

A Mathematical Model For Light and Nutrient Modulated Growth of Phytoplankton Species Under the Influence of Benthic Grazing and Nutrient Forcing

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Abstract

It is well documented that the recent colonization of Lake Michigan by dreissenid bivalves lead to a dramatic reconfiguration of the lake's ecosystem. These changes resulted in benthification, which is a transport of a substantial part of the ecosystem's biomass to the bottom of the lake's water. While various datasets support this observation, a quantitative evaluation of overall ecosystem productivity, its spatial distribution and its effects on the dynamics of the lake ecosystem are not fully understood. The formulation, parametrization and numerical solution of mathematical models representing the major components of the altered lake ecology could help the understanding and quantitative evaluation of the new ecological dynamics. We present a detailed formulation of a simplified mathematical model and a numerical method for its solution. The model takes into account the competition among primary producer species for the varying light and two different nitrogenous nutrient sources in the pelagic, as well as the impact of the grazing and nutrient recycling by a substantial and changing dreissenid mussel population in the benthos.

1 Introduction

Despite human efforts to keep them robust and viable all natural ecosystems are subject to continuous change. When there is external pressure forced upon an ecological structure, at some scale the system will adjust. Determining the robustness and intrinsic stability of an ecosystem and the specific implications of such transforming events is difficult. Most of the time a multitude of feasible implications can be conjectured but without the appropriate tools to analyze and approximate the underlying dynamics and complexity of a the system such forecasting efforts essentially stay at the level of informed guessing. The ecological structure within Lake Michigan is an example of one ecosystem that has gone through a dramatic transformation recently. Within the past two decades Lake Michigan has been subject to the large impact colonization of an invasive bivalve species, the quagga mussel.

Since the late 1990's many research endeavors document the colonization and its impact on the ecosystem[1, 2, 8]. The quagga mussel has thrived in the conditions present in Lake Michigan because of derived niches[5]. As a result of this, there is an overall reduction of phytoplankton biomass in the lake which is evident with the loss of the spring bloom for diatoms[1, 6]. Fundamentally the success of these mussels have drawn a large portion of the lake's biomass to its benthic region, a process referred to as *benthification*.

Such transformation can be particularly influential for larger species within the food-web and gives reason for investigation. In order to evaluate the impact of the quagga mussel on phytoplankton biomass, now two major actors in the lake ecosystem, we model their interactions. Our model involves one spatial dimension (depth), contains two phytoplankton densities subject to light availability and two nitrogenous compounds, nitrate and ammonia that include a preferential factor for ammonia uptake. This model incorporates a quagga mussel growth model component in the benthos and enforces the impact of mussel grazing as a boundary condition on the phytoplankton and nutrient dynamics. This research endeavor makes a step towards quantifying the impact of the quagga mussel, and can help infer probable outcomes in the reformulated ecosystem.

2 Mathematical model

To model the ecological impact of a generalized water column strictly related to the colonization of quagga mussels we consider the physical and biological processes involved. To construct qualitative representation for a simplified ecological dynamics, we can use conservation laws for the nutrients considered. This basic conservation concept means that the time rate of change of a distributed quantity in some spatial domain is equal to its rate of growth within the domain and its net rate of transport, or flux, through the boundaries of the domain:

$$\frac{d}{dt} \int_a^b \mu(z,t) dz = \phi(a,t) - \phi(b,t) + \int_a^b f(z,t) dz = - \int_a^b \phi_z(z,t) dz + \int_a^b f(z,t) dz.$$

