Spatial and Temporal Phytoplankton Dynamics in Response to Environmental and Anthropogenic Stressors in Lake Seminole, Georgia

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ABSTRACT

Alteration to landscapes by humans can seriously impact dynamics of aquatic ecosystems. Examples of such alterations include urbanization and agriculture in which introduced effluent and materials are either directly or indirectly deposited into rivers. In large rivers, reservoirs alter natural flows creating lentic ecosystems susceptible to allochthonous inputs from up-river. In this investigation, phytoplankton community change over a multi-year period in a large shallow reservoir, Lake Seminole, Georgia, links primary producer change to environmental and anthropogenic stressors. Inflows into Lake Seminole differ in that one arm is primarily from urban/industrial areas and the other two are mainly from agricultural regions providing a unique natural experiment regarding land-use effects on phytoplankton dynamics. Phytoplankton community structure was estimated by measuring and analyzing photosynthetic pigments. Stressors to the system included precipitation, temperature, water flow, and the presence of the invasive macrophyte *Hydrilla verticillata* which is seasonally known to cover up to 50% of the lake. Results show that average phytoplankton abundance is increased from up-reservoir to down-reservoir and in the presence of *Hydrilla verticillata*. The phytoplankton community of Lake Seminole demonstrates the complexity and multivariate integration of anthropogenic stressors in large reservoirs showing the difficulty of management efforts targeting a single stressor.

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DEDICATION

This thesis is dedicated to my father, Ted F. West II, who has taught me to never give up, even when it seems futile to continue. His persistence to live despite his health barriers continue to drive my sister, brothers, and I to live the best life we possibly can and to face any adversity we encounter with overwhelming contention. I miss him every day, but I am overjoyed that he saw this thesis through to completion while relentlessly fighting his own battles.

Chapter I

INTRODUCTION

Reservoir Dynamics

Reservoirs are lacustrine environments formed behind dams in which the physical, chemical, and biological features are strongly conditioned by water level fluctuations, due to rainfall and dam operation (Thornton et al., 1990). In their ecological structure and function, reservoirs have been conceptualized as disruptions to river systems (Vannote et al., 1980) and as intermediates or transitions between rivers and lakes (Lind 1971). Reservoirs have relatively large watersheds compared to natural lakes and therefore can receive large inputs of nutrients and other materials (Kimmel et al., 1990; Wetzel 1990). Because of the influence of hydrological inflows, reservoirs often exhibit pronounced gradients in light and nutrients, resulting in rapid changes in the distribution of photosynthetic organisms (Kimmel et al., 1990). The sediments stored in reservoirs can contain large amounts of particulate materials thus disrupting downstream transport. For example, nutrient storage in reservoirs has decreased nutrient delivery to shallow marine areas by 700% (Górniak 2002). In addition, the amount of water globally held by reservoirs has increased seven fold in the last 40 years (Górniak 2002). Hydrology determines the rates of sedimentation and nutrient export by altering the natural water residence time of the reservoir (Hillbricht-Ilkowska 1999; Vanni et al., 2001). During high flows, surface runoff and drainage are often the dominant mechanism for nutrient input (Burns et al., 2001; Ocampo et al., 2006; Torak et al., 1996). Furthermore, variations in hydrologic regimes, such as shifts from drought to flood conditions, result in a change in the primary transport mechanism for nutrient input (Meixner et al., 2007; Rodriguez-Blanco et al., 2009). Floods are one of the most important influences on total nitrogen (TN) and total phosphorus (TP) retention and cause the greatest amounts of N and P export (Mhamdi et al., 2007; Irfanullah & Moss 2008; Spieles & Mitsch 2000). Such variations in nutrient dynamics directed by flow can alter the biomass, diversity, and abundance of phytoplankton populations in lakes and reservoirs. High temperature can also cause nutrient release by creating anoxic conditions which activates internal P loading in deeper areas of reservoirs (Hillbricht-Ilkowska 1999). Eutrophication in lakes and reservoirs often results in the proliferation of various phytoplankton species, some of which can be detrimental to aquatic ecosystems.

