Modeling Phytoplankton Heterogeneity in a Consumer-Resource Agent-Based Model

by

Melissa Mattwig

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Thesis Committee:
Dr. Casey Godwin, Primary Advisor
Dr. Michael Fraker
Dr. Gregory Dick

ABSTRACT

Increased eutrophication and climate-induced environmental change in freshwater ecosystems are exacerbating Harmful Algal Blooms (HABs) through the proliferation of dominating phytoplankton species such as *Microcystis*. To help mitigate HABs, it is important to have effective predictive tools, such as models, that will adequately inform management decisions. Consumer-resource models are one such application to describe phytoplankton interactions with their environment, however they typically employ population-level estimates for functional traits despite research showing intra- and inter-specific variability. To address this, I adapted phytoplankton consumer-resource models—such as the Droop equation to describe growth rates based on internal stores of limiting resources—to an Agent-Based Model (ABM) framework. With this framework, I developed 5 models to test the effects of functional trait variability on the consumption and use of an extracellular resource: no variation, variation of 3 functional traits (maximum specific uptake rate, minimum quota, maximum growth rate) concurrently, and 3 models of varying each functional trait separately. Overall the model with 3 varied functional traits had the largest population, lowest extracellular resource, and largest C:P ratio than the other models. This indicates that the more variable phytoplankton population will be better competitors, have a higher biomass, and a higher overall population than its homogenous counterparts given the same nutrient environment. These findings raise important considerations for future phytoplankton consumer resource models and ultimately for freshwater management decisions.

ACKNOWLEDGEMENTS

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INTRODUCTION

Freshwater ecosystems are becoming increasingly altered due to land-use change, anthropogenic inputs of nitrogen (N) and phosphorus (P) from agricultural fertilizers and wastewater, and climate change (Conley et al. 2009). This has led to an increase in eutrophication, or the excess primary production or algal biomass. The increase of primary production is due to increased availability of one or more growth limiting factors, with N and P being the most influential nutrients in freshwater (Schindler 2006, Elser et al., 2007). As a result, some have found that harmful algal blooms (HABs)—most of which are caused by cyanobacteria in freshwater (Paerl, 1988)—are becoming more frequent and intense (Paerl & Huisman, 2008, O'Neil et al., 2012, Ho et al., 2019). However, Wilkinson et al. (2021) found that significant bloom intensification has not been widespread in U.S inland lakes as previously thought but that large lakes (>100km^2) were more likely to experience an increase of HABs. To better manage HABs, it is important to understand how predominant cyanobacteria play a role in HABs formation.

      Microcystis is a prevalent bloom-forming cyanobacterium in freshwater environments (Harke et al., 2016) and has dominated 78% of freshwater cyanobacterial blooms that were reported globally over the last 30 years (Xiao et al. 2020b). Some strains of *Microcystis* produce peptides called microcystins which can be dangerous to humans and wildlife. Moreover, *Microcystis* benefits from climate-induced environmental change (Paerl et al., 2011, Paerl and Otten, 2013), with higher temperatures resulting in higher growth rates (Robarts and Zohary, 1987, Fujimoto et al., 1997), especially for toxic strains (Davis et al., 2009). Another factor that makes *Microcystis* a widespread HAB in freshwater is that this genus is composed of multiple strains or genotypes that differ in their physiology and ecological traits (Dick et al., 2021, Bramburger et al., 2023). *Microcystis* also aggregates to form colonies which can be clonal or a mix of different strains (Smith et al., 2021, Otten et al., 2017. Jackrel et al., 2019) The interspecific and intraspecific variation of *Microcystis sp*. highlights the need to develop models that can describe and forecast how different environmental scenarios will affect phytoplankton productivity and response to these environmental drivers.

      Many management efforts for controlling eutrophication and HABs are based around the response of algal growth and biomass to nutrient inputs. The overarching principle is that nutrient demands of phytoplankton—determined by their physiological requirements—leads to a positive and often saturating relationship between the availability or delivery of nutrients and the size or extent of the phytoplankton population or bloom. Models, especially ecosystem-scale models, are becoming increasingly valuable to management of inland waters through a range of

purposes, such as forecasting and understanding patterns on a spatio-temporal scale (Manno et al. 2007, Schmolke et al., 2010, Ralston & Moore, 2020). This response can be based upon statistical relationships observed across similar systems, but there is more recent interest in using process-based models to predict how a lake's state would respond to potential changes in nutrients. Statistical modeling provides essential tools in HAB prediction and management by using patterns observed in the past to inform the model and make predictions. While statistical models are primarily used for hindcasts and near-term forecasts, they often lose their effectiveness for long-term forecasting (Ralston & Moore, 2020, Flynn & McGillicuddy, 2018). There are a handful of statistical models used at the ecosystem level to evaluate the role of *Microcystis* in freshwater HABs. In Lake Erie, a Baysian modeling framework (Obenour et al., 2014) and regression models (Stumpf et al., 2016) have been used to forecast HABs severity, effects of phosphorus, and potential HABs-reducing scenarios. In Chesapeake Bay, a habitat model using a neural network is used to forecast the probability of *Microcysti*s blooms (Brown et al. 2013). While these models are useful to make broad predictions about HABs, they do not always provide accurate representations of the underlying physiological or biological processes that affect the nutrient use of a single species or competition between species (Ralston & Moore, 2021), which can limit their applicability as tools for understanding rather than prediction.