Here μ represents the spatially distributed density of a quantity under consideration, ϕ is its flux/transport and $f(z,t)$ is its local rate of growth. In this context we assume that $\mu(z,t)$ represents a nitrogen density in the water column in the form of phytoplankton biomass or dissolved nutrient at time instant t and depth z in the body of water, taken to be uniform along the other two spatial dimensions. The domain is considered to be a watercolumn with a small constant area. The conservation law in this case can be simplified and formulated as a one-dimensional integro-differential equation. For instance we can consider the model to represent the dynamics in an offshore basin within a large lake. The above conservation law implies that the density μ considered also satisfies at any depth z and time t the partial differential equation

$$\mu_t(z,t) = -\phi_z(z,t) + f(z,t).$$

2.1 Phytoplankton Biomass

Lake Michigan has a large variety of phytoplankton species that can be organized into a number of functional species groups. Species within and across these species groups have different adaptations and varying growth potential under different light and nutrient conditions. We demonstrate our modeling approach on the simple case of competitive growth of two phytoplankton species in the water-column with biomass densities $\omega_1(z,t)$ and $\omega_2(z,t)$. Generalizing the model for higher number of species is relatively straightforward.

We additionally assume that phytoplankton species have the capacity to orient their position in the water column by regulating their buoyancy to enhance their growth potential. This capacity is represented by $v_i(N_1, N_2, I)$ in the model, that stands for a nutrient and light dependent buoyancy or rate at which the i th phytoplankton species rises and sinks in the watercolumn. An additional parameter considered important for the flux of phytoplankton biomass throughout the watercolumn is the effective diffusion $D(z)$, which may be depth dependent.

The other main variable in our model represents the density of nutrient sources in the pelagic available for uptake for the phytoplankton. We consider densities of two nitrogen based compounds, ammonia $N_1(z, t)$ and nitrate $N_2(z, t)$. Ammonia metabolism is biologically more efficient and therefore it is a preferred source of consumption by the phytoplankton. Because of this we include a preferential factor that suppresses the consumption of nitrate when ammonia is present in sufficient quantities.

Light availability also regulates phytoplankton photosynthesis and growth. The light intensity $I(z, t)$ acts as an external forcing in the model and is being attenuated in the watercolumn with increasing depth. Additional to the impact of water, light attenuation is also influenced by the biomass densities present in the system. This phenomenon is quantitatively described by the Lambert-Beer Law with absorbance being determined by background attenuation and the concentration of the phytoplankton species.

2.2 Nutrient Densities

As a simplifying choice we incorporate ammonia and nitrate as nitrogen nutrient source in the model, ignoring phosphorus or other nutrients. This is because the densities of alternative nitrogen sources are substantially impacted by the presence of the benthic mussel population, and may drive a more complex and structured phytoplankton growth that can be observed in the formation of thin differential growth layers of phytoplankton.

Unlike the phytoplankton densities that have a convective flux component due to buoyancy, nutrient densities N_1 and N_2 are subject to diffusive fluxes only. Nutrient accumulation is affected by an instantaneous resupply from decomposing phytoplankton and a constant seeping rate from the benthic layer into the system. Both N_1 and N_2 are approached in a similar fashion with the addition of the preferential factor for N_1 (ammonia). We also consider the contribution of ammonia to the system via the mussel density at the bottom boundary. Additional to an assumed nutrient release from sediment, ammonia is also resupplied through

excretion by large mussel biomass in the benthos.

2.3 Mussel Density

The drastic change in phytoplankton biomass and nutrient distribution over recent years is correlated to the quagga mussel colonization[3]. The adult population of this species is in the benthic layer. We ignore in our model the likely substantial, but short-term impact of mussel spawning on the pelagic phytoplankton population. This restricts mussel dynamics to the bottom boundary, and thus it can be represented by an ordinary differential equation (or a system of ODEs if the size-structure of the mussel population would be modeled). This in turn can be used as boundary condition or boundary forcing to the dynamics in the pelagic represented by a system of partial differential equations (PDEs) derived from conservation laws. The mussels' activity at the bottom boundary of the watercolumn is observed to cause an increase in ammonia concentration and a decrease in phytoplankton. The bulk mussel biomass density in the benthos in the model is represented by the variable $M(t)$.