Longitudinal Gradients in Reservoirs

Large reservoirs tend to result in various longitudinal gradients occurring within the reservoir consisting of three different zones of riverine, transitional, and lacustrine (Figure 1.1) (Kennedy et al., 1982). Each individual reservoir is different in terms of gradient dynamics however overall trends for each zone generally occur (Figure 1.1) (Thornton et al., 1981). Riverine regions are located in the narrow, shallow, up-reservoir region (Leavitt 2015). This zone is characteristic of a well-mixed and aerobic water column with increased light attenuation from allochthonous organic matter and fine suspended particles (Thornton et al., 1981). Significant sedimentation occurs through the transition zone with a subsequent increase in light penetration either increasing gradually or abruptly depending on the flow regime (Thornton et al., 1981). In some reservoirs, an area known as the plunge point is located in transitional areas where sediment-laden inflowing water sinks to a depth of comparable density (Thornton et al., 1981; Leavitt et al., 2015). At some point within this mixed layer of the transition zone, a compensation point between the production and processing of organic matter should be reached (Thornton et al., 1981). Autochthonous production of organic matter past this point within the mixed layer should increase (Thornton et al., 1981). Plunge points are variable in location, especially in large, shallow reservoirs. They expand or contract based on specific conditions within individual reservoirs such as water temperature, flow regimes and material inputs (Thornton et al., 1990). In the lacustrine region of reservoirs, sedimentation of inorganic particulates is low, light penetration is sufficient to promote primary production with the potential for nutrient limitation and production of organic matter exceeding processing within the mixed layer (Thornton et al., 1981).

Phytoplankton Dynamics in Longitudinal Gradients and Reservoirs

Phytoplankton dynamics in reservoirs can be variable along the longitudinal gradient (Leavitt et al., 2015). Algae in riverine zones are typically represented in low abundance and biomass due to increased flushing and high turbidity caused by the riverine conditions (Thornton et al., 1981). Transitional zones typically represent the highest primary productivity of the three but can vary from each individual reservoir based on the location of the plunge point (Figure 1.1) (Thornton et al., 1990). Lacustrine zones can also contain increased primary productivity depending on certain factors such as the location of a reservoir's withdrawal and flow regimes.

Reservoirs usually have a wide array of mechanisms that alter nutrient dynamics that directly influence phytoplankton community structure (Happey-Wood, 1988). Hydrologic variability and seasonal factors appear to control retention dynamics within reservoirs which generally act as a sink for inorganic nutrients and a source for dissolved organic carbon (DOC) (McEntire 2006). Reservoirs, due to their large watershed size, receive larger nutrient loads than natural lakes (Wetzel 1990). Water temperature, along with rainfall, regulates the seasonal dynamics of phytoplankton community structure in reservoirs (Talling Can 2001; Schagerl & Oduor, 2008). In addition, high discharge rates from the reservoir may disrupt assemblage structure, leading to low assemblage persistence (Schneck et al.,, 2010). Furthermore, the hydrological regime also greatly influences phytoplankton assemblages, as precipitation governs dam operation and water retention times, producing pulses of material and nutrients in suspension, stimulating material cycling and biomass loss (Calijuri et al., 2002).