Mechanistic, or process-based, models are informed by data but ultimately based on fundamental laws and assumptions of processes in the natural world by a single or set of differential equations. Mechanistic models can be advantageous for long-term forecasting since anthropogenic and climate change increases uncertainty, causing predictions to conform less to past circumstances (Flynn & McGillicuddy, 2018, Ralston & Moore, 2021). They are also better for understanding dependence and ecological effects by being able to manipulate one or more variables at a time. This modeling flexibility was the basis for the development of ecological resource competition theory (Tilman, 1977). Consumer resource models are a mechanistic modeling framework that relate phytoplankton growth and physiology to abiotic factors like nutrients, light, and temperature. These tools are especially useful when developing models that predict or forecast how changes in climatic or environmental trends will affect the presence of HABs for various temporal scales.

Most consumer-resource models for phytoplankton define nutrient uptake using Michaelis-Menten kinetics and, separately, growth using the cell quota model frameworks (Droop, 1968). The Droop model relates the growth rate to the intracellular concentration of the limiting nutrient, which is determined by uptake of extracellular resource and dilution of intracellular resource from growth. Experiments by Tilman (1977) showed that this growth model

accurately predicts the outcome of competition of two species limited by two resources under steady-state conditions. Many consumer-resource models for phytoplankton assume singular rates for growth and uptake on the population level for model simplicity and computational efficiency (Schuler, 2005). However, it is becoming more important to consider interspecific and intraspecific variation of HABs taxa. *Microcystis* has many strains that vary in growth rates and colony formation under different environmental conditions (Komárek & Komárková, 2002, Dick et al., 2021). Xiao et al., (2020b) found differences in growth parameters between strains of the same species (*M. aeruginosa*) from the same lake in Michigan based on changes in light and temperature, indicating that there is intraspecific variation among Microcystis strains. In addition to intraspecific variation, unicellular morphologies of *Microcystis* lead to morphological heterogeneity in colonies throughout the growing season as a result of formation strategies (cell division vs. cell adhesion), grazing stress, nutrient availability, and temperature (Xiao et al., 2018). On the other hand, colony disaggregation can also occur as a result of higher temperatures and specific nutrient concentrations (Ma et al., 2014, Zhu et al., 2016). The effects of nutrient concentration on colony formation, however, have been contradictory (Ranjbar et al. 2021). Thus, there is a need to explore this heterogeneity in HABs modeling and forecasting that accounts for individual diversity. One way to do this is through agent-based (ABM), or individual-based (IBM), modeling.

ABMs are tools for modeling heterogeneity within and across species that cannot be represented in population-level models (Hellweger and Bucci, 2009). The ABM framework can also account for colony-level variability during bloom formation. The interaction between individuals through shared resources and their impact on higher levels of ecological organization, such as colonies, emphasizes the potential that ABMs have for increasing our understanding of phytoplankton dynamics (Hellweger et al., 2016). While ABMs are useful for understanding behaviors of individual organisms, they can also be coupled with ecosystem-level models to determine the effects of individual heterogeneity on system-level properties (Hellweger et al., 2016). This utility requires that ABMs simulating phytoplankton growth, division, and colony formation also need to explicitly maintain mass balance in a way that can be easily integrated within other modeling frameworks, such as the agent-based marine ecosystem model that was coupled with the Massachusetts Institute of Technology (MIT) Ocean General Circulation Model (OGCM) by Clark et al. (2013). Historically the use of ABMs in research on phytoplankton growth and competition has been limited due to their high complexity and computational demand (Acevedo-Trejos et al., 2022, Hellweger et al., 2016). Some adaptations, such as the concept of "super-individuals" introduced by Sheffer et al. (1995),

increase the amount of represented individuals while reducing the computational requirements of ABMs. Hellweger and Kianirad (2007) developed a deterministic cell size ABM for cell growth and division where the growth of the cell is directly related to cell size and found that their model replicated data from chemostat laboratory experiments by Droop (1974) and Rhee (1974). Ranjbar et al. (2021) discusses the importance of including colony formation within phytoplankton ABMs, but recent phytoplankton ABMs have only simulated colonies as opposed to individuals and colonies in this study (Wang et al., 2017, Feng et al., 2018). There are currently no ABMs for phytoplankton growth and division that simulate colony formation as well as the effects of individuals and colonies concurrently competing for shared resources (Hellweger and Bucci, 2009). Wu and Forget (2022) developed a phytoplankton life-cycle ABM in Julia, however this model has not been applied to specifically explore how heterogeneity affects the phytoplankton consumer-resource relationship.

Here I present an ABM that simulates phytoplankton uptake, growth, division, colony division and formation through sloughing. The model is based on a chemostat-like environment and allows the introduction of variability for various growth and uptake parameters to represent intraspecific variability that is often missing in phytoplankton models. Moreover, this model explicitly maintains mass balance through monitoring the change in external nutrient concentration and biomass nutrient content as explicit state variables. This model was developed using R, an open-source programming language that will be easily accessible, expandable, and can be integrated within larger ecosystem models. Through incorporating functional trait variability I investigated the following questions: 1) how does intraspecific trait variability within colonies affect consumer-resource relationships and competitive ability? 2) how does intraspecific variability affect individual or colony structure within or across colonies? and 3) are there specific traits for which trait variability has a larger effect on resource use? It is important to note that this model was used to generally study the effects of variability on consumer-resource dynamics since there are both genetic and environmental drivers that can influence functional traits. The investigation of these questions in this study will elucidate future directions for this model, such as the incorporation of multiple resources and integration into larger ecosystem models.

