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A Predator-Prey Food-web Model in A Lake

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Abstract

Acid rain decreases the pH level in a lake and the lake acidity has an effect on organisms and can reduce their body size, reproduction capacity, egg viability and mortality rate. In this paper, a predator-prey model consisting of algae (cyanobacteria), an herbivore (*Daphnia magna*), and a predator (yellow perch) is developed and the coefficient functions governing dynamics of growth rate and death rate of organisms with respect to pH value in this model are determined. Parameter values in this model are adopted from experimental data in published references. This paper is based on a summary report on an ecological modeling problem from Graduate Student Math Modeling Camp at Rensselaer Polytechnic Institute in 2009.

Key Words: Predator-Prey, Algae, Daphnia, Perch, pH, Acid Rain

1. Introduction

Over the past 50 years, human beings have changed the ecosystem more rapidly and extensively than in any comparable period of time in human history, largely to meet rapidly growing demands for food, fresh water, timber, fiber, and fuel. Many recognized changes including global warming, biodiversity loss and land degradation have already caused significant harm to human beings. There are major problems associated with our management of the world's ecosystem which has already caused significant harm to some people, particularly the poor, and unless addressed will substantially diminish the long-term benefits we obtain from ecosystems. (Reid et al., 2005). Unfortunately, as technology progresses to improve the lives of the human race, these same advancements play a key role in the destruction and disturbance of many other species. When it precipitates, these detrimental chemicals are sent back down to earth in the form of acid rain. It is increasingly necessary to raise awareness of the negative effects of acid rain on our lakes' inhabitants.

Acid rain increases the hydrogen ion concentration of a lake, thus increasing the acidity of the water. An acidic lake leads to the early death of many species who live within the habitat. Experimental and field studies suggest that pH 6.0 is a critical biological threshold. Anything less is detrimental to the species within the environment and causes the inhabitants to begin to die off. Most species cannot exist once the pH drops below about 4.5. Acid deposition also causes other toxins to emerge, being that associated with the acidification of water is increased leaching of toxic trace elements from the soil and rock in the water (Kwong, 2014). The situation is particularly serious in the Adirondacks. To illustrate, it is not uncommon to find lakes in the Adirondacks with a pH less than 5.5, and there are a fair number with a pH below 5.0. Conditions are improving, however, with one indication of this being a slowly increasing lakewater pH, with a mean increase of 0.01/yr. This is why certain ecologists state that chemical balances might return by about 2060. Once this balance is restored, lake zooplankton are expected to rebound within 10 years and some fish populations returning to normal five or 10 years after that (Rinke and Vijverberg, 2005). It is one of the objectives of this project to examine the plausibility of this claim. Investigating the damaging effects of acid rain on an aquatic ecosystem may bring more awareness to the issue, as its toxic effects may lead to the loss of a species.

Acid deposition affects both young fish and mature fish, although pH tolerance tends to increase with maturity, as exhibited in a study conducted at Evo Inland Fisheries and Aquaculture Research Station in southern Finland (Rask, 1984). The research concludes that with a decreasing pH and during early stages of development, the fish are more sensitive to pH. Being that young fish cannot tolerate acidic environments, exposure to low pH levels during development is not conducive to growth and flourishing populations. The idea that some species may be acid tolerant or intolerant is also corroborated in a study (Weisse, Laufenstein, & Weithoff, 2013) by the researchers who determined that the rotifer, *Cephalodella acidophila*, is an acidophil. It was revealed that the specimen had a low survivability in neutral pH. Throughout the investigation, the rotifer was placed in various environments that depended on parameters such as water temperature and food (alga) availability, both coupled with pH.

Along with studying the pH sensitivity of fish, it is important to take a look at the diet of a fish as it grows and matures. In size-structured communities where individuals grow in size over their life cycle, interactions between species will shift between competitive and predatory interactions depending on size relationships (Persson, De Roos, & Byström, 2007). In this study, the interaction of blue-green algae (Cyanobacteria), water flea (Cladocera, also known as daphnia), and yellow perch (*Perca flavescens*) are observed. However, the yellow perch possesses a varying diet. When young, the fish typically consumes both algae and plankton. However as the fish matures it tends to include aquatic insects, small fish, and leeches in its diet. It is critical to take this into account when crafting the models.