Macrophyte Effects on Reservoir, Nutrient, and Phytoplankton Dynamics

Macrophyte presence in lakes and reservoirs can exhibit profound effects on nutrient dynamics, flow, and phytoplankton biomass (Wetzel 2001). Large beds of macrophytes decrease water velocity, increase water residence time and affect rates and patterns of sedimentation by acting as filters for suspended particulate inorganic and organic material (Kufel & Kufel 2002; Knight et al., 2003; Clarke 2002; Schulz et al., 2003). Biomass, seasonality, and environmental variables such as light, temperature, and nutrient availability are important factors in determining nutrient uptake and retention by submerged aquatic vegetation in reservoirs (Pietro et al., 2006; Sollie & Verhoeven 2008). Macrophytes act as short-term sinks for nitrogen and phosphorus by incorporating these nutrients into their biomass (Kufel & Kufel 2002; Chimney and Pietro 2006) potentially creating a nutrient limiting environment for phytoplankton. In addition, they may promote aerobic phosphorus release as they increase water pH through intensive photosynthesis (Solim & Wanganeo 2009). Macrophytes affect resuspension, a process where sediment and nutrients are transported back to the water column because of physical (e.g., waves and currents) or biological (bioturbation) activity. Submerged aquatic macrophyte beds attenuate wave action and increase the wind velocity needed for resuspension to occur (Madsen et al., 2001), thereby reducing the rate of sediment resuspension (Holmroos et al., 2015). Furthermore, aquatic macrophytes affect other physical and chemical parameters of surrounding waters by altering the availability of dissolved oxygen (DO), light and temperature within the water column (Carter et al., 1991; Pagano et al., 2004). Additionally, macrophyte stands can alter the location of the plunge point along the reservoir gradient altering the movement and processing of materials through the system.

Given that reservoirs experience significant influence from human impacts, invasive species are a common occurrence in reservoir systems. Invasive macrophytes can enter waterways via inputs from humans at up-stream sources or by indirect methods such as transplantation by boats. The invasive macrophyte *Hydrilla verticillata* is one of the most studied aquatic vascular plants (Langeland 1996) and contains extensive adaptive attributes to survive in the aquatic habitat which allows it to be an aggressive and competitive colonizer (Langeland 1996). Dense beds can encompass the entire water column in shallow depths (~3m), obstructing boating areas and modifying fish communities (Patrick 2015). Optimum water temperatures for growth varies between 25 and 36°C (Sousa 2011) so as global temperatures continue to rise, *Hydrilla* has the potential to spread to more northern waterways.

Land-use Effects on Phytoplankton and Reservoir Dynamics

Past research has convincingly demonstrated that alterations to landscapes by humans can seriously impact the trophic status, health, and benefits of the once unaltered land (Knight et al., 2003). Examples of anthropogenic land-use changes include urbanization and agriculture that lead to leeched materials and effluent deposited into rivers by direct or indirect means. Watersheds dominated by agricultural or urban lands typically export nutrients at higher rates than undisturbed watersheds (Puckett 1995). These nutrient inputs increase the growth of primary producers thus altering the physical and chemical characteristics of the aquatic ecosystems. The Environmental Protection Agency (EPA) reported in 2004 that approximately 44% of the streams, 64% of the lakes and 30% of the estuaries around the nation were altered due to excessive nutrient loading, hydrologic modifications, urban and agricultural runoff and sewage input (EPA 2009). Among the various nutrients involved in runoff, phosphorus is regarded as the most important factor for determining the water quality of lakes (Søndergaard et al., 2003) while nitrogen also contributes to the quality due to its combined effects with phosphorus (Conley et al., 2009). High loads of phosphorus lead to high phytoplankton biomass, turbid water, and often undesired biological changes such as loss of biodiversity, disappearance of submerged aquatic macrophytes, decreases in water clarity, fish stock changes, decreased oxygen concentration, and decreasing top-down control by zooplankton on phytoplankton (Paerl 2009; Schindler 2006; Søndergaard et al., 2003). Phosphorus entering waterways has increased 2.5 to 5-fold in the last 50 years as a consequence of chemical fertilizers, application of animal manure and disposal of raw and treated human waste (Schaefer & Alber 2007; Williamson et al., 2008). The effects of eutrophication in lakes and reservoirs are numerous, deleterious, and typically characterized by shifts towards cyanobacterial dominance of phytoplankton (Skulberg et al., 1984; Carmichael 1991). As a result, phytoplankton are commonly used as indicators of water quality and therefore help to gain insight into how biotic and abiotic stressors affect aquatic systems and water quality.