2.4 Parameter and Variable Definitions

Table 1: Parameter and Variable Definitions

v_1, v_2	Sinking/Buoyancy Rates for Phytoplankton Species
$D(z)$	Depth Dependent Diffusive Coefficient
N_1	Ammonia Density
N_2	Nitrate Density
ω_i	Phytoplankton Biomass Densities
I	Light Intensity
ρ_{max}^i	Phytoplankton's Maximal Growth Rate
$K_{N_j}^i$	Saturation Constant for Nutrient Uptake Limitation Phytoplankton Species
K_m	Saturation Constant for Mussel Uptake of Phytoplankton Species
K_l^i	Saturation Constant for Light Limitation Phytoplankton Species
λ_i	Ammonia Preference Factor
ε_{ij}	Instantaneous Release of Nutrients (i.e. Recycling Fractions)
ℓ_i	Loss Parameters (Viral Lysis, Grazing etc.)
M	Mussel Density
r_{max}	Maximal Growth Rate for Mussel Population
M_{max}	Maximal Carrying Capacity for Mussel Population
a_b	Light Attenuation Constant Through Water
a_i	Light Attenuation Constant for Phytoplankton Species
α	Ammonia Release Constant
β_r^i	Sediment Release of Ammonia and Nitrate From Benthic Layer
r_i	Mussel uptake rates of phytoplankton species

2.5 Model

$$\frac{\partial \omega_1}{\partial t} = -(\nu_1 \omega_1)_z + D_z \omega_{1z} + D \omega_{1zz} + G_1(\omega_1, N_1, N_2, I), \quad (1)$$

$$\frac{\partial \omega_2}{\partial t} = -(\nu_2 \omega_2)_z + D_z \omega_{2z} + D \omega_{2zz} + G_2(\omega_2, N_1, N_2, I), \quad (2)$$

$$\frac{\partial N_1}{\partial t} = D_z N_1 + D N_{1zz} - H_1(\omega_1, \omega_2, N_1, N_2, I), \quad (3)$$

$$\frac{\partial N_2}{\partial t} = D_z N_2 + D N_{2zz} - H_2(\omega_1, \omega_2, N_1, N_2, I), \quad (4)$$

$$\frac{dM}{dt} = r_{max} \left(1 - \frac{M}{M_{max}}\right) \left(\frac{\omega_1 + \omega_2}{k_M + \omega_1 + \omega_2}\right) M - qM, \quad (5)$$

where

$$G_1(\omega_1, N_1, N_2, I) = \left(\rho_{max}^1 \left(\frac{N_1}{K_{N_1}^1 + N_1} + \frac{N_2}{K_{N_2}^1 + N_2} \cdot \frac{1}{\lambda_1 + N_1} \right) \mathcal{L}_1 - \ell_1 \right) \omega_1$$

$$G_2(\omega_2, N_1, N_2, I) = \left(\rho_{max}^2 \left(\frac{N_1}{K_{N_1}^2 + N_1} + \frac{N_2}{K_{N_2}^2 + N_2} \cdot \frac{1}{\lambda_2 + N_1} \right) \mathcal{L}_2 - \ell_2 \right) \omega_2$$

$$H_1(\omega_1, \omega_2, N_1, N_2, I) = \rho_{max}^1 \left(\frac{N_1}{K_{N_1}^1 + N_1} \right) \mathcal{L}_1 \omega_1 + \rho_{max}^2 \left(\frac{N_1}{K_{N_1}^2 + N_1} \right) \mathcal{L}_2 \omega_2 \\ - (\varepsilon_{11} \ell_1 \omega_1 + \varepsilon_{12} \ell_2 \omega_2)$$

$$H_2(\omega_1, \omega_2, N_1, N_2, I) = \rho_{max}^1 \left(\frac{N_2}{K_{N_2}^1 + N_2} \right) \Upsilon_1 \mathcal{L}_1 \omega_1 + \rho_{max}^2 \left(\frac{N_2}{K_{N_2}^2 + N_2} \right) \Upsilon_2 \mathcal{L}_2 \omega_2 \\ - (\varepsilon_{21} \ell_1 \omega_1 + \varepsilon_{22} \ell_2 \omega_2)$$

with

$$\mathcal{L}_1 = \left(\frac{I}{K_I^1 + I} \right), \quad \mathcal{L}_2 = \left(\frac{I}{K_I^2 + I} \right), \quad \Upsilon_1 = \left(\frac{1}{\lambda_1 + N_1} \right), \quad \Upsilon_2 = \left(\frac{1}{\lambda_2 + N_1} \right),$$

and

$$I = I(z, t) = I_0(t) e^{-\int_0^z a_b + a_1 \omega_1(s) + a_2 \omega_2(s) ds}.$$