Most food-webs involve hundreds of interacting species, producing a rather complicated mathematical problem. The objective of this project is to develop a fundamental understanding of the role of pH in a food-web, and for this reason a prototype system will be considered. Specifically, it will be a three species system consisting of blue-green algae (cyanobacteria), a herbivore (*Daphnia magna*), and a predator (yellow perch). These species are used because there are some experimental data (Livansky, 1981) on how they interact and how their reproductions are affected by pH.

We usually think of food chains as simple models of what typically happens in nature among a number of species. A food web extends the food chain concept incorporating the complex interaction within the system. In this project, the model we will consider shows that the interplay of two predators and two prey, with no transitivity among the predators. That is, each predator has only one prey in the model. In addition, we examine the effects of acid rain on the food-web model. And although it is a complication, we also briefly consider the influence that our organisms have on lake pH.

The rest of the paper is organized as follows. In Section 2, we formulate a food-web model consisting of algae, daphnia as well as fish, outline all the assumptions and parameters involved, and determine the coefficient functions in this system with experimental data from some references. In Section 3, we present the lake-pH model and explain the terms involved. In Section 4, we present our results.

2. The Model

Prior researchers have used predator-prey models in order to study the changing aspects of a system. The general predator-prey model analyzes the interaction between two species, as opposed to mapping the interaction of three. In one such study, researchers observed the resistance of amoebae grazing activity on blue-green algae (cyanobacteria). (Simkovsky et al, 2012). The team investigated the mechanisms on a molecular level by screening genetic variances of Cyanobacteria and their defenses against amoebae grazers. A predator-prey system (Garbutt, Little, & Hoyle, 2015) investigated the maternal food availability and its effects on offspring feeding rate in daphnia. They used two models, one without the maternal effects incorporated and one with the incorporation of maternal effects. The Hollings type II model (Scheffer et al, 1997) was utilized in their model as the functional response for the system, considering growth rates, consumption rates, carrying capacity, efficiency, and handling.

The three organisms in our study are a part of a very critical interrelationship. The model investigates the balance of an aquatic environment influenced by acid rain. Food chains are usually thought of as simple, though our model incorporates the interaction of two predators and two prey, along with no transitivity existing amongst them. In other words: each predator only has one prey. The organisms in this complex food web model are Cyanobacteria (blue-green algae), *Ceriodaphnia dubia (Daphnia magna*, water flea), and *Perca flavescens* (yellow perch). Ecologically significant, the water flea serves as feed for larger aquatic organisms as they consume algae. The daphnia is critical to freshwater ecosystem, as it aids in the overall health of the habitat (*New World Encyclopedia*, 2013). The omnivore feeds on the algae, which would otherwise suffocate the environment if the growth becomes out of control. The yellow perch, as aforementioned, is carnivorous, dieting on smaller fish and fish eggs. For the purpose of this study, the yellow perch will feed solely on the daphnia, which will feed only on algae.

Each organism in our model participates in a delicate interrelationship between its environment and the fellow members in the food web. The balance in this relationship, required for the organism to thrive, can be upset by any number of variations in the environment. In our model, this interrelationship---along with the parameters that influence it---is described in terms of a coupled dynamical system, which models the effect of lake pH on the system's population dynamics.

The physical data of the blue green algae (Table 1) is adopted from the paper (Rai and Rajashekhar, 2014) and algae is served as the prey for the *Daphnia magna* in the model. The background information for Daphnia (Table 2) and yellow perch (Table 3) are obtained from several research papers and resources (Daphnia: Clare, 2002; Ebert, 2005; *New World Encyclopedia*, 2013. Yellow Perch: Rai and Rajashekhar, 2014; Maryland Fish Facts; State of New Jersey Official Website).