METHODS

Model Description

The aim of the model is to simulate phytoplankton resource consumption, growth, division, and mortality within an agent-based framework in a continuous culture environment akin to a chemostat (**Figure 1**). The model keeps track of all the individuals and their functional traits related to resource use within each colony while separately monitoring all of the colony sizes and state variables. The process of resource uptake, growth, and division occur on the individual level while dilution and sloughing alter the colony characteristics. This model explicitly conserves resource mass by following the movement of resource from the extracellular medium into the cell and rationalizing it to cell size (as carbon) to generate a cell quota. Many of the trait values in this model are based on similar phytoplankton ABMs developed by Hellweger & Kianirad (2007).
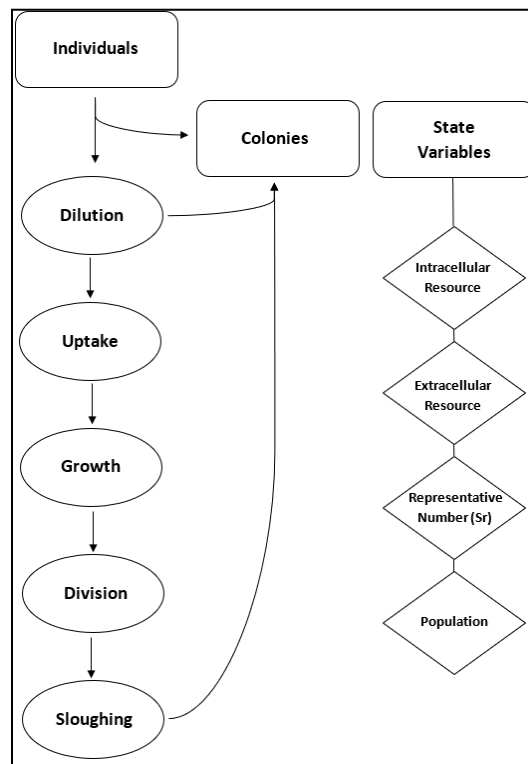

Figure 1: Model description. Dataframes in the model used to track individuals, colonies, and state variables are represented by squares. Biological and physiological processes that occur to individuals and colonies are represented by circles. The diamonds represent state variables that are continuously calculated throughout the model.

Parameter or State Variable	Unit	Value (or range)
Maximum specific uptake rate (V_{MAX})	$\frac{nmol}{nmol\ C * hr}$	0.0485 - 0.1456
Half-saturation constant (K_M) for uptake	$\frac{nmol}{L}$	510
Minimum cell size (m_0)	$\frac{nmol\ C}{cell}$	0.00022
Minimum quota (q_0)	$\frac{nmol}{nmol\ C}$	0.00117 - 0.0035
Internal resource concentration (S_I)	$\frac{nmol}{cell}$	0 - 0.35
Extracellular resource concentration (S)	$\frac{nmol}{L}$	0 - 0.35
Resource inflow concentration (S_{IN})	$\frac{nmol}{L}$	0.35
Resource flow rate (Q)	$\frac{L}{hr}$	0.0104167
Maximum Colony Size	$cells$	3000
Maximum growth rate (μ_{MAX})	$\frac{1}{hr}$	0.02083 - 0.0625
Population level intracellular resource (S_P)	$\frac{nmol}{L}$	0 - 0.35

Table 1: Parameters and state variables within each model. Most values are adapted from phytoplankton ABMs developed by Hellweger and Kianirad (2007) except for the maximum colony size which was derived from Bridgeman et al., (2013) and Watzin et al., (2006).

Resource Uptake

Resource uptake rate (*V*) follows Michaelis-Menten kinetics following the concentration of the limiting resource as in equation 1:

$$V = V_{MAX}(\frac{S}{K_M+S}) \tag{1}$$

Where V_{max} (nmol/nmol C*hour) is the maximum specific uptake rate, *S* (nmol/L) is the extracellular resource concentration, and K_M (nmol/L) is the half-saturation constant for uptake under resource-limited conditions. The predicted uptake rate, V, is multiplied by an individual's size to determine the mass of resource moving into a cell to increase internal resource (S_I,

nmol/cell). This is different from other models where uptake affects the quota directly (q, nmol/nmol C) by changing the ratio of internal resource to carbon. This allows for explicit conservation of mass by tracking uptake as a mass rather than a quota. If the calculated uptake exceeds S, then S is distributed equally between all individuals in the model.

Growth and Division

Growth in this model occurs on the individual level and follows the Droop model of growth (1974) which relates individual growth rate (in carbon) to the resource quota, q:

$$\mu = \mu_{MAX}(1 - \frac{q_0}{q})$$
<div align="right">(2)</div>

where μ is the growth rate, μ_{MAX} is the maximum growth rate, q_0 is the minimum cell quota below which growth cannot occur, and q is the cell quota. Growth in this model also affects the quota through dilution of the internal limiting resource. Once the growth rate is calculated for each individual based on their quota, division is induced through the model introduced in Hellweger & Kianirad (2007) that is consistent with existing theory and data of phytoplankton cell size distributions:

$$\frac{dm}{dt} = \mu m$$
<div align="right">(3)</div>

Where m (nmol C * cell^{-1}) represents the cell size based on cell carbon. Cells divide once $m \geq 2m_0$ and the cell size for each individual in the model is initialized to $1.5m_0$ at the start of each model run. Divided individuals inherit all traits from the parent individual and S_I is divided equally between the cells.

Sloughing

When a colony reaches a maximum colony size of 3000 individuals, it experiences sloughing and 60% of the colony breaks off to form a new colony. Sloughing was incorporated to represent biological processes that affect large colonies, such as shear stress, and to add a computational convenience to avoid exceedingly large colonies that may otherwise dominate

the population. The maximum colony size was chosen arbitrarily based on colony size observations in Lake Erie (Bridgeman et al., 2013), and the natural unit counting protocol for large *Microcystis* colonies by Watzin et al., (2006). While the maximum colony size can impact the number and size of the colonies in the model, it should not affect the underlying consumer-resource relationship that this model simulates.

