right)^2},$$

where T_0 is the optimal germination temperature, and q is a dispersion parameter, which determines how much less likely germination becomes for every degree $T(t)$ differs from T_0 . Equation (4) can also serve as a nonlinear version of Equation (3): when T_0 is greater than all observed temperatures, $E_T(t)$ is an increasing function of $T(t)$.

A third possibility is that an environmental driver may serve as a germination threshold, that is, the driver may need merely to exceed a certain value to enable germination. For example, if lake temperatures are below freezing, Gloeo does not germinate, and other, less-obvious threshold effects may exist. There are many ways to model thresholds; we used a step function, switching from 0 to 1 at a threshold value.

Decisions, Decisions

Many linked decisions are needed to complete the model. First, which environmental drivers should be modeled? Since our goal was to determine which drivers are most important, we had to try a variety of combinations. We rejected the idea of modeling GDD by itself because GDD increases through the season and Gloeo recruitment has peaks and troughs. We did consider models in which temperature or PAR was the only driver. Otherwise, we tried *all* combinations.

Next, how should the drivers be combined? Were they additive, multiplicative — or something else? Because multiplying drivers slows germination precipitously if any one driver drops to low values, we chose multiplying over adding.

Another issue was discretization. Temperature and PAR data were available every ten minutes; GDD was computed daily; Gloeo recruitment was measured approximately once per week. We could have used a numerical method like Euler’s or Runge-Kutta. We chose to convert to a set of difference equations:

$$(5) \quad G_1(t) = -k \cdot E(t) \cdot G_1(t - 1),$$

$$(6) \quad G_2(t) = k \cdot E(t) \cdot G_1(t - 1) - G_2(t - \delta),$$

where $E(t) = E_T(t)E_P(t)E_G(t)$ is a product of the three environmental drivers (when all are present). In (5) and (6), the time step t is one day, and δ , the time delay from germination to recruitment, is in days.

Finally, it was necessary to identify appropriate values for the model parameters. A literature search and group-wide discussions generated biologically likely ranges for each parameter across which we allowed them to vary.

All these choices led to many models. For each, we modeled the number of recruited Gloeo per day and compared the model’s predictions with weekly data, summing daily model values over the intervals between field visits during which recruited Gloeo were collected. We then compared model predictions with observed data and sought to minimize the differences between predictions and data using least-squares computations.

Figure 5 shows two of these many models: one in which only temperature is modeled (Figure 5(a)), and one in which all three environmental drivers are included (Figure 5(b)). The data used to generate these graphs appear in a web supplement [5]. As might be

expected, using all three drivers allows a closer fit of model to data, in the sense of least-squares error. Additional work could be done here to determine whether it is worth it to allow the additional parameters. We can balance the increased accuracy with the goal of keeping the total number of parameters low. Measures such as the Akaike Information Criterion (AIC) (see [2], e.g.) can be helpful here.

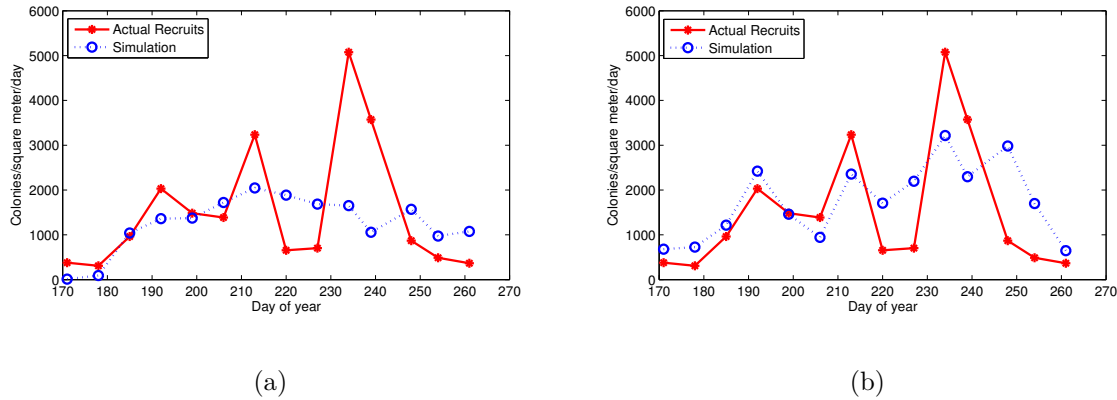


FIGURE 5. Two model-based simulations compared with Gloeo recruitment data.