Table 1: Blue-green Algae (cyanobacteria), producer

Scientific Name	Cyanobacteria
Optimal Water Temperature	20-30 C
Optimal pH	7.5

Table 2: Daphnia magna, primary consumer

Scientific Name	Ceriodaphnia dubia
Family	Daphniidae
Lifespan	50 days
Average Length	0.5 mm -6 mm
Optimal Water Temperature	18 -22 C
Optimal pH	6.5-9.5

Table 3: Yellow Perch, secondary consumer

Scientific Name	Perca flavescens
Family	Percidae
Lifespan	13 years
Average Length	12 inches
Optimal Water Temperature	19-24 C
Optimal pH	4.5-5.0

2.1 Differential Equation Formulation

In the construction of our model system, the following concepts and assumptions were applied:

- 1. Aquatic organisms possess a sensitivity to pH changes.
- 2. Wet acid deposition, i.e. acid rain, causes an increase in the hydrogen ion (H⁺) concentration in lakes; thus causing a decrease in pH.
- 3. Cyanobacteria reproduce rapidly, with the population doubling in about half a day.
- 4. Cyanobacteria contain hydrogenases that can either metabolize or produce hydrogen ions. These enzymes are termed uptake hydrogenase and bidirectional hydrogenase respectively.
- 5. Maturity is observed in the daphnia at seven days, and the average life span is 50 days. For this matter, only adult daphnia are considered in our model.
- 6. In optimal conditions, the yellow perch matures between 2 to 4 years with an average lifespan of 13 years. It is observed that young yellow perch are more sensitive to changes in pH. The optimal pH for reproduction is 5.5.
- 7. Yellow perch prey on the daphnia, as the daphnia preys on the algae.
- 8. In order to address the ability of the subsystems to sustain population growth when acknowledged independently, we place an "interaction carrying capacity." This is posited between both the perch-daphnia and daphnia-algae subsystems.

9. The interaction of the algae and daphnia serves to reduce the algae population, while the interaction of the daphnia and perch serves to reduce the daphnia population.

Our basic model involves an equation for each organism in the system (three total). By integrating the assumptions outlined above, we attained the following dynamical system, a modification of a predator-prey model:

$$\begin{aligned} \frac{dA}{dt} &= \beta_A A (A^* - A) - \alpha_2 D A - \mu_A A, \\ \frac{dD}{dt} &= \beta_D D (A D^* - D) - \alpha_1 F D - \mu_D D, \\ \frac{dF}{dt} &= \beta_F F (D F^* - F) - \mu_F F, \end{aligned}$$

where the variables and parameters are defined as follows:

- A, D, and F represent the population density of the cyanobacteria, *Daphnia magna*, and yellow perch, respectively;
- *t* is the time, measured in days;
- β_{A}, β_{D} , and β_{F} represent the birth rates of cyanobacteria, daphnia, and yellow perch, respectively;
- μ_A, μ_F , and μ_D represent the death rates of cyanobacteria, and yellow perch and daphnia;
- A* is the carrying capacity of the cyanobacteria;
- D* and F* are the capacity/interaction terms for the daphnia and yellow perch;
- α_1 and α_2 serve as "nutrition parameters."

When in more acidic environments, the birth rate (β_A) of cyanobacteria is negatively impacted. However, similar to the yellow perch, the death rate of the algae (μ_A) is not particularly sensitive to alterations in their aquatic environments. Due to this, we consider the parameter μ_A to be constant. We assumed these rates to follow a normal distribution, and our parameters were estimated using data fitting. Using data from (Livansky, 1981) and the method described above, the birth-rate parameter for algae was defined. The exponential form of the pH-dependent birth and death rate parameters thus obtained are given by

$$\beta_A = 4.479^{\left(-\frac{pH-7.033}{3.39}\right)^2}$$

In our model parameters α_1 and α_2 serve as "nutrition parameters." These parameters are indicative of the influence a predator has on its prey. The population density of a species will be negatively influenced by the presence of its predator. The nutrition parameters describe how adverse this effect will be. In our model, we assume that appetite is not affected by alterations in pH; the parameters α_1 and α_2 are not dependent on pH.