Lake Seminole and the Apalachicola-Flint-Chattahoochee River Basin

A prime example of a reservoir experiencing an occupation by an invasive submerged macrophyte with different inputs from both agricultural and urban/industrial watershed land-uses is Lake Seminole (Figure 1.2). Lake Seminole is a large and shallow reservoir in southwestern Georgia, USA, with a surface area of 152 km^2, mean depth of 3m and a maximum depth of 10m (Sammons & Maceina 2005). The reservoir is utilized for a variety of uses that include navigation, hydroelectric power, and recreation. *Hydrilla verticillata* is an invasive macrophyte infecting this reservoir, is seasonally abundant and can account for over 50% of the reservoir's area (Gholson 1984). The Chattahoochee River, Flint River, and Spring Creek drain into and join to form Lake Seminole (Figure 1.2). The Apalachicola River forms at the Jim Woodruff Lock and Dam, built in 1952 so forming Lake Seminole, which was then opened to the public in 1957 (Dalton et al., 2004). The reservoir is owned and maintained by the Army Corps of Engineers (Dalton et al., 2004).

Lake Seminole is located in the Apalachicola-Flint-Chattahoochee (ACF) River Basin which spans through Georgia, Florida, and Alabama and drains an area of 51,800

km^2 (Frick et al., 1998). Two different land-uses characterize the drainage basin of the ACF: urban/industrial and agricultural (Patrick 2015). The Chattahoochee drains a more urban and industrial watershed, while the Flint River and Spring Creek drains a more rural and agricultural watershed (Frick et al., 1996; Patrick 2015). The ACF basin provides freshwater into Apalachicola Bay, which provides 90% of Florida and 10% of the United States' oyster industry (Oczkowski et al., 2011).

Research Objectives

Few studies exist on phytoplankton abundance and community structure in Lake Seminole, as most studies focus on *Hydrilla* management and fishery systems (Patrick 2015). This study is designed with two objectives:

Objective 1: To assess the effects of *Hydrilla verticillata* on phytoplankton abundance and community structure along the longitudinal gradients of Lake Seminole.

Objective 2: To determine the effects of different land-use practices on phytoplankton abundance and community structure and determining environmental and anthropogenic drivers for two unique phytoplankton bloom events in Lake Seminole.

Chapter II

SPATIO-TEMPORAL EFFECTS OF HYDRILLA VERTICILLATA ON PHYTOPLANKTON DYNAMICS IN A SHALLOW RESERVOIR

Abstract

Reservoirs alter natural rivers creating a longitudinal gradient by dividing the reservoir into riverine, transitional, and lacustrine zones. Along this gradient, turbidity typically decreases and phytoplankton increase as allochthonous materials deposit and the reservoir transitions into a more lacustrine environment. Dense macrophyte coverage can alter these dynamics by decreasing flow rate and increasing light attenuation promoting phytoplankton growth in each reservoir section. In this study, phytoplankton community structure was inferred from photosynthetic pigments measured from water samples within each zone of Lake Seminole, GA, a large reservoir currently dominated by the invasive macrophyte species *Hydrilla verticillata*. Comparisons of phytoplankton abundance and community structure were made between reservoir zones and macrophyte growing seasons. Results show that algal abundance increased down the longitudinal axis while community structure diversity is greatest in the mid-reservoir zone where the invasive macrophyte predominates. Phytoplankton increased in abundance during *Hydrilla* growing seasons when compared to periods of die-off. It is inferred that *Hydrilla* presence increases phytoplankton growth, raising concern for ecological and economical management for other shallow reservoirs that are occupied by invasive macrophytes.

Introduction

Reservoirs have been conceptualized as disruptions to river systems (Vannote et al., 1980) and as intermediates or transitions between rivers and lakes (Lind 1971). Large reservoirs tend to result in various longitudinal gradients occurring within the reservoir consisting of three different zones of riverine, transitional, and lacustrine (Kennedy et al., 1982). Each individual reservoir is different in terms of gradient dynamics however common trends for each zone generally occur (Thornton et al., 1981). The riverine zone is typically high in nutrients and exhibits increased light attenuation (Pickett & Harvey 1988). The transitional region traditionally exhibits a decrease in light attenuation and contains high nutrient abundances. Low nutrient concentrations and high light penetration represent the lacustrine region (Thornton et al., 1981). In addition, flow is variable for each gradient, with the riverine zone flowing at the highest rates and decreasing down-reservoir (Figure 1.1).

