MODEL OF NUTRIENT CYCLING IN MACROPHYTE LAKES

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Abstract

The aim of this research is to determine the trophic state of Lake Matoaka, assess the viability of introducing triploid grass carp into the lake, and predict the effect the fish would have on the its ecosystem. A mathematical model is proposed for a qualitative representation of the dynamics of a macrophyte dominated freshwater system. The focus of the model is the relationship between phytoplankton and macrophyte populations in order to assess the effect the introduction of grass carp would have on the nutrient cycling of a eutrophic water body. This model is then used to analyze the stocking rates for grass carp recommended by the Virginia Department of Game and Inland Fisheries (VDGIF).

Introduction

As a result of long-term nutrient enrichment from sewage spills and other campus sources, Lake Matoaka has been listed as a hypereutrophic system (Pensa and Chambers, 2003). Consequences of nutrient loading include low oxygen levels and high primary production, the most obvious manifestation of which is the presence of harmful algal blooms that can reduce the lake's biodiversity and recreational value. Given the extent that the College values Lake Matoaka as an important resource for recreation and research, it in the best interest of the college community to take steps to improve the water quality of the lake. Fortunately, there is a large body of research pertaining to the eutrophication process in freshwater lakes, as well as the use of grass carp as a biomanipulation agent in freshwater systems. This report has 3 components: (1) an assessment and analysis of the trophic state of Lake Matoaka using the Vollenweider-OECD Eutrophication Model; (2) a review of literature on the carp's possible ecological impact and (3) a mathematical model predicting how many grass carp should be introduced into Lake Matoaka and its comparison with Virginia VDGIF recommended stocking rates.

Procedure for Determining the Trophic State of Lake Matoaka

Eutrophication is the process through which elevated levels of nutrients, often nitrogen or phosphorus, stimulate the primary production of a water body; thereby causing algal mats, depletion of dissolved oxygen, fish kills and loss of biodiversity (Carpenter *et al.*, 1998). In lake ecosystems, phosphorus is considered the most likely nutrient controlling primary production (Vollenweider, 1976; Schindler, 1977; Correll, 1999) and is availible in soluble inorganic concentrations within the ecosystem, which in turn depend on external loading, release from the sediments and decaying plant matter within the system (Sigee, 2005).

In oligotrophic lakes, most phosphorus remains stored in sediments, and waters are oxygenated throughout the year. However, in nutrient enriched systems, high primary

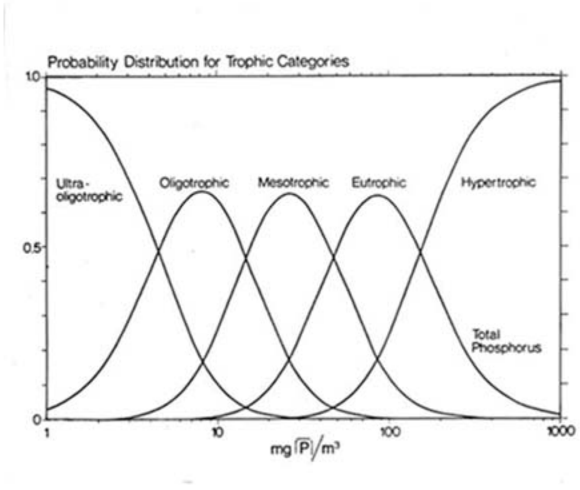

Figure 1: OECD Probability distribution curve for the average lake phosphorus

productivity leads to increased bacterial populations and respiration rates, which can cause bottom waters to become hypoxic or anoxic during the summer growing season. Low levels of dissolved oxygen contribute to the loss of aquatic animals and the release of phosphorus normally bound to bottom sediments (Correll, 1999). This nutrient release causes a positive feedback loop that increases the rate of eutrophication within a system (Carpenter and Cottingham, 1997). While more extensive research on Matoaka's recent transition to a hypereutrophic state has been performed by Pensa and Chambers (2003), a brief analysis of Matoaka's trophic status is useful to determine the sensitivity of the system's equilibrium.

Perhaps the most popular model for eutrophication control programs was developed by Vollenwieder and Kerekes in 1982, and successfully employed by the Organization for Economic Cooperation and Development (OECD) in a variety of different lakes and reservoirs worldwide (Rast *et al.*, 1983). The model relates the effect of retention time and inflow concentration to determine the total annual phosphorus concentration in a lake. Assuming that algal production is driven to a large extent by phosphorus availability, Vollenwieder plotted the chlorophyll a concentration for over two hundred different water bodies as a function of their respective normalized phosphorus loads (Rast *et al.*, 2009). From this data, Vollenweider and Kerekes developed the OECD Probability Distribution (Figure 1), which can be used to determine the trophic state of Lake Matoaka. The OECD data collected in the United States suggests that, since the phosphorus residence time generally decreases inversely with degree of eutrophy, lakes with high primary productivity respond more rapidly to phosphorus control measures (Rast *et al.*, 1983). Hence, estimating Matoaka's degree of eutrophy would be beneficial for predicting its response to phosphorus reduction.

It should be noted that since it focuses on largely on the planktonic response to nutrient loading, the OECD eutrophication modeling approach is less reliable in macrophyte dominated lakes such as Matoaka (Rast *et al.*, 2009). Furthermore, it only calculates phosphorus pollution from point sources. However, I believe that it is sufficient to use this model as a general inquiry into Lake Matoaka's trophic state because of its wide applicability.