Figure 1: The growth rate of algae decreases as pH decreases when pH is less than 7. The growth rate almost goes to zero when pH is less than 3.5. y-the rate of biomass production and the corresponding unit is gL⁻¹d⁻¹

The products involving the starred terms in the daphnia and perch equations are "interaction carrying capacities" influenced by population models described by the logistic equation. Our reasoning is that the reproduction rate of each organism depends on the interaction within this predator-prey subsystem. The parameters involving μ in each equation describes the death rate for each organism. Daphnia, our primary consumer in the model, unlike the yellow perch, are extremely sensitive to alterations in pH (Xu and Cui, 2008). Thus the μ_D term has a dependence on pH, whereas, as mentioned above, μ_F does not. Both birth rate (female fecundity and egg viability rate) and death rate of daphnia are significantly affected when pH value gets below 6.5. Details of daphnia's death rate with regard to pH value are given in the study (Lampert and Sommer, 1997), while the intrinsic birth rate under the influence of water pH is given in the research (Xu and Cui, 2008). We assumed these rates to follow a normal distribution, and our parameters were estimated using data fitting. The exponential form of the pH-dependent birth and death rate parameters thus obtained are given by

$$\mu_D = 1.037 \left(-\frac{pH - 3.866}{0.4347} \right)^2$$

and

$$\beta_D = 0.3796^{\left(-\frac{pH-7.127}{2.596}\right)^2}$$



Figure 2: The birth rate of daphnia changes with pH.

Figure 3: The death rate of daphnia changes with pH.

The final equation considers the yellow perch population dynamics, and the parameter β_F is interpreted as the growth rate of the population, after taking the interaction of both predator and prey into consideration. By multiplying the current yellow perch population and the death rate (parameter μ_F), we obtained the negative term in the equation. Based on the assumption that the adult yellow perch are only slightly affected by decreasing changes in pH, we regard μ_F as a constant in our model (Rask, 1984). However, lower pH does affect the spawning, thereby affecting the birth rate of the yellow perch. The parameter β_F can be seriously affected by alteration of pH value, and fry survivability drops off considerably with low pH. We implemented exponential interpolation on experimental data of fry survivorship with respect to pH value, obtaining

$$\beta_F = 1.066^{\left(-\frac{pH-7.045}{1.744}\right)^2}$$



Figure 4: The birth rate of Yellow Perch decreases with the pH less than 7

2.2 The Equilibrium Points:

In order to analyze the stability of our model, equilibrium points of the system are calculated and the steady state analysis was completed. After setting the rate of changes, or derivatives, in the given system equal to zero, we found eight equilibrium points. In the consideration of population density dynamics of this model, we eliminated those with negative components. Furthermore, steady states in which equated to the non-existence of an organism was also eliminated. For our model, the following equilibrium points are those that we considered of theoretical interest:

$$A = \frac{-\alpha_2 \alpha_1 \mu_P + \alpha_2 \mu_D \beta_F - \mu_A \beta_D \alpha_1 - \mu_A \beta_D \beta_F + A^* \beta_D \beta_A \alpha_1 + A^* \beta_D \beta_A \beta_F}{\beta_D (\alpha_1 \beta_A + \beta_A \beta_F + D^* \alpha_2 \beta_F)}$$
$$D = \frac{\alpha_1 \beta_A \mu_F - \beta_D D^* \mu_A \beta_F + \beta_D D^* A^* \beta_A \beta_F - \mu_D \beta_A \beta_F}{\beta_D (\alpha_1 \beta_A + \beta_A \beta_F + D^* \alpha_2 \beta_F)}$$
$$F = \frac{-\beta_D D^* \mu_A + \beta_D D^* A^* \beta_A - \mu_D \beta_A - \mu_F \beta_A - \mu_F D^* \alpha_2}{\alpha_1 \beta_A + \beta_A \beta_F + D^* \alpha_2 \beta_F}$$

Given a set of parameter values, we examine the system for any periodic solutions.

3. The Lake Equations

It is critical to our system to efficiently model the rate at which the hydrogen ion concentration changes in a lake. Hydrogen ion concentration is predominantly measured by the pH scale, in which pH is defined by:

$$pH = -\log_{10}\left[\frac{moles\ H^+}{V}\right],$$

where V represents volume in liters. Though the quantity $\left[\frac{moles H^+}{V}\right]$ is dimensionless, we disregard this point in the interest of our model. In moles, the amount of hydrogen ions per liter is given by:

$$p = 10^{-pH}$$

when adjusted for the volume dimensions we will be using (cubic meters) we achieve:

$$p = 10^{3-pH}$$

Hydrogen ions will flow into and out of the lake (termed inflow and outflow respectively) based upon the following occurrences:

- Rain
- Evaporation
- Runoff as a result of rain
- Inflow from streams leading into the lake
- Outflow into streams leading from the lake

Cyanobacteria present within the system also aids in moderating the hydrogen ion concentration of the lake.