Collaborative Conclusions

An important feature of all our graphs is that while some models captured the observed peaks in Gloeo population early in the season, they did not show the last, biggest, peak. They either failed to have a late-season peak, or it was much smaller than the observed peak. This led us to reassess our assumptions.

Insight #2. Perhaps Gloeo can germinate without overwintering.

We assumed that Gloeo akinetes overwintered, but had no experiments to confirm that overwintering was necessary. We took this to mean that we should eliminate compartment G_4 (Figure 4), allowing sinking colonies from G_3 to go directly into G_1 or perhaps into a

different compartment from which germination could occur in the same season. To complicate matters, however, we do not have good data on how long Gloeo colonies remain in the water, how many akinetes are formed by sinking Gloeo colonies, how much variation there is in either of these processes, and what factors affect them.

Insight #3. Even a simplified model should consider lake water dynamics.

This brought us to the end of the 2010 field season. For summer 2011, we had a new group of students working on the project. Some did field and lab work; some looked at our mathematical modeling approaches; everyone did some of each so that we all understood each other's work better. We met weekly to share what we had done and to think about the implications for Gloeo.

One math-oriented undergraduate, Cristina Herren, took on the question of what happens to Gloeo in the lake water. Recruitment is a necessary contributor to the population of Gloeo in the water, but division in the water may be the key to noticeably high Gloeo populations, sometimes called *blooms*. The exact contributions of recruitment and division to lake water Gloeo population are not fully known, and may vary by lake [3, 10]. We needed to understand better the factors that drive Gloeo division.

We have data on Gloeo abundance in the water of Lake Sunapee, taken daily during summer months since 2008 by a citizen scientist. Adding a statistical component to our work, Cristina used many different time series approaches to evaluate the extent to which Gloeo abundance in the water was associated with abiotic drivers such as light, temperature, wind speed, and other factors. No strong correlations with abiotic drivers were detected. However, Gloeo's response to its own population density on consecutive days suggested the possibility of density-dependence: rates of change in Gloeo density from one day to the

next were sometimes *positively* density dependent (in that growth was faster with increased density in the water), but more often *negatively* density dependent (in that growth declined with increased density), especially at high densities. Data from 2011 are shown in Figure 6.

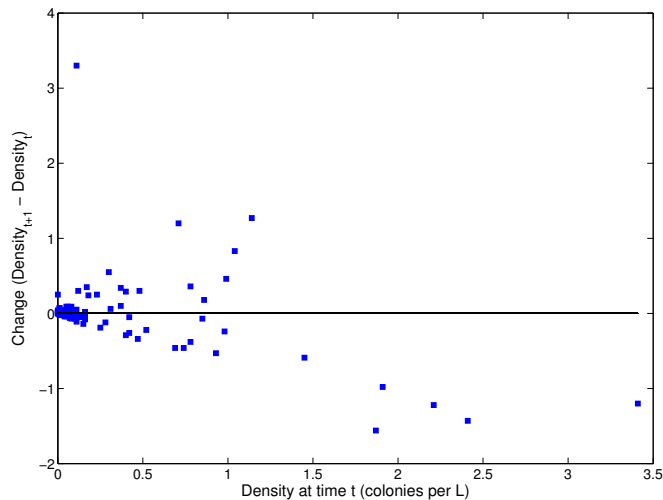


FIGURE 6. Change in Gloeo density in the water compared with starting density. Density always decreases for initial densities greater than ≈ 1 .