Application of the Vollenweider-OCED Eutrophication Model

Vollenweider (1969) described the mass balance of phosphorus in a lake as:

$$\frac{dV}{dt} = W - QP - \sigma VP \tag{1}$$

where V is the lake volume (m^3), W is the annual phosphorus input (mg), Q is the annual volume of water discharged (m^3), P is the lake phosphorus concentration ($\frac{mg*P}{m^3}$) and σ is the net sedimentary loss coefficient (day^-1). This equation describes the mass of phosphorus stored in the lake as the difference between the input and amount lost from flushing and sedimentation. Finding the equilibrium solution of this equation yields:

$$P = \frac{W}{QP - \sigma V} \tag{2}$$

Depending on how limnologic variables such as surface area, lake volume, mean depth and residence time are taken into account, equation (2) can be configured in a number of different ways. One of the most widely applied formulations to determine the expected total annual phosphorus concentration, P_λ, was developed by Vollenwielder (1977):

$$P_\lambda = \frac{L_p \tau_\omega}{z(1 + \sqrt{\tau_\omega})} \tag{3}$$

where τ_ω is the hydraulic residence time (days), z is the mean depth (m), and L_p is the mass of phosphorus entering the system, normalized to the surface area of the water body ($\frac{mg}{day*m^2}$):

$$L_p = \frac{\text{total phorporus input from inlets}(\frac{mg}{day})}{\text{surface area } (m^2)} \tag{4}$$

According to calculations using the parameters in Table 1, the total annual phosphorus concentration of Lake Matoaka is $239.27\frac{mgP}{m^3}$, indicating that it most likely to be eutrophic. The reason this value yields a lower trophic catergory than other estimates is probably the high hydraulic retention time for the lake, suggesting in terms of the equation that a large amount of phosphorus is lost to the sedements. Since other indexes have placed Lake Matoaka at hypereutropic, this application of the Vollenwieder-OECD model and its unexpected result suggest that the macrophyte dominance in lake may make it exceptional to this model. Regardless, this model's catergorization of Matoaka as having a greater than 50% probability of being eutrophic and $\geq 40\%$ probability of being hypereutrophic implies a degree of enrichment that suggests efforts to reduce loading in the Matoaka watershed should be considered.

Review of Grass Carp Research

Ctenopharyngodon idella, known as the the grass carp or white amur, is an herbivorous, freshwater fish native to the large rivers of eastern China and Siberia. The species was introduced into the United States for aquatic vegetation control in 1963 and has since been stocked in most states. Furthermore, Eades and Stinkoenig (1994) found that VDGIF issued approximately 549 permits requesting 9,000 carp each year since the development of sterile, triploid grass carp in 1984.

The triploid carp is considered an ideal method to manage a wide variety of submersed and floating vegetation because of the longevity of the method, low cost, and contol over its replication. It is also considerably less invasive than alternative methods such as the use chemical herbicides or dredging. Furthermore, there is an abundance of available data evaluating the grass carp's effectiveness as a tool to reduce aquatic vegetation. Most reports published in the 1970s address how the physiology of the grass carp affects its viability as a biological agent for weed control (Sills, 1970; Stott and Robson, 1970; Shireman and Maceina, 1981; Shireman, 1984; Leslie *et al.*, 1987). It seems that these studies were prompted by the apparent success of grass carp as an effective management tool for reducing and eradicating macrophyte communities. However, by the late 1980s, literature on grass carp shifted from research of the direct impact of the fish on aquatic plants to investigations its indirect impacts on water quality and other environmental parameters (Shireman and Hoyer, 1986; Maceina *et al.*, 1992; Leslie, 1990; Bonar *et al.*, 2002; Dribble and Kovalenko, 2009). Since the possible effects of grass carp introduction ecosystem are complex, it is important to first develop an understanding of the carp's direct and indirect ecological impacts before assessing the feasibility of its introduction into Lake Matoaka.

EFFECT OF GRASS CARP ON MACROPHYTE COMMUNITIES

Parameter	**Value**
Surface area	160,000 m^2
L_p	4230.69 $\frac{mg}{year*m^2}$
z	2.5 m
τ_ω	0.21 $years$

Inlet	**Average P concn.** ($\frac{mg}{L}$)	**Flow rate** ($\frac{mL}{day}$)	**P inflow** $\frac{mg}{day}$
College Creek	0.43	2592	1123,970.36
Crim Dell stream	0.56	1,036.8	578,041.9
Strawberry stream	0.09	691.2	64,226.88
Pogonia stream	0.09	518.4	48,170.16
Berkeley stream	0.09	432	40,141.8
Total			**1854,551.09**

Table 1: Paramter values for the Vollenweider equation were constructed based on streamflow estimates of the precipitation and evaporation measurements collected by the Keck Lab weather station for the Lake Matoaka water budget. The surface area was collected from GIS and hypsography measurements were calculated based on bathymetry data collected by Pensa and Wilkin (2002). The phosphorus concentrations for the inlets were averaged from data collected over the past six years.

Aquatic Plant Infestation	Slight (< 30)	Moderate ($30 - 60$)	Heavy (> 60)
Stocking Rate (fish/acre)	2	5	10
Number of fish recommended for Matoaka (40 acres)	80	200	400

Table 2: VDGIF Recommended Stocking Rate as found attached to the Exotic Species Application/Permit to import certified triploid grass carp for aquatic vegetation control in private ponds.

There is consensus that grass carp eliminate plant species in order of decreasing palatability and have an order of preference (Fischer, 1968; Cross, 1969; Michewicz, *et al.*, 1972; Edwards, 1974; Fowler and Robson, 1978; Leslie, *et al.*, 1987; Pine and Anderson, 1991; Pipalova, 2006; Dribble and Kovalenko, 2009) which varies with the age of the fish (Osborne and Sassic, 1981; Pine *et al.*, 1990) and climate (Leslie *et al.*, 1993). Generally the best predictors of palatability were calcium and lignin, while cellulose, silica, and iron content were indicators of unpalatability (Bonar et al. 1990). Furthermore, VDGIF recommends grass carp introduction to control plants of genus *Elodea, Chara, Potamogeton, Nitella* and *Hydrilla* (VDGIF, 2008). There is also evidence that grass carp feed significantly on phytoplankton, although this preference is considerably less than for macrophytes (Pipalova, 2002).

Scientific Name	**Common Name**	**Order of Preference**
Potamogeton cripsus	Curled Pondweed	1
Najas flexilis	Bushy Pondweed	2
Elodea canadensis	Waterweed	3
Utricularia sp.	Bladderwort	4
Wolffia papulifera	Watermeal	5
Lemna minor and *Spirodela polyrhiza*	Duckweed	6
Azolla sp.	Water fern	6
Ceratophyllum demersum	Coontail	7

Table 3: Grass Carp Order of Preference for Aquatic Plants: The following reflects grass carp preference for the plants found in a general survey of macrophytic vegetation in Lake Matoaka (Capelli, 1993). Data for preference rankings was reported by Masser (2002).