Our model considers the conservation of the overall volume of the lake, for convenience of computations. Thus, any water flowing into the system will be equivalent to that flowing out, in order to analyze the system at a constant volume. The water that runs out is presumed to be at a pH that reflects the current state of the lake. The following is the general form of the H⁺ rate:

$$\dot{p} = \frac{S}{V} \left[\left((p_R + 0.62p_N)R(t) + p_C C(t) \right) - (1.62R(t) + C(t)) \right] - \delta_1 p V A + \delta_2 A$$

S = surface area; V = volume; $p_R = H^+$ concentration in rain; $p_N = H^+$ concentration in runoff; $p_C = H^+$ concentration in incoming stream channels; R(t) = rain (m/day); C(t) = stream-inflow rates (m/day); A = population of algae; δ_1 and δ_2 are both proportionality measures.

Overtime, the pH levels of both rain and runoff will generally vary. In the interest of this model, we assumed these values to be constant.

We considered a lake occupying (and completely filling) a hemispherical basin with a radius of 1.5 kilometers in order to test the qualitative behavior of the hydrogen ion rate model. To prove this concept, we find that the ratio of the lake's surface area to its volume is

$$\frac{S}{V} = \frac{3}{2r} = 10^{-3}$$

It is noted that $\frac{s}{r}$ describes the interface between a particular volume and the environment. The greater the ratio's value, the greater the influence of "surface effects" on the system. Listed below are the constants chosen to be incorporated into the model:

- $p_R = 10^{-1.2} \text{ (pH= 4.2)}$ $p_N = \frac{p_R}{5} \text{ (pH= 4.9)}$ $p_C = 10^{-4} \text{(pH= 7)}$ $R(t) = 3 \times 10^{-3} m/d$

- $C(t) = 3 \times 10^{-2} m/d$

Solving the model (when A= 0) with an initial condition of $p(0) = 10^{-4}$ (which corresponds to a pH of 7, or neutral, when t=0) yields

$$p(t) \approx e^{-0.00003t} (0.006e^{0.00003t} - 0.006),$$

Whose plot over a period of 60 years is given in Figure 5.

behavior of this system is shown in Figure 6.



Figure 5. A plot showing the influence of acid rain on a hemispherical lake of initially neutral pH over a period of 60 years.

This model qualitatively matches our expectations, considering that water at a greater pH is being replaced by water at a pH lower than that of the lake's original state. As t approaches infinity, the limit of $\rho(t)$ is 0.006, which corresponds a pH of approximately 5.2, suggesting that this is the lowest pH the lake will assume given the above parameters.

There is an immediate physical interpretation for this value. We know that the main source of hydrogen ions is the water entering the lake from outside via rain, runoff, and stream channels. The pH of 5.2 therefore must correspond to the pH of the *mixture* of this incoming volume of water. The time at which the lake's concentration of hydrogen ions becomes essentially constant therefore corresponds to a point at which almost all of the water in the lake at t = 0 has been replaced by the inflowing water.

We can support the above statement by noting that the inflow of rain at pH 4.2 is an order of magnitude less than the inflow from the streams at pH 7. That is, the ratio for rain-runoff-stream is approximately 100:62:1000. A sample of this mixture with volume 1,162 liters will have $10^{-2.2} + 62 \times 10^{-4.9} + 10^{-4}$ moles of hydrogen ions. That equates to a hydrogen ion concentration of about $10^{-5.2}$ mol/L, or a pH of 5.2 as anticipated.

With some confidence in our model, we may now consider alternate geometries. Consider, for instance, a hypothetical lake shaped like an above-ground swimming pool, which we can consider as a cylinder. In this case, the $\frac{s}{v}$ term is simply the reciprocal of the lake depth. We will again assume that our lake has the same radius mentioned above, 1.5 km, but this time we will assume its depth to be 20 meters, giving $\frac{s}{v} = 0.5$. Since this term has now changed by an order of magnitude, we can expect an acceleration of the process shown in Figure 1. The limiting value, however, should be determined entirely by the pH of the incoming mixture of water, as it was above. A plot of the



Figure 6: A plot showing the influence of acid rain on a cylindrical lake of initially neutral pH over a period of 60 years. The change in pH essentially stops after about 16.5 years.