Macrophyte presence in reservoirs can incur profound effects on nutrient dynamics, water flow, and phytoplankton biomass (Wetzel 2001). Invasive macrophytes can enter waterways via anthropogenic inputs at up-stream sources which deposit down-stream in reservoirs or by indirect methods such as transplantation by boats. The invasive macrophyte *Hydrilla verticillata* is one of the most studied invasive aquatic vascular plants (Langeland 1996) and contains extensive adaptive attributes to survive in the aquatic habitat which allow it to be an aggressive and competitive colonizer (Langeland 1996). Dense beds can encompass the entire water column in shallow depths (~3m), obstructing boating areas and modifying fish communities (Patrick 2015). Additionally, optimum water temperatures for growth varies between 25 and 36^{o}C (Sousa

2011) and as global temperatures continue to rise, *Hydrilla* has the potential to spread to more northern waterways.

Phytoplankton dynamics can be variable along the longitudinal gradient in reservoirs (Leavitt et al., 2015). Algae in riverine zones are typically represented in low abundance and biomass due to increased flushing and high turbidity due to the river-like conditions (Thornton et al., 1981). Primary production can show a definite increase at mid-reservoir transitional zones (Leavitt et al., 2015). In some reservoirs, an area known as the plunge point is located in transitional areas where sediment-laden inflowing water sinks to a depth of comparable density (Leavitt et al., 2015). At some point within this mixed layer of the transition zone, a compensation point between the production and processing of organic matter should be reached (Thornton et al., 1981). Autochthonous production of organic matter past this point within the mixed layer should dominate (Thornton et al., 1981). As a result, once the plunge point is reached in a reservoir, phytoplankton production can increase but this occurrence depends on specific conditions within individual reservoirs, e.g. temperature which determines water density of inflows, and most importantly flow regimes which can have significant effects on the location of the plunge point (Thornton et al., 1990). In lacustrine zones, sedimentation of inorganic particulates is low but sufficient light penetration for primary production prevails. Regarding autochthonous nutrient loading, top withdrawal reservoirs are known to conserve more nutrients in the hypolimnion than bottom withdrawal due to minimal removal of nutrients in the hypolimnion and sediments (Fischer et al., 1979).

Dense macrophyte stands can decrease flows and cause a rapid deposition of the terrestrial load traveling down a river. This decreases water mixing, increases light, and alters biogeochemical cycles thus improving conditions for phytoplankton growth. In addition, macrophyte stands could alter the location of the plunge point along the reservoir gradient altering the movement and processing of materials through the system. Phytoplankton abundance and community structure in Lake Seminole, GA, were measured in this study with the objectives:

1) What is the abundance of phytoplankton in the three zones of an invasive macrophyte dominated reservoir?
2) How does phytoplankton abundance vary along longitudinal gradients during *Hydrilla verticillata* growth and die-off periods?
3) How does phytoplankton community structure vary along longitudinal gradients during *Hydrilla verticillata* growth and die-off periods?

Methods

Study Site

Lake Seminole (Figure 2.1) is a large and shallow reservoir in southwestern Georgia, USA with a surface area of 152 km^2, mean depth of 3m and a maximum depth of 10m (Sammons & Maceina 2005). Uses for the reservoir consist of navigation, hydroelectric power generation, and recreation. Large beds of the submerged aquatic macrophyte *Hydrilla verticillata*, can account for over 50% of the reservoir's area, and are seasonally abundant in the transitional region (Gholson 1984). The reservoir is part of the Apalachicola-Flint-Chattahoochee (ACF) River Basin, which spans through Georgia, Florida, and Alabama and drains an area of 51,800 km^2 (Frick et al., 1998). Lake Seminole is at the confluence of the three rivers making up the ACF (Figure 2.1) with the Chattahoochee River and Flint River joining to form the Apalachicola River.