Despite extensive research categorizing grass carp feeding preferences (Table 3), the results of field studies seem to vary depending on environmental conditions (Dribble and Kovalenko, 2009). A common concern is that the grass carp's preferential feeding patterns will have a negative effect on plant diversity or increase the aboundance of less palatable non-native species. Lake Matoaka presents an interesting situation because of its infestation by the carp's most preferred species, the invasive *Potamogeton crispus.* According to a study on plant and algal distribution in Lake Matoaka by Pensa and Wilkin (2002), *P. crispus* was found to be the dominant aquatic plant after proliferating rapidly over a ten year period. The plant stores nutrients absorbed from the soil and water column, and at the end of its life cycle in the middle of June, decaying strands of *P. crispus* release a pulse of these nutrients into the water column, stimulating the growth of algal blooms (Capelli, 1993). Observers of Lake Matoaka, especially in the spring, will probably note that some kind of reduction of *P. crispus* would be highly desirable for both the recreational and aesthetic value of the lake. However, since *P. crispus* is only abundant during the spring and early summer, consideration should be given to whether other plants exist in sufficient concentrations to avoid eradication by grass carp consumption. From the observations of Professor Gregory Capelli, I have gathered that since there isn't any unusual, rare, or endangered vegetation in Lake Matoaka, there isn't great concern over whether a plant species may be eliminated by the introduction of the grass carp.

There is also evidence that the overabundance of macrophytes in Lake Matoaka has had a negative affect on fish populations. Excess vegetation reduces nesting sites for fish and provides too many hiding areas for small fish, allowing them to overpopulate (Eades and

Stinkoenig, 1994; VDGIF, 2008). A survey done on Matoaka fish populations found that no bluegill larger than 5 oz were collected, demonstrating what appears to be a stunted population of numerically abundant but undersized individuals. It was further speculated that the dense vegetation allows small blue gill to avoid bass predation, resulting in both excess bluegill and underfed bass (Cappelli, 1993). Hence, if accompanied by a long-term fish monitoring program, the reduction of macrophytes by the grass carp may prove to have a very positive impact on fish populations.

Effect of Grass Carp on Water Quality

Before considering the indirect effects the grass carp may have on the water quality of Lake Matoaka's ecosystem, it is important to understand how the system itself functions. As previously mentioned in this paper, excessive macrophyte abundance contributes to reduced oxygen in bottom waters, the release of nutrients into the water column and harmful algal blooms. While these qualities seem to imply that the reduction of macrophytes would reduce the high nutrient and low oxygen levels that characterize eutrophic waterbodies, macrophytes also play an important role in limiting these qualities. For example, while an abundance of vegetation may reduce oxygen in bottom waters, macrophyte photosynthesis helps maintain suitable dissolved oxygen levels elsewhere in the water column. Lake restoration research has shown two stable states of lakes at the same intermediate level of total phosphorus concentration: one with turbid water dominated by phytoplankton and another with clear water dominated by macrophytes (Hosper, 1989; Scheffer *et al.*, 1993; Blindow *et al.*, 1997; Moss *et al.*, 1996; Jeppesen, 1997; van Donk and van de Bund, 2002; Zhang *et al.,* 2004). Several mechanisms could be at work in Lake Matoaka to reinforce a stable state of macrophyte dominance and limited phytoplankton growth.

Firstly, it is well known that macrophytes compete with phytoplankton for nutrients such as nitrogen, phosphorus or carbon compounds in the water column (van Donk and van de Bund, 2002). Macrophyte species are able to absorb nutrients from the sediments, providing them with a competitive advantage over phytoplankton although their decomposition releases these otherwise unavailable nutrients. Furthermore, although oxic-anoxic gradients in macrophyte beds can cause the release of phosphorus from the sediments, they can also reduce mixing of the water column and the availability of that phosphorus to planktonic growth (Jeppesen *et al.*, 1997; Barko and James 1997). Experimental sediment resuspension has shown an increase nutrient availability and algal biomass (Dzialowski *et al.*, 2008), indicating that macrophytes play a crucial role in limiting resuspension and hence algal blooms.

Perhaps the most interesting aspect of competition between macrophytes and phytoplakton is the potential for aquatic macrophytes release allelopathic substances to suppress phytoplankton growth (Hutchinson, 1975). Of particular interest to the Lake Matoaka system is the secretion of a sulfur compound from *Ceratophyllum demersum* that may have allelopathic properties regarding algal blooms (Wium-Anderson *et al.*, 1983). Experiments have found that *C. demersum* hampers phytoplankton development (van Donk and Gulati, 1995) over a wide range of phosphorus concentrations (Mjelde and Faafeng, 1997). Considering that *C. demersum* appears to be the dominate macrophyte species in peak growing season, more research is warranted on its possible allelopathic interaction with phytoplankton. Fortunately, *C. demersum* is the least favored food of the carp and should not experience excessive predation that would reduce its allelopathic impact.

Other mechanisms may be at work in maintaining a macrophyte dominated state and reducing the eutrophy of freshwater systems. Macrophyte induced oxic-anoxic gradients may also increase denitrification and hence promote the removal of biologically available nitrogen from the lake system (Weisner *et al.*, 1994; Erikkson and Weisner, 1997, 1999). Submerged aquatic plants in eutrophic lakes are generally light limited and large amounts of vegetation growth clear the water, creating a positive feedback mechanism that allows more vegetation to grow. This vegetation-turbidity feedback is one of the major mechanisms for macrophyte dominance in lakes (Scheffer, 1998). Gradual enrichment starting from low nutrient levels will cause the system to proceed along a lower equilibrium curve until critical turbidity is reached at which macrophytes disappear. In order to restore the macrophyte dominated state, nutrient level must be reduced to a value where algal biomass is sufficiently low to reach the critical turbidity for macrophytes again, even when nutrient levels subside. The relationship between vegetation and turbidity demonstrates how macrophytic dominance can effectively limit algal growth at varying nutrient levels below a critical turbidity (Scheffer, 1998).