Agent Accounting

This model—like many ABM frameworks—reduces the computational demand through the use of super-individuals. We define an individual in this model as a single phytoplankton cell. Individuals are grouped into colonies based on their colony identification (ID) number. Each colony in this model is considered a super-individual and each super-individual is assigned a representative number (S_R), which is the number of identical entities that a specific super-individual represents. That reduces computational demand by only simulating the individuals in one colony and upscaling the values of those simulated individuals by the S_R. Unfortunately this substitute can also challenge computational capabilities when the number of super-individuals grows too large. Some models address this issue by varying the number of super-individuals and fixing the S_R (Fredrick et al., 2013). Other models have varied both the number of super-individuals and their S_R (Hellweger & Kianirad, 2007). In all approaches a range of values is specified for either the super-individuals or the S_R to determine at which population size merging or splitting occurs. Splitting a super-individual is straightforward and effectively the same as dividing an organism through reproduction: half of the cell size and half of the resource quota are partitioned to each daughter cell. Merging super-individuals or reducing the S_R is often done through re-sampling a population and using an average for the newly-merged individual. While efficient, that step can introduce gains and losses of resource when the sum product of size and quotas does not equal the actual sum of resource in biomass. The ABM that I developed for this study models colonies as super-individuals, each assigned a variable S_R that is altered through death and dilution.

Dilution and Death

All colonies have an equal probability (5%) of being advected from the environment in each timestep using a uniform distribution. This density-independent mortality affects the S_R. Colonies are removed from the dataset when their S_R reaches 0. Once a colony is removed, all the

individuals within that colony are also completely removed from the mode without assuming the regeneration of nutrients through processes such as cell lysis, as opposed to assigning a value for being dead or alive as other ABMs (Frederick et al., 2013).

Maintaining Mass Balance

A feature of this model is that it allows for individual heterogeneity within colonies while maintaining mass balance in a continuous culture. In each timestep, the extracellular resource (S) is determined by:

$$\frac{dS}{dt} = QS_{in} - VN \tag{4}$$

where Q is the flow rate for the continuous culture (dimensionless), S_{IN} is the resource inflow concentration, V is the resource uptake rate and N is the total population. The total population encompasses all the individuals in the model—including the additional colonies represented by S_R. In this model, the change in S does not occur at the same time in each timestep. Loss of S from dilution out of the continuous culture based on Q occurs at the beginning of each timestep. Reduction of S based on resource uptake by individuals occurs during uptake. The addition of resources into the continuous culture occurs at the end of each timestep. The population level intracellular resource (S_P) is calculated after the addition of incoming resource by summing the S_I of all individuals within a colony and multiplying by the S_R.

Description of Model Runs

The model was run under five different conditions:

- No Variation
- 3 Parameter Variation (V_{MAX}, q_0, and μ_{MAX})
- Variation of μ_{MAX}
- Variation of V_{MAX}
- Variation of q_0

These traits were chosen as they directly affect how much resource an individual can take up (V_{MAX}) and use for growth (q_0 and μ_{MAX}). Trait values were randomly assigned using a uniform distribution 50% above and below the fixed value used in the No Variation model. Each run used a different seed, but all starting conditions except for the variation in trait values were identical for each run. Each model was run for 500 timesteps with each step representing 1 hour. The model was developed in R version 4.2.2 (R Core Team, 2022) and the plots were made using the ggplot2 package (Wickham, 2016). All models were run using the Great Lakes High Performance Computing (HPC) environment through the University of Michigan.

RESULTS & DISCUSSION

Consumer-resource relationships and competitive ability

The first question I explore using this model is how the variation of trait values changes the consumer-resource relationship or competitive ability within and across colonies. **Figure 2** and **Table 2** show a mean S_I of 0.26 nmol/cell and an S of 0.09 nmol/cell for the 3 Parameter Variation model and a mean S_I of 0.19 nmol/cell and an S of 0.16 nmol/cell for the No Variation model. In **Figure 2**, the sharp spikes in the population for the No Variation model represent synchronous division that is occurring as a result of a homogeneous population without variation of trait values. The mean population at the end of the 3 Parameter Variation was 410,955 total individuals and the population mean at the end of the No Variation model was 182,455 total individuals. The variation of trait values does not have an effect on the quality of consumer-resource relationship across all the individuals or colonies but rather the quantity. The S_I is higher and the S is lower in the 3 Parameter Variation model than in the No Variation model under the same environmental conditions. This shows that variation in trait values related to resource use allows for individuals across colonies to consume more resources than a homogenous population. This result also highlights the improvement of competitive ability in populations with variable trait values since S near equilibrium is equal to its R* value, or the lowest resource level that can support non-negative net growth in a chemostat given a specific dilution rate (Tilman et al., 1982). It is not, however, specific to one colony as the improved competitive ability is seen across the entire population. These results align with trait-based

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approaches to phytoplankton ecology and show how functional traits can be translated to fitness (Litchman & Klausmeier, 2008).

       Table 2 also shows that increased variability leads to an increase in total biomass (as total cell carbon) as well as a higher C:P ratio. This means that despite each model having the same amount of extracellular resource, the introduction of variation allows for flexible internal stores of resource that ultimately lead to higher competitive ability and larger populations. The flexibility of C:P in this model is seen in other studies that report intraspecific plasticity of their elemental composition. (White et al., 2006, Gabraith & Martiny, 2015). Thus, models used to predict the HABs will result in larger blooms when including variability. This can have implications for HABs management since historically the largest solution for HABs management has been a reduction in nutrients essential to phytoplankton growth and metabolism (N and P).