Initial conditions :

$$\omega_1(z, 0) = \omega_1^0(z), \quad \omega_2(z, 0) = \omega_2^0(z), \quad N_1(z, 0) = N_1^0(z), \quad N_2(z, 0) = N_2^0(z), \quad M(t) = M_0$$

Boundary conditions for $t > 0$ on the top

$$\begin{aligned} \left. \frac{\partial \omega_1}{\partial z} \right|_{z=0} &= 0, & \left. \frac{\partial \omega_2}{\partial z} \right|_{z=0} &= 0, \\ \left. \frac{\partial N_1}{\partial z} \right|_{z=0} &= 0, & \left. \frac{\partial N_2}{\partial z} \right|_{z=0} &= 0, \end{aligned}$$

and on the bottom

$$\begin{aligned} \left. \frac{\partial N_1}{\partial z} \right|_{z=d} &= \left(\alpha \frac{\omega_1 + \omega_2}{k_M + \omega_1 + \omega_2} + \beta q \right) M + \beta^1, & \left. \frac{\partial N_2}{\partial z} \right|_{z=d} &= \beta^2, \\ \left. \frac{\partial \omega_1}{\partial z} \right|_{z=d} &= r_1 \left(\frac{\omega_1}{k_M + \omega_1 + \omega_2} \right) \Big|_{z=d} M, \\ \left. \frac{\partial \omega_2}{\partial z} \right|_{z=d} &= r_2 \left(\frac{\omega_2}{k_M + \omega_1 + \omega_2} \right) \Big|_{z=d} M. \end{aligned}$$

3 Analysis of the Model

In this section we outline the numerical solution of the model. We implement a spatial discretization scheme to approximate the solution of the system of partial differential equations using Matlab's built-in ODE suite.

3.1 Discretization of the Water Column

To simplify the partial differential equations representing phytoplankton biomass and nutrient densities we discretize depth into a uniform mesh of size N on $[0, d]$. Biomass densities, $\omega_i(z, t)$, and nutrient densities, $N_i(z, t)$, are approximated at the mesh points, and this in turn, lets us use a finite volume type method to approximate the partial derivatives in the convective and diffusive terms on the right side

of the partial differential equations. For the convective terms we use a second order upwinding scheme, while for the diffusive terms we utilize a central difference approximation. Our model contains an integral term to represent light intensity, which is influenced by phytoplankton densities in the whole watercolumn above the given depth. The integral is approximated by the trapezoidal rule. This development follows the treatment of a similar problem in [4] and [7]. Along with the equation for the mussel dynamics, such an approach results in a large nonlinear system of $4N + 1$ ordinary differential equations that is integrated by a stiff solver in Matlab's ode suite.

3.2 Simulation Results

Model parameter values, except for the mussel dynamics parameters were obtained from [9]. Through simulations we investigated various parameter values associated with the quagga dynamics in our simplified model to see if we could qualitatively mimic documented dynamics of recent years. Of a particular interest is the way the mussels' excretion of ammonia impacts phytoplankton density.

In Figure 1 below we can see layering of the phytoplankton densities. Specifically, the first phytoplankton species (ω_1) forms a layer between 5-10 meters and species two lies closer to the benthic region around 20 meters. In Figure 2 we see a similar layering effect with identical parametrization for the phytoplankton species. However, we see that species (ω_2) in the bottom layer carries a substantially larger biomass, due the increase in the value of the parameter describing the ammonia excretion by the mussels. We can therefore conclude that the mussel density aids in the layering effect and modifies phytoplankton distribution in the benthic region.