The complex dichotomy of macrophytes and phytoplankton serve to buffer lake ecosystems against fluctuation nutrient inputs and highlight the importance of the balance between these populations. Previous research indicates that shallow lakes can possess up to three alternative stable states at the same level of nutrient saturation, dominated by either macrophytes, phytoplankton or cyanobacteria (Wallsten and Forsgren, 1989; Blindow *et al.*, 1997). The profusion of literature concerning the introduction of grass carp supports this observation by demonstrating that the fish's effect on water quality varies greatly with the management strategy used. The stocking density of grass carp and consequently the rate at which aquatic plants are eliminated seems to determine the magnitude of the carp's impact (Lembi *et al.*, 1978, Leslie *et al.*, 1983, 1987, Richard *et al.* 1984, 1985; Pipalova, 2006; Dribble and Kovalenko, 2009). In studies where high densities of grass carp were utilized to quickly eliminate all aquatic vegetation major changes in phytoplankton biomass occurred (Holdren and Porter, 1986; Maceina *et al.*, 1992). However, at low stocking densities the effects of grass carp on phytoplankton assemblages appears to be minimal (Terrell, 1975; Von Zon *et al.*, 1976; Hestand and Carter 1978; Lembi *et al.*, 1978; Mitzner, 1978; Terrell, 1982; Leslie *et al.*, 1983; Cassani *et al.*, 1995; Bonar *et al.*, 2002; Pipalova, 2002).

Although most studies that evaluated water quality parameters (total alkalinity, calcium, magnesium, potassium, total phosphorous, turbidity, chlorophyll and secchi disk transparency) noted an initial decrease in water quality following vegetation control by grass carp (Dribble and Kovalenko, 2009), many longer-lasting experiments at low grass carp stocking density noted that these chemical changes began to return to pre-introduction levels (Lembi et al. 1978; Canfield *et al.*, 1983; Small *et al.*, 1985; Shireman and Hoyer, 1986; Leslie, 1990; Maceina *et al.*, 1992; Bonar *et al.*, 2002). These experiments seem to suggest that overall lake quality changes will occur in the short term due to aquatic macrophyte removal, but will return to their limnological potential based on chemical loading rates, hydrology and sedimentary losses.

Conclusions of Grass Carp Introduction

The diversity of scientific findings concerning how the introduction of grass carp can impact an ecosystem seems reasonable when considering the ecology of freshwater systems. In cases where macrophytes were eliminated, the lake achieved a new stable state dominated by phytoplankton growth. However, when macrophytes were removed very gradually and in limited amounts, they were able to successfully inhibit algal growth and also maintain a stable state. Since the grass carp primarily feeds on the surface and in shallow water, it is not likely to engage in benthivorous behavior that could increase nutrient release from the sediment (Leslie, 1990). An initial spike in phytoplankton populations following the introduction of grass carp seems to be the inevitable result of the carp's fecal matter releasing nutrients from undigested plant material into the water column.

Considering available data, I think that it is possible to hypothesize the best case senario that could arise from putting a certain amount of grass carp into Lake Matoaka. Introducing the carp would help eliminate *P. Crispus* which is desirable for several reasons. Firstly, it would reduce the pulse of nutrients responsible for algal blooms in June, which would instead diffuse throughout the lake in fecal deposits or be converted to fish flesh. Hence, while phytoplankton may be more apparent throughout the spring, I predict that reduction of *P. Crispus* by the grass carp will decrease harmful algal mats in the early summer and the subsequent reduction in dissolved oxygen. Secondly, grass carp predation might limit the invasive qualities of *P. crispus* and restore diversity to the macrophyte population of the lake. Finally, the reduction of macrophytes in general would help restore normal fish populations.

However, care should be taken when considering the reduction of aquatic plants to maintain a stable macrophyte dominated state. While the death of plants in a pulse causes algal blooms, consistent macrophyte cover and dominance limits photoplankton aboundance. Furthermore, compared to other eutrophic lakes, Matoaka does not generally exhibit excessive algal blooms (Capelli, 1993) suggesting that macrophytes play a crucial role in phytoplankton inhibition. I can recommend the introduction of grass carp at a very low stocking rate to beneficially reduce the abundance of *P. Crispus*, but the data on grass carp introduction shows that the carp is not a viable means to improve water quality in Lake Matoaka. Moreover, in eutrophic sytems like Matoaka, the introduction of grass carp risks destabilizing the macrophyte dominated state. It is unfortunate that grass carp introduction will not restore the Matoaka watershed. However, neither grass carp stocking nor other types of aquatic plant control remove the factors that cause excessive growth of aquatic plants. I can confidently recommend the introduction of grass carp only in conjunction with reducing nutrient loading into Lake Matoaka.

My conclusions about grass carp suggest that the VDGIF stocking recommendations could have a negative affect on euthropic water bodies in general. I would like to create a model that simulates the interesting mix of competition and mutualism that characterizes phyotplankton-macrophyte dynamics to try to analize this prediction.

Model Description

One of the benefits of qualitative modeling is that it reduces highly complex ecological systems into relatively simple component parts from which it is possible to conduct meaningful theoretical analysis. Furthermore, models that describe eutrophication processes in lakes have been used for environmental management since the seventies (Jorgensen, 2010).

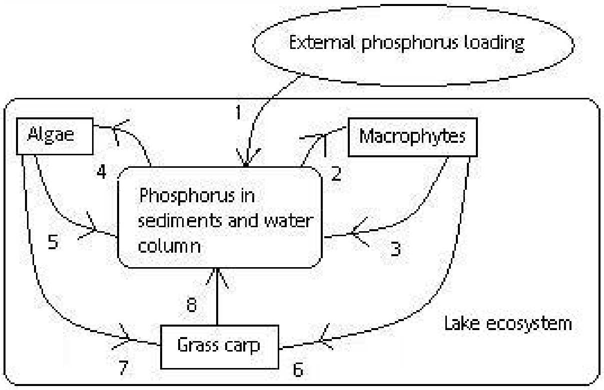

Figure 2: Flow diagram of material in a lake ecosystem. Numbers indicate: 1 – phosphorus loading from point and nonpoint sources; 2 – nutrient uptake from sediments and water column by macrophytes; 3, 5 – mortality of macrophytes and algae, respectively ; 4 – nutrient uptake from water column by algae; 6,7 – consumption of macrophytes and algae by grass carp, respectively; 8 – release of nutrients from grass carp waste.