Model	Population-level Intracellular Resource* (S_P)	Extracellular Resource* (S)	Ending Population	Cell Size*	Total Cell Carbon (nmol C)
3 Parameter Variation	0.26 SD: 0.0178	0.09 SD: 0.0054	410,955	0.000304 SD: 6.147e-05	124.93
No Variation	0.19 SD: 0.025	0.16 SD: 0.0097	182,455	0.000354 SD: 3.775e-05	64.59
Variation of μ_{MAX}	0.20 SD: 0.024	0.16 SD: 0.012	221,956	0.0003 SD: 6.537e-05	66.59
Variation of V_{MAX}	0.22 SD: 0.027	0.13 SD: 0.014	233,963	0.000302 SD: 6.253e-05	70.66
Variation of q_0	0.24 SD: 0.023	0.12 SD: 0.0061	377,726	0.0003 SD: 6.164e-05	113.32

Table 2: *Total population-level intracellular resource, extracellular resource, and population at the end of each model. The * denotes a mean across all 10 runs for each model at the last time step. SD represents standard deviation.*
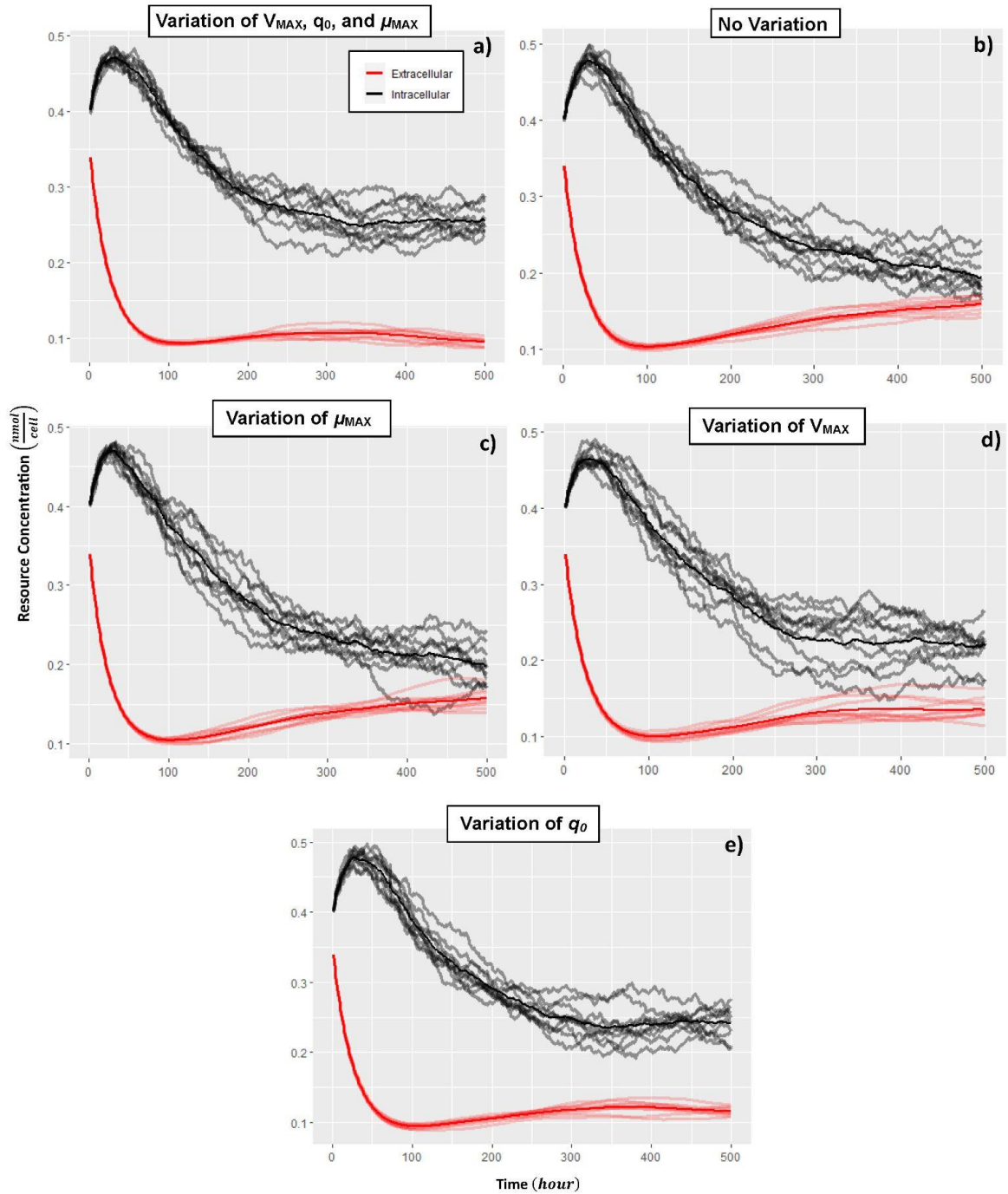
Figure 2: Intracellular (black) and extracellular (red) resource concentration in nmol/cell over time for all models. In each plot each run is represented by the lighter, opaque lines and the mean value is represented by the darker, solid line.
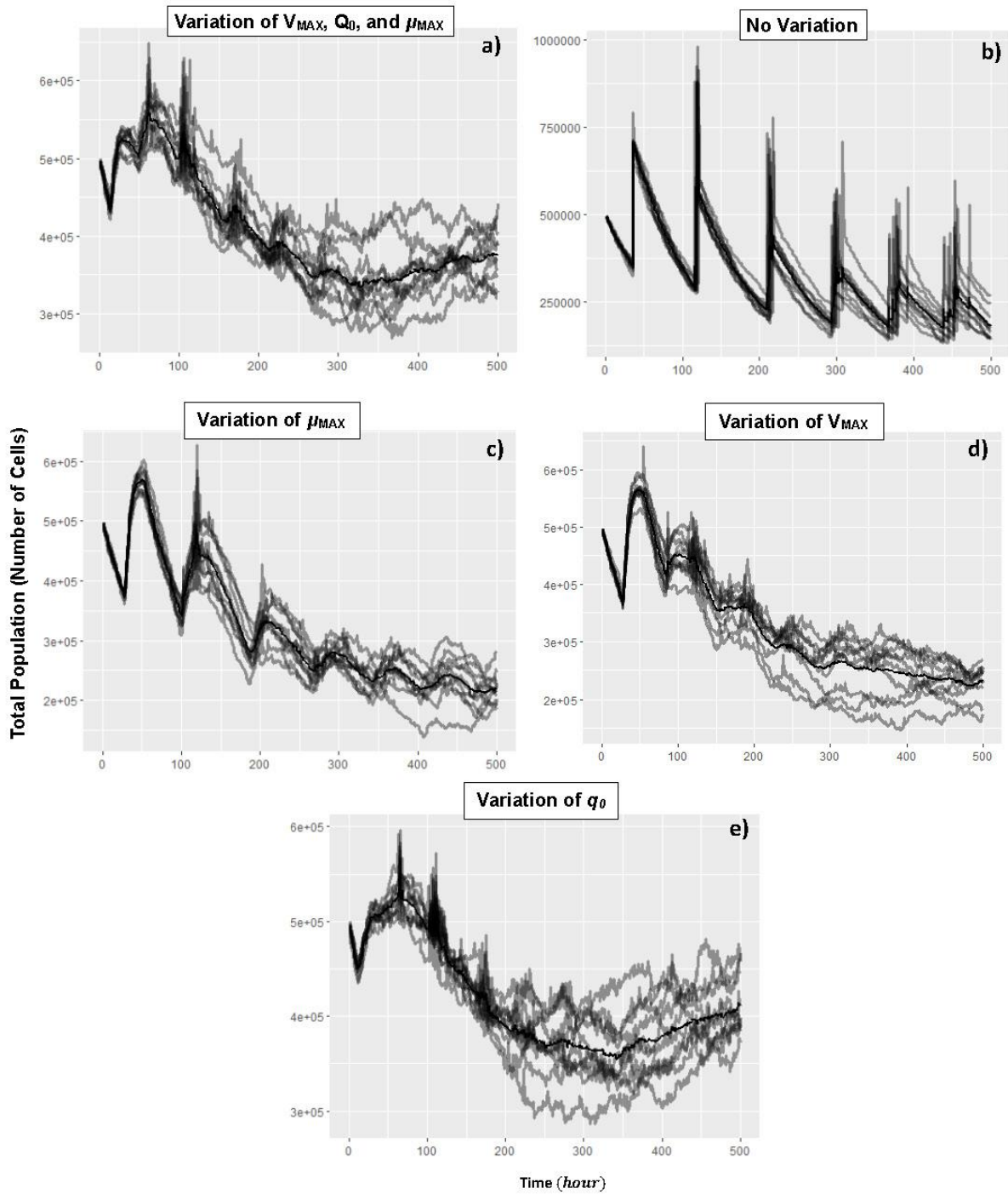
Figure 3: *Total population over time for all models. In each plot each run is represented by the opaque lines and the mean value is represented by the solid line. The sharp spikes in the population for the No Variation model represent synchronous division that is occurring as a result of a homogeneous population without variation of trait values.*