This model has been constructed to explore a possible way to quantify the impact the quagga mussel has had on Lake Michigan. Our simulations qualitatively match the layered phytoplankton population structure observed in the lake. In the future, we plan to impose an age structure on the mussel population to better predict potential ecological changes as the first generation colonizers come to the end of their life cycle. The model is also flexible enough so that it could accommodate more phytoplankton or nutrient species.

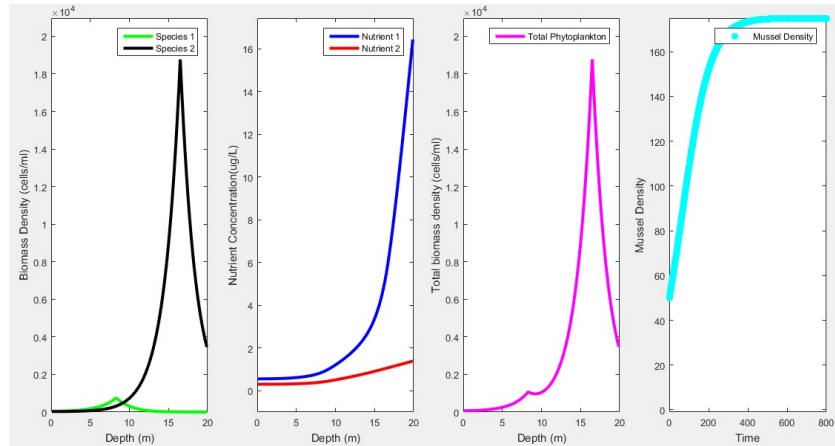


Figure 1: Parameter values for mussel dynamics: max mussel growth rate $r_{max} = .08$ ($time^{-1}$), carrying capacity $M_{max} = 200$ ($mussel/m^2$), half-saturation for growth limits $k_M = .1$ ($cells/ml$), mortality rate $q = .003$ ($time^{-1}$), nutrient excretion factor $\alpha = .1$, nutrient release from death factor $\beta = .5$ and uptake of phytoplankton factors $r_1 = r_2 = .2$.

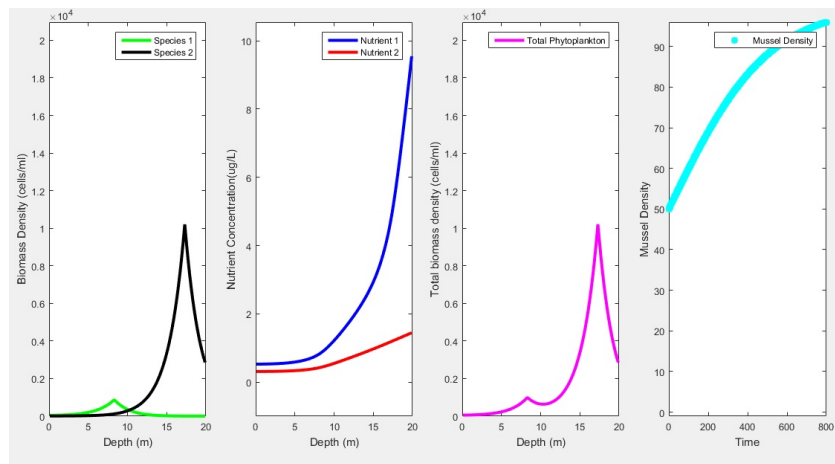


Figure 2: Parameter values for mussel dynamics: max mussel growth rate $r_{max} = .08$ ($time^{-1}$), carrying capacity $M_{max} = 200$ ($mussel/m^2$), half-saturation for growth limits $k_M = .1$ ($cells/ml$), mortality rate $q = .003$ ($time^{-1}$), nutrient excretion factor $\alpha = .35$, nutrient release from death factor $\beta = .5$ and uptake of phytoplankton factors $r_1 = r_2 = .2$.

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