Recently, several structurally dynamic models demonstrating the competition between phytoplankton and macrophytes have accurately predicted how shallow lakes respond to changing phosphorus levels (Muhammetoglu and Soyupak, 2000; Zhang *et al.*, 2004). However, many of these models require extensive parametrization and the appeal of designing a minimal model with only a few aggregated variables is obvious. Several minimal models that have successfully described behavior of a lake system have been developed (Rosenzweig 1973, Voinov and Tonkikh, 1986; Scheffer, 1991), although none of these models include the introduction of grass carp. Noting previous research in ecological modeling I believe that several complex features of phytoplankton and macrophyte competition can be understood from using a system of nonlinear differential equations to illustrate general characteristics of freshwater ecosystems. Furthermore, I would like to use this model to venture a reasonable hypothesis for how the introduction of grass carp at VDGIF stocking rates will effect Lake Matoaka.

Figure 2 demonstrates the interaction scheme on which the model is based. Differential equations are used to model phytoplankton and macrophyte competition for phosphorus based on a Lotka-Volterra system.

PHYTOPLANKTON GROWTH MODEL

Possibly the best known growth model is the logistic equation, which describes population increase, $\frac{dA}{dt}$, as a function of population density, A:

$$\frac{dA}{dt} = r_A(1 - \frac{A}{K})A \tag{5}$$

where A is algal density, r_A is the growth rate (days^{-1}), and K is the carrying capacity of the environment for algae (mg/l). In this model, the population density increases over time until it plateaus at a carrying capacity (Figure 4). Note that as a result, there are two

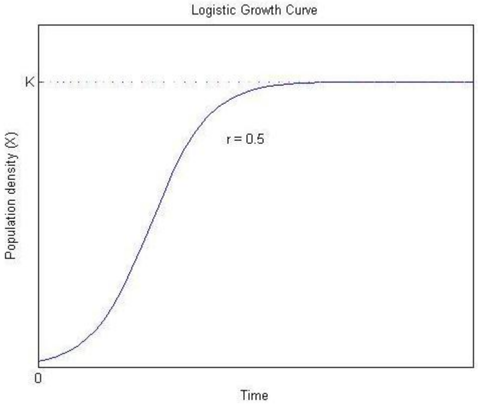

Figure 3: A graphical representation of the classic logistic growth equation demonstrates the change of population density over time. The two equilibrium solutions can be seen to occur when X = 0, or X = K

equilibrium states, when A = 0 or when A = K. Logistic growth is often termed density dependent growth because the relative growth rate can be seen to decrease linearly with population density. While certainly a profound simplification of the mechanisms underlying algal growth, many natural algal communities in lakes fit the logistic equation reasonably well (Heyman and Lundgren, 1988; Scheffer, 1998). In the case of Lake Matoaka, algae is unable to reach its maximum density due to competition with macrophytes for nutrients. The addtion of a term to account for this interaction in the logistic dynamics of algal density will be discussed in the context of a Lotka-Voltera system of algal-macrophyte competition in the following section.

As previously stated in this paper, phosphorus inputs and recycling establish the potential productivity of lakes. The early work of Ketchum and Redfield (1949) established that under optimal conditions, algal biomass contains C:N:P in a fixed atomic ratio of 106:16:1. This ratio, known as the Redfield ratio, has been shown as a constant feature of both photoplakton and zooplankton populations (Sigee, 2005). One important ramification of the Redfield ratio is that it relates algal chemical composition to environmental nutrient availability. Since the ratio indicates that the requirement for phosphours in freshwater systems is considerably less than for nitrogen, it may make the assumption that most lake systems are phosphorus limited seem counter intuitive. However, phosphorus limitation can explained by considerably lower levels of phosphorus supply and the ability of blue-green algae to carry out nitrogen fixation (Sigee, 2005). This relationship combined with the similarity of between bacterial and algal nutrient uptake has lead to scientific consensus that algal growth rate and therefore algal biomass is generally nutrient limited (Sigee, 2005). Additionally, while it is certainly true that algae growth can be limited by other factors, such as light and zooplankton predation, by applying the Liebig law of the minimum, I am going to assume growth is only affected by the factor that poses the strongest limitation. Hence, in the case of Lake Matoaka, I am going to continue to assume that algal aboundance is limited by phosphorus availability rather than by any other nutrient.

Nutrient uptake and algal growth rate have been widely studied and lead to the devel-

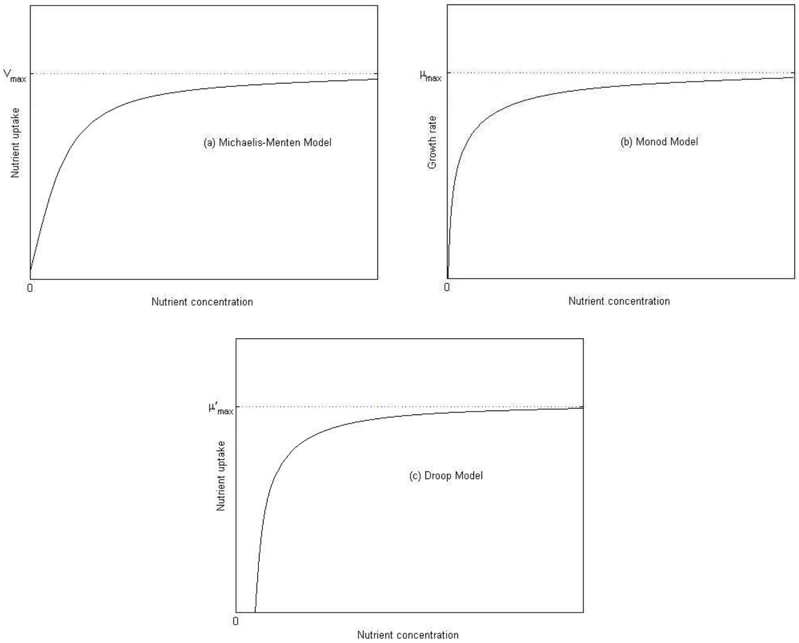

Figure 4: Different representations of algal nutrient uptake and growth rate described by (a) Michaelis-Menten, (b) Monod, and (c) Droop models.