<u>Selection of Trait Values</u>

To better understand what contributed to increased competitive ability when introducing variation among resource use traits, the second question that I examined through this model was how intraspecific variability changes individual or colony structure. **Figure 4** shows that by the end of the 3 Parameter Variation model overall the population had higher values of V_{MAX} and μ_{MAX} and lower values of q_0 compared to the fixed values of the No Variation model shown in red. At the beginning of the model the trait values were uniformly distributed and the trend towards higher or lower trait values can be seen in the middle (t = 250) of the model run. Selection for V_{MAX} and q_0 was more pronounced than for μ_{MAX}, i.e they had higher counts of trait values farther from the median value of the No Variation model than μ_{MAX}. This could be due to μ_{MAX} being strongly correlated with traits not included in this model, such as light availability or stoichiometric ratios (Inomura et al., 2020) or because V_{MAX} and q_0 more strongly affect individual resource allocation. Ultimately, these results indicate that variation in resource use trait values allows colonies to select for trait values that will provide a competitive edge for resource consumption. The function of consumer resource models is to explain how organisms convert resources from their environment to their mass and this model shows that variability of resource use traits matters by affecting the quantity and speed at which a resource is converted to biomass. This is similar to research done by Inomura et al., (2022) which showed that phytoplankton exhibited plasticity in their stoichiometric—and by correlation their underlying trait—values due to acclimation to local environmental conditions through resource allocation. Moreover, the diversity in stoichiometric values arose naturally as a result of a range of growth conditions similar to my study where trait selection arose naturally from a range of values.
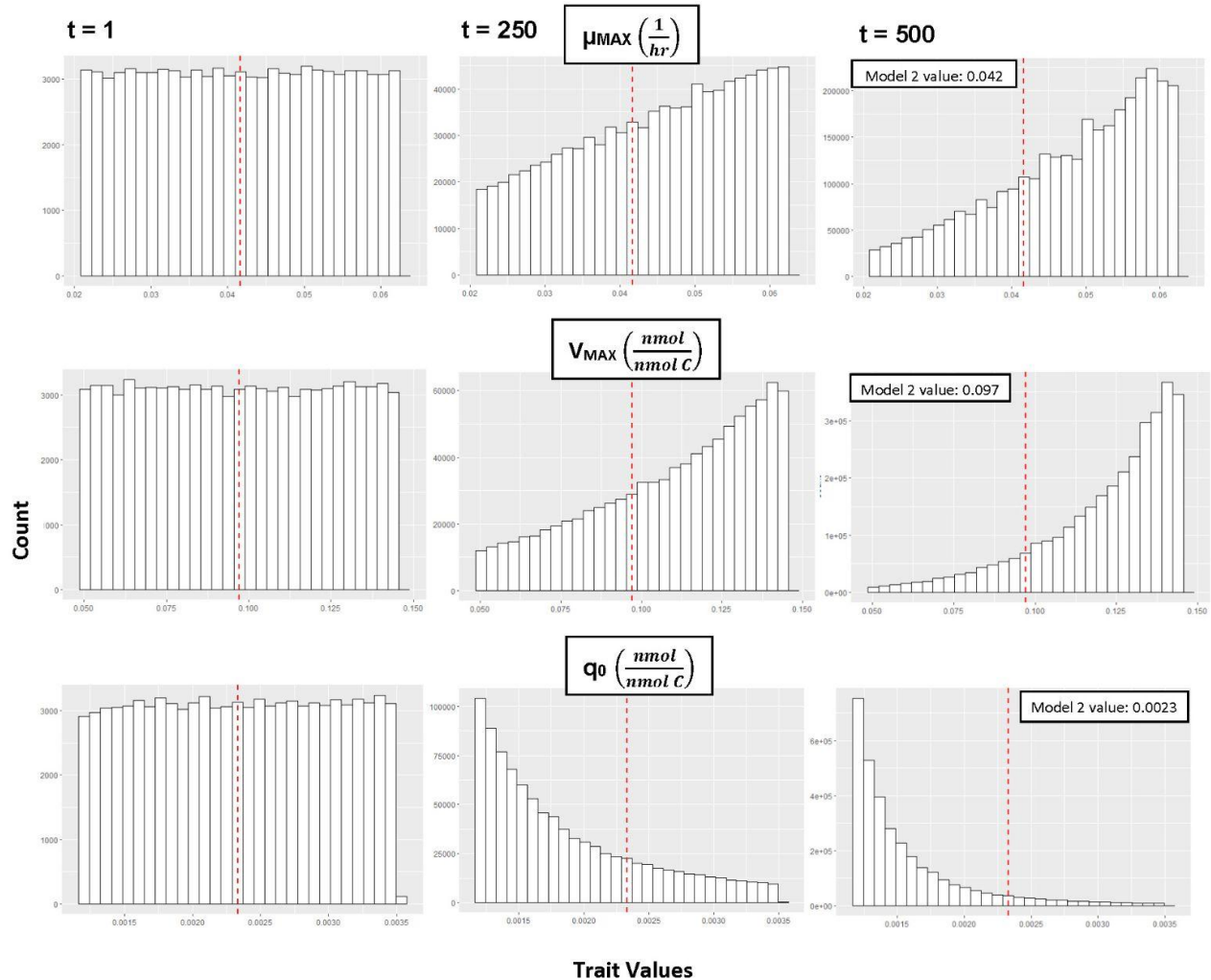
Figure 4: Comparison of trait value distributions in the 3 Parameter Variation model at t = 1 (left), 250 (middle) , and 500 (right) for μ_{MAX}, V_{MAX}, and q_0. The fixed value for each of the trait values from the No Variation model are represented by the dashed red lines in each plot.

Comparing Impact of Variation of Individual Resource Use Traits

My third question for this study was to explore whether variability in one of the resource use traits had a larger effect on resource use than other traits. **Figure 2** compares S_I and S and **Figure 3** compares the total population for the 3 Parameter Variation model (**panel a**), No Variation model (**panel b**) and the models with Variation of μ_{MAX} (**panel c**), V_{MAX} (**panel d**), and q_0 (**panel e**). The S_I for each model was 0.20, 0.22, and 0.24, respectively (**Table 2**). The model for Variation of q_0 had the strongest competitive ability by having both the largest S_P and lowest S, which can be interpreted as the lowest R* of all the models. This competitive ability was not