Interestingly, in data from both 2008 and 2009, it looked like only the negative density dependence occurred for densities greater than one colony per liter, whereas in 2010, the negative density dependence occurred above approximately five colonies per liter. We therefore designed an experiment to test whether we could directly observe negative density-dependence. The idea for the experiment and its design came out of the weekly meetings of the whole group.

Insight #4. Without mathematical modeling *and* ecological knowledge, the experiment would not have happened.

Our experiment was conducted at two lakes in August 2011, using collapsible plastic containers holding 20 liters of lake water (Figure 7) with initial densities of one, five, or eight

Gloeo colonies per liter. Consistently, Gloeo showed no positive population growth rates at densities greater than one colony per liter, suggesting that even at relatively low densities Gloeo had negative density dependence.

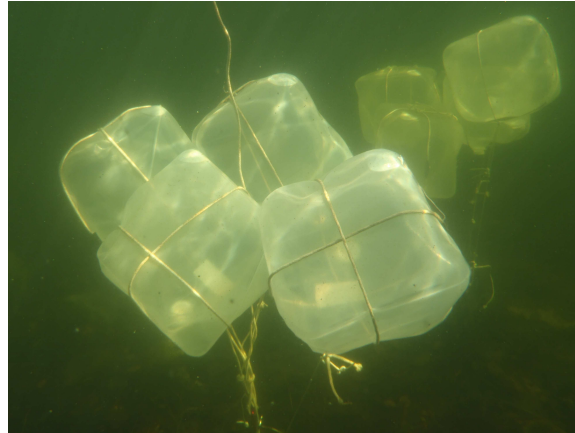


FIGURE 7. Floating experimental Gloeo colony containers. They are anchored to the lake bottom by rope and float about one meter below the surface.

(credit: Kathryn L. Cottingham and Elizabeth Traver)

What might cause this? Was it nutrient limitation? The answer to this question has big implications for lake management, so we set about designing another experiment where nutrient availability and colony density varied. However, we were surprised at the end of the experiment to find that many of the colonies had disintegrated into a gelatinous mass rather than having divided further. Our Gloeo were sinking to the bottom of the lake. They were done for the season. And so were we.

Insight #5. It can be hard to get information in the field, no matter how desirable.

Sometimes you have to wait another year.

Onward

In the future, we will investigate whether the degree of density dependence is modified by availability of N and P in the lake water, possibly accounting for the differences in the threshold density for negative density dependence. We also want to explore end-of-season effects on Gloeo. Outcomes from these experiments will inform our model, helping us to determine how to represent mathematically each phase of the Gloeo life cycle. Our group continues to work together, along with other interested people, to understand Gloeo and its role in eutrophication of New England lakes.

A unique feature of our project is the role of engaged citizens. Members and affiliates of the LSPA (Lake Sunapee Protective Association) attend some research meetings, engage with students and faculty reviewing and debating our results, and provide access to the lake. They alert us to important events that should be sampled (e.g., unusual blooms), provide longer term views of the system (e.g., “I recall that when I was a kid the rocks were less slimy, so there were probably fewer algae attached to them than today”), and are actively engaging the next generation in lake monitoring (e.g., Midge Eliassen, an LSPA member who has sampled Gloeo for many years, brings her granddaughters out to collect data).

Our experience leads us to urge that all mathematicians interested in the future of planet Earth consider collaborating with people in other disciplines. It may mean a lot of background reading, working in Word as well as \LaTeX , learning how to translate between mathematics and other disciplines, explaining to others how you do what you do, and asking more and different kinds of questions than you ever imagined you would. You may not always be sure how best to proceed and may have to try several paths. If you have chosen to work with others who are willing to do the same, this can lead you to places neither foresaw. To

get started, find some fellow adventurers, and get your feet wet.

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Summary

We describe a collaboration between mathematicians and ecologists, studying the cyanobacterium *Gloeotrichia echinulata* and its possible role in eutrophication of New England lakes. The mathematics includes compartmental modeling, differential equations, difference equations, and testing models against high-frequency data. The ecology includes field observations and experiments, and parameter estimation based on our data and related literature. Mathematically and ecologically, a collaboration progresses in ways it would never have if either group worked alone.

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