opment of three empirical models of algal growth kinetics (Figure 2). These models relate nutrient uptake to external nutrient concentrations (Michaelis-Menten model), cell growth to external nutrient concentrations (Monod model), and cell growth to internal nutrient concentrations (Droop model) by a rectangular hyperbola function. The Monod model has been successfully applied to data in laboratory cultures for a variety of nutrients (Tilman, 1982; Grover, 1990; Van Donk and Kilham, 1990) and is expressed as:

$$\mu(P) = \mu_{max} \frac{P}{K_\mu + P} \tag{6}$$

where μ is the specific growth rate (days^{-1}), μ_{max} is the maximum growth rate when phosphorus is not limiting, P is the immediately available phosphorus (mg l^{-1}) and K_μ is the half saturation coefficient. K_μ is a measure of the relative ability of a species to use low levels of nutrient.

Unfortunately, the model has been unsuccessful at low growth rates where changes in growth rate are mostly governed by internal nutrient storage rather than external mechanisms (Droop, 1968; Auer and Canale, 1982). Derivations from the formula may also have occurred due to problems with measuring very low concentrations of nutrients and when the growth-substrate relationship changes with substrate concentration (Sigee, 2005). Noting these limitations, however, I believe that the Monod equation is the most useful for a model of the relationship between algae, macrophytes and external nutrient concentrations. Considering Matoaka's degree of nutrient enrichment, I hope to bypass inaccuracies associated

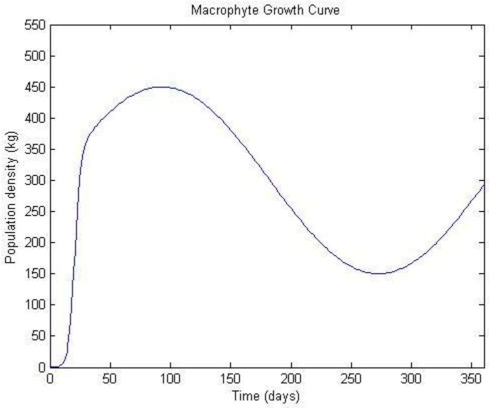

Figure 5: A graphical representation of the annual change in macrophyte population, begining in the spring.

with low growth rates and nutrient levels.

Hence, substituting μ for the algal growth rate into equation (3) yields a new equation for algal growth:

$$\frac{dA}{dt} = \mu_{max}(\frac{P}{K_\mu + P})(1 - \frac{A - a_{A,M}M}{K_A})A \tag{7}$$

Macrophyte Growth Model

Most phosphorus models have been developed with the assumption that the primary response of a waterbody to nutrient loading is manifested in phytoplankton populations and hence few studies are available for macrophyte modeling (Muhammetoglu and Soyupak, 2000). Traditionally, work on modeling aquatic macrophytes has concentrated on modeling their distribution along a depth gradient in terms of light and turbidity limitations (Scheffer, 1998). Although there are several conceptual models that have striven to quantify macrophyte growth for specific lakes and conditions (Chambers and Kalff, 1985; Duarte and Kalff, 1986), the development of deterministic models related to macrophyte problems is relatively sparse (Muhammetoglu and Soyupak, 2000).

Assuming that vegetation grows logistically, seasonal fluctuations in macrophyte density contribute significantly to the internal nutrient cycling of a system. To model this temporal variation, consider a non-autonomous logistic equation with a time-varying carrying capacity $K_M(t)$:

$$\frac{dM}{dt} = \mu_M(1 - \frac{M}{K_M(t)}) \tag{8}$$

when

$$K_M(t) = K_0(1 + sin(\omega t)) \tag{9}$$

and where $K_M(t) > 0$, r_M is the growth rate and K_0 is the average carrying capacity. With a carrying capacity that varies periodically, macrophyte density peaks during the summer and declines during the winter, reflecting a fluctuating environment with deterministic variability

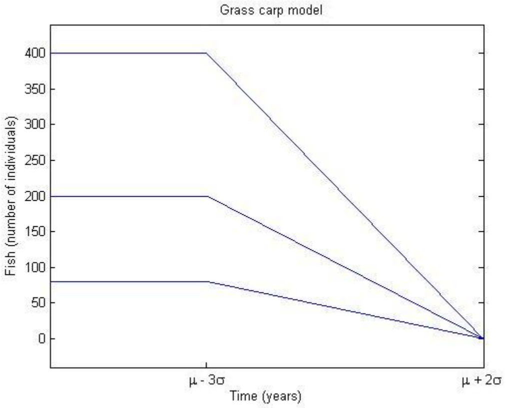

Figure 6: A graphical representation of the change in grass carp population at the VDGIF recomended stocking rates: when g_0 = 80, 200, 400.

(Figure 5). Hence, independently from the initial value, $M(0)$, macrophyte populations will tend to a unique sinusoidal solution with a period that represents an annual cycle.

Next, formulating macrophytic-algal competition as a Lotka-Volterra system yields the following equations:

$$\frac{dA}{dt} = \mu_{max}(\frac{P}{K_\mu + P})(1 - \frac{A - a_{A,M}M}{K_A})A \tag{10}$$

$$\frac{dM}{dt} = \mu_M(1 - \frac{M - a_{M,A}M}{K_M})M \tag{11}$$

where $a_{A,M}$ and $a_{M,A}$ are the respective algal and macrophyte unitless competative coefficients. In a Lotka-Volterra system for two species, i and j, the term $a_{i,j}$ represents the effect species j has on the population of species i.

MODELING NUTRIENTS

The equation to model nutrients is:

$$\frac{dP}{dt} = L_{p2}P - r_A A - r_M M \tag{12}$$

where L_{p2} is the rate at which biologically availible phosphorus is added to the system, r_A percent of of algal biomass that is phosphorus and r_M is the percent of macrophyte biomass that is phosphorus. Hence, when the algae or macrophyte population growth is positive and greater than the rate at which phosphorus is added to the system, it causes the amount of nutrient in the system to decrease. However, when the algae or macrophyte population growth is less than the rate at which phosphorus is added to the system, it should cause the growth rate in algal population to increase and therefore cause a spike in the algae population over time. This also occurs when the macrophyte growth becomes negative, causing the nutrient growth to be negative and hence the algal growth rate to increase.