With suitable values for δ_1 and δ_2 , the parameters that define the influence of algae on the lake pH, we are now prepared to perform numerical simulations of the pH dynamics of a lake of arbitrary geometry. We can also incorporate variable rainfall rates and pH values of the incoming water to describe the effect of changing environmental conditions on lake pH. This must correspond to the pH of the mixture of the inflow of water, being that the main source of H⁺ is the water flowing into the lake from sources (i.e. rain, runoff, stream channels). The point at which the hydrogen ion concentration becomes constant is the point at which all of the initial water initial (t = 0) has been replaced by the inflowing water.

4. Main Results

Due to the many orders of magnitude difference in the population size, birth rates, and death rates of the different organisms, we non-dimensionalized the system in order to more effectively analyze the model. We chose to scale each of the populations by a maximum carrying capacity, and we used the algae growth rate to determine the time scale:

$$\bar{t} = t\beta_A A^*, \qquad \bar{A} = \frac{A}{A_{max}}, \qquad \bar{D} = \frac{D}{D_{max}}, \qquad \bar{F} = \frac{F}{F_{max}}$$
(4.1)

We chose an algae-related time scale in order to observe the effects of all the organisms in the system and not only the ones that live longer. Our new dimensionless model becomes:

$$\begin{split} \frac{d\bar{A}}{dt} &= \bar{\beta}_A \bar{A} \left(1 - \bar{A} \right) - \bar{\alpha}_2 \overline{D} \bar{A} - \mu_A \bar{A}, \\ \frac{d\bar{D}}{dt} &= \bar{\beta}_D \overline{D} \left(\bar{A} \overline{D}^* - \overline{D} \right) - \alpha_1 \overline{F} \overline{D} - \bar{\mu}_D D, \\ \frac{d\bar{F}}{dt} &= \bar{\beta}_F \overline{F} \left(\overline{D} \overline{F}^* - \overline{F} \right) - \bar{\mu}_F \overline{F}, \end{split}$$

with the dimensionless parameters defined as:

$$\bar{\alpha}_{1} = \frac{F_{max}\alpha_{1}}{\beta_{A}A^{*}}, \ \bar{\alpha}_{2} = \frac{D_{max}\alpha_{2}}{\beta_{A}A^{*}}, \ \bar{\mu}_{A} = \frac{\mu_{A}}{\beta_{A}A^{*}}$$
$$\bar{D}^{*} = \frac{A^{*}D^{*}}{D_{max}}, \ \bar{\beta}_{D} = \frac{\beta_{D}D_{max}}{\beta_{A}A^{*}}, \ \bar{\mu}_{D} = \frac{\mu_{D}}{\beta_{A}A^{*}}$$
$$\bar{F}^{*} = \frac{D_{max}F^{*}}{F_{max}}, \ \bar{\beta}_{F} = \frac{\beta_{F}F_{max}}{\beta_{A}A^{*}}, \ \bar{\mu}_{F} = \frac{\mu_{F}}{\beta_{A}A^{*}}$$

Note that we have also eliminated two parameters, since \bar{A}^* and \bar{A} both scale to be 1. Here we have chosen non-dimensionalized constants:





Figure 7: The food web model test.

A mutual interaction exists between algae density and hydrogen ion concentration, which is influenced by cation absorption, carbon fixing, and recycling. Many papers remark on pH's impact on algae growth, but we selected (Livansky, 1981) as the source of our data, which were used to extrapolate the overall growth rate of algae with respect to pH value. With the model in the first section and the relationship between pH and hydrogen ion concentration defined in the second section, we numerically approximated the solution to this ODE model using *ode45* in MATLAB. The results of these simulations and their corresponding pH values are shown in the figures below. Incorporating the complicated interaction between changing lake pH, modeled in Section 3, and the food-web model described earlier can be the object of future work, combined with controlled experiments in order to future examine the model system.



Figure 9: The food web model test at pH=4.



Figure 8: The food web model test at pH=5.



Figure 10: The food web model test at pH=6.5.

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