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larger than the model for 3 Parameter Variation which shows that heterogeneity across multiple trait values has the largest effect on competitive ability. The Variation of q_0 model displayed the highest ending population than the other two single parameter variation models, which could be explained by the fact that a lower q_0 means that each individual needs less nutrient to grow. This means that more individuals can use less resource to grow given the same input nutrient concentration in the other models. Additionally, the Variation of μ_{MAX} model had more periodic changes in the population akin to synchronous division. In **Figure 5** the trait selection for the One Parameter Variation models occurs more slowly and aggregated than in the 3 Variation Model (**Figure 4**), especially for μ_{MAX}. This shows that trait values undergo selection at a quicker rate when more than one trait value is varied, which aligns with results by Litchman et al., (2007) showing correlations between nutrient-dependent growth and uptake parameters. This shows that colonies with favorable values for two or three resource use trait values more quickly outcompete colonies with only one competitively variable trait.
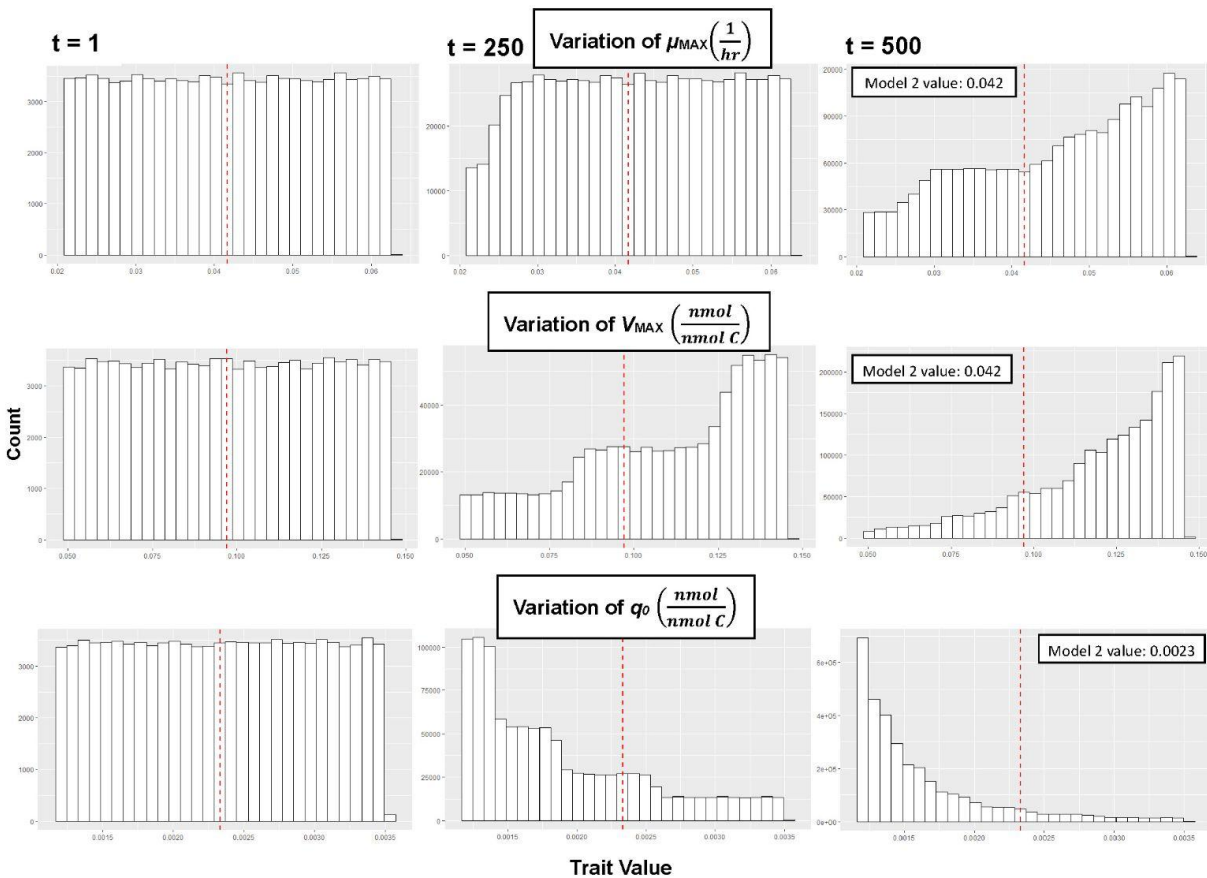

Figure 5: Comparison of trait value distributions in the One Parameter Variation models at t = 1 (left), 250 (middle) , and 500 (right). The fixed value for each of the trait values from the No Variation model are represented by the dashed red lines in each plot.

Model Limitations

One limitation of this model is the mechanism for increasing the S_R of super-individuals when it falls too low. Since new colonies are formed through sloughing once a colony reaches a maximum colony size, there is no need for super individuals within the colony as the colonies are never growing large enough to be too computationally demanding. This approach also allows for maximizing variation within colonies by simulating each individual cell. Averaging the values of all individuals when merging colonies to increase their S_R would not conserve overall resource mass in this model. This is a result of the model structure since the intracellular resource concentration is tracked on the level of each modeled individual within a colony. Additionally, merging colonies that have the lowest S_R that may not reflect phytoplankton behavior, especially when this model is used to simulate various species.

Conclusions and Future Directions

The model I developed for this study explores how heterogeneity among resource use trait values leads to increased competitive ability through a lower R* as a result of individual selection of optimal trait values. It shows that populations will naturally select for optimal resource use functional traits when given a range of trait values, which tells us that increasing heterogeneity ultimately changes how resources in the environment are converted to biomass. This model is a starting point for how ABM frameworks can be used to emphasize individual heterogeneity to explore various consumer-resource scenarios and test those predictions from experiments or sampling data. It predicts that—given the same starting conditions and resource availability—the modeled phytoplankton population will be better competitors, have a higher biomass, and a higher overall population than its homogenous counterparts. Additional resources as well as traits can be easily incorporated into the model, and its availability via open-source programming software makes it easily accessible to the public. Other additions could include characteristics that influence functional traits, such as an effect on growth rate as a result of colony size as was shown by Wilson et al., (2010). Moving forward, it will be necessary to see how individual variation affects community composition models. Moreover, the model's explicit conservation of mass allows for easy integration within larger ecosystem models that will allow for a more accurate representation of phytoplankton resource consumption to see how variation plays a role on a larger, ecosystem scale.

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