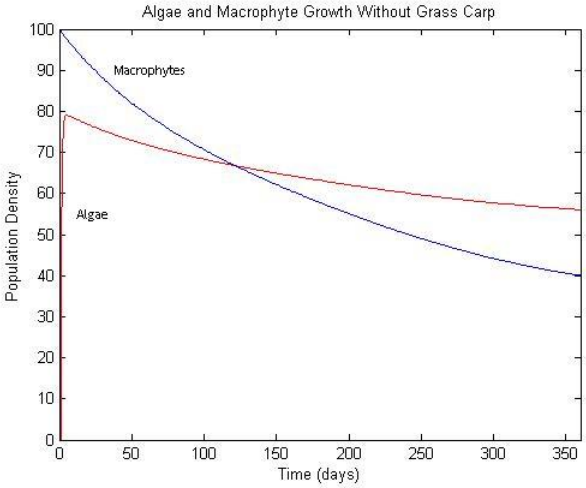

Figure 7: Solution curves for macrophyte and algae growth without the grass carp. Algal growth is indicated by the red line and macrophyte growth by the blue.

Average life span (μ)	**Source**
11	Kirk and Socha, 2003
10	Sutton and Vandiver, 1986
13	Allen and Wattendorf, 1987
8	Berg, 1949
10.5 ± 1.80	

Table 4: Estimated values for grass carp life span and corresponding sources.

Other models have distinguished between nutrients and detritus, noting the competitive advantage of macrophytes to attain nutrients from the soil (Voinoz and Tonkikh, 1986). Rather than separating these nutrient sources, I have attempted to represent this process by making the parameter for phosphorus absorbtion greater for macrophytes than phytoplankton. Since nutrient loss to sedementation is contained in the L_P term as determined in the previous system, I have also assumed that phosphorus is continuously supplied to the lake from outside sources at a rate greater than it is being deposited in the sediments.

The resulting solution curves from running simulations are not what I predicted and indicate that the model needs more work. Discussion of how the model can be improved will follow in the conclusion.

ACCOUNTING FOR GRASS CARP IN THE MODEL

Since the grass carp is sterile, its population can not increase or fluctuate. However, the naturally stochastic nature of grass carp mortality can be estimated by a time period when the carp population remains continuous at its initial value until it reaches a point at which it declines sharply until it reaches zero (Figure 6). This decline begins at about 3 standard deviations before the carp's average life span, at which point, assuming that grass

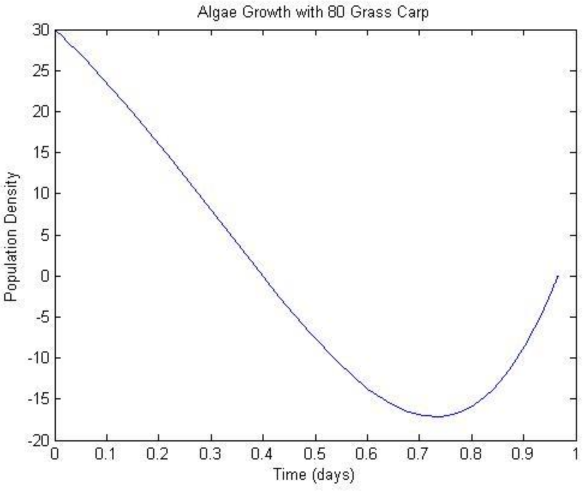

Figure 8: Solution curve for algae growth with grass carp stocked at low density. Algal growth is indicated by the red line and macrophyte growth by the blue.

carp mortality has a normal distribution, about 99% of the initial population will remain. Then the population will decrease linearly, reaching zero at about two standard deviations from the average where only about 5% of the initial carp population is expected to will remain. This behavior can be modeled by a piecewise function:

$$g(x) = \begin{cases} g_0 & : 0 \geq t \geq \mu - 3\sigma \\ \frac{-g_0}{5\sigma}(t - \mu - 3\sigma) & : \mu - 3\sigma \leq t \leq \mu + 2\sigma \end{cases} \tag{13}$$

where g_0 is the amount of grass carp that enter the lake, μ is the average life span and σ is the standard deviation as determined in Table 4. A term for carp population can then be substituted into the equations (8), (9), and (10):

$$\frac{dA}{dt} = \mu_{max}(\frac{P}{K_\mu + P})(1 - \frac{A - a_{A,M}M}{K_A})A - p_A g(t) \tag{14}$$

$$\frac{dM}{dt} = \mu_M(1 - \frac{M - a_{M,A}A}{K_M(t)})M - p_M g(t) \tag{15}$$

$$\frac{dP}{dt} = L_p P + r_A A + r_M M + a_1(p_A + p_M)g(t) \tag{16}$$

where p_M and p_M are the respective amount of macrophytes and algae consumed by grass carp (day$^-1$) and $p_2 >> p_1$. It should be noted that these values are relative to both body size and temperature of the grass carp, the relationship of which has been modeled by Stewart and Boyde (1999). However, since this remains a minimal model, a constant value representing an average estimate will suffice at the moment.

PLANT BIOMASS ESTIMATES

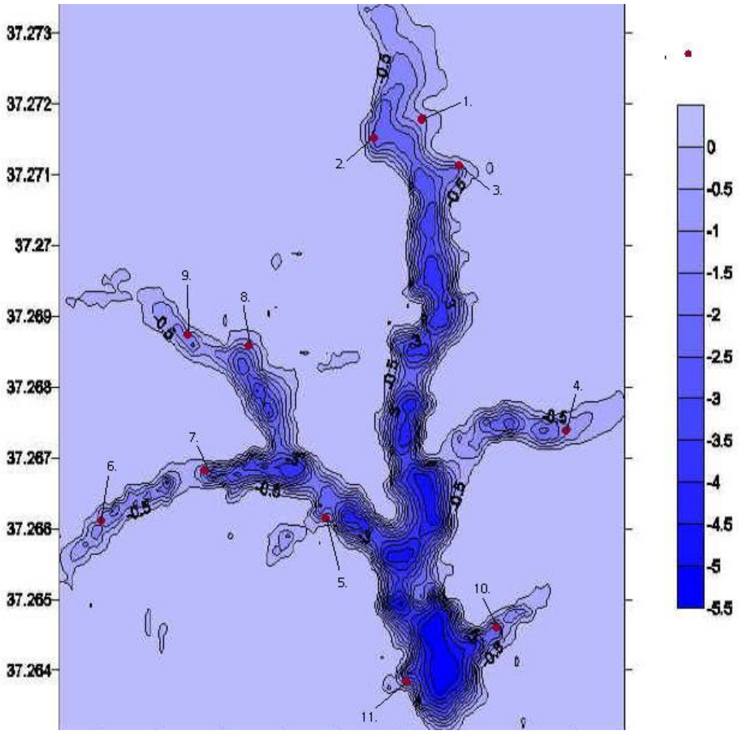

Figure 9: A map of locations where samples were taken. The image of Lake Matoaka is taken from a bathymetry study by Pensa and Wilkin (2002).

Biomass data were collected from $0.25m^2$ quadrats for 11 disperse locations in Lake Matoaka during the summer growing season in July (Figure 7). Samples were dried outside and then in an Isotemp oven at 75^o before their dry. Scheffer (1998) suggests most plant beds are found in water shallower than 1 m and the probability of finding vegetation decreases with depth almost asymptotically. I hope to determine what percent of Matoaka's total volume is $\leq 1m$ based on bathymetry of Lake Matoaka by Pensa and Wilkin (2002) and multiply that by the average mass per volume of the quadrat samples to try to estimate Matoaka's total plant biomass. I would also like to do chl-a testing to estimate the mass of algae in the lake. I would then subtract that amount from the total biomass estimate to determine peak macrophyte mass. I would like to do a similar biomass data collection in the winter, to estimate the minimum algae and macrophyte biomass.

Sample	**Dry weight**	**Depth (m)**	**Mass per volume ($\frac{g}{m^3}$)**
1	96.79	0.64	604.96
2	243.37	0.65	1497.67
3	308.48	0.75	1645.21
4	237.32	0.63	1506.82
5	150.95	0.59	1023.38
6	81.12	0.51	636.23
7	76.43	0.36	849.22
8	212.64	0.48	1772.03
9	213	0.59	1444.07
10	106.04	0.50	848.32
11	224.24	0.63	1423.75
Average			1204.7 ± 420.4

Table 5: Measurements from quadrat samples collected in July for vegetation estimates

CONCLUSION

Although I believe that I am able to provide a recommendation for whether grass carp should be introduced into Lake Matoaka based on the research of other scientists, the model itself is not complete and requires more research to parametrize. I have acquired a good mathematical understanding of the biological mechanisms I would like to represent, but the model is not yet able to assess the effect that introducing different stocking rates of fish may have on Lake Matoaka's ecosystem. As a result, I can not make an estimate of exactly how many grass carp could potentially be introduced into Lake Matoaka. I would also like to be able to focus more specifically on the dynamics between macrophytic-algal competition and examining the isoclines of different simulations without grass carp introduction. Trying to represent the relationship between macrophytes and algae mathematically has been especially interesting because they seem to demonstrate either competition or mutualism at annual cycles, a quality absent from traditional Lotka-Voltera systems. One of the major flaws in the model is accurately portraying the time dependent carrying capacity for macrophytes on which I have based this relationship. I now believe that seasonality may force the intrinsic growth rate to fluctuate instead of the carrying capacity. I may also have to modify my equation for phosphorus to make it more biologically nuanced in order to get a more meaningful result from my solution curves. The problem with the model also may

Parameter	**Value Estimated**	**Plan for acquiring data for better parameter estimate**
M_0	100 u	Plant biomass estimates, bathymetry, chlorophyll a testing
A_0	30 u	Plant biomass estimates, bathymetry, chlorophyll a testing
P_0	2 u	P_λ as determined in equation (3) or data from Physics dept Algae Project
a_1	0.5	Grass carp bionergetics; Pipalova, 2006
L_p	0.1 kg	To be determined based on data in first section
r_A	0.015	More research and perhaps nutrient testing
r_M	0.010	More research and perhaps nutrient testing
K_μ	0.7	More research and or data from Physics dept Algae Project
p_A	1	Better estimated based on grass carp feeding rates and literature or experimentation in the lab
p_M	9	Better estimated based on grass carp feeding rates and literature or experimentation in the lab
$a_{A,M}$	0.4	sSeveral estimates should be tested/ determined based on volume
$a_{M,A}$	0.2	Several estimates should be tested/ determined based on volume
K_0	175 u	Determined based on volume, more simulation testing necessary
K_a	40 u	Determined based on volume, more simulation testing necessary
ω	$\frac{2\pi}{360}$	Developed to simulate periodic annual cycle of macrophyte growth
μ_{max}	0.6	More research on algal populations and data from literature

Table 6: Parameter estimates and rough outline for how to acquire data for better estimates.

revolve mainly around its parameters, for which I have mostly estimates. Fortunately, a lot of the data I need is being collected by the physicists working on the Algae Project and after a year of data, I should have much better estimates. Lastly, I also would like to do a more rigorous mathematical assessment of the model in order to determine whether it provides unique solutions. I hope to complete an independent study spanning two semesters during which I can complete this model and answer these questions.

Finally, it should be noted that this study largely ignores the effect of zooplankton grazing on phytoplankton density. Macrophytes have been shown to provide crucial habitat to *Daphnia* and other planktivorous organisms (Jeppesen *et al.*, 1997) that may help reinforce a macrophyte dominated stable state. Furthermore, several models have been developed focusing on zooplankton-phytoplankton interactions (Scheffer, 1991; Genkai-Kato, 2004) and it would be interesting to include macrophytes. However, since the focus of my study is the effect of grass carp on the balance primary production, I have chosen not to consider the influence of zooplankton. As my research continues, I would like to include phytoplankton-zooplankton dynamics.

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