The Flint River and Chattahoochee River headwaters begin in the upper ACF basin south of Atlanta and in north Georgia, respectively.

Although the two rivers are similar regarding geologic position, they differ in upriver land use and human population densities, as well as in the number of dams, sewage treatment discharges and hydrological variability (McEntire 2009). The Chattahoochee is known for its higher density of urbanization from Atlanta and Columbus, Georgia, contains 22 wastewater treatment plants, four large reservoirs, and nine low storage "run-of-the-river" reservoirs. The Flint River has only two "run-of-the-river" reservoirs and the flow from Spring Creek, a former tributary of the Flint, is unimpeded (Frick et al., 1996; Abbott 2005). Agricultural practices account for 49% of the land use in the lower ACF and are predominantly located around the Flint River and Spring Creek corridors (Frick et al., 1996). For Spring Creek and the Flint River, base flows are provided by the Upper Floridan aquifer whereas the Chattahoochee River's base flow is determined by the Army Corps of Engineers operation of reservoir release at up-stream dams. Lake Seminole discharges at the Jim Woodruff Lock and Dam forming the Apalachicola River, which runs unimpeded into the Gulf of Mexico at Apalachicola Bay. Apalachicola Bay is a crucial fishery for the state of Florida and the United States containing 90% of Florida's and 10% of the United States' oyster industry (Oczkowski et al., 2011).

Field Collection

Samples from 277 water column locations from various depths were collected usually monthly over the course of 2 years from seven different sampling sites (Figure 2.1) on Lake Seminole as part of the monthly water quality monitoring plan by the Joseph

Jones Ecological Research Center; June 2012 – August 2014. Only surficial and mid depth samples (up to 2m) were included in the study to ensure samples were obtained from the photic zone. Deeper samples were excluded in *Hydrilla* beds because of increased light attenuation. Sampling stations that included more than one sample were averaged to generate a single value. The stations included are three riverine stations, three transitional stations (where *Hydrilla verticillata* is seasonally present in the reservoir), and one lacustrine station (Figure 2.1). Months in which no samples were collected are July and November of 2012, along with January and December 2013 and February 2014. Whole water samples were filtered at the Joseph Jones Ecological Research Center immediately after sampling, and the filters containing all seston material were placed in aluminum foil to prevent UV decay of pigments, and stored in a freezer at -20° C. The samples were analyzed for pigment type and concentration via High Performance Liquid Chromatography (HPLC).

Photosynthetic Pigment Analysis

Photosynthetic pigments (carotenoids and chlorophylls) were measured by an HPLC system using the methods of Leavitt and Hodgson (2001) and Waters et al., (2012). The filter samples were extracted using a solvent mixture (80% acetone, 15% methanol, and 5% HPLC grade H_2O) and injected into a Shimadzu HPLC system using the mobile phase and time sequence of Leavitt and Hodgson (2001). Chlorophylls and carotenoids were separated by passing through a Phenomenex Luna Microsorb C18 column and measured using a photodiode array detector set at 435 nm for carotenoids and a fluorescence detector for chlorophylls. Pigment identification was made using retention times of known standards and pigment specific spectra recorded by the detectors (Waters et al., 2012). A list of the photopigment associations with phytoplankton groups are referenced in Table 2.1. Regression analysis and multivariate analysis was used to determine any spatial and temporal differences between the samples. Outliers are determined by the Thompson tau outlier test.

Results

Spatial and Temporal Dynamics of Total Phytoplankton and Degradation

The lacustrine zone accounts for the maximum primary producer abundance (PPA) and the riverine zone accounts for minimal PPA (Figure 2.2). Concerning river basins, the Chattahoochee River has the highest phytoplankton abundance and Spring Creek has the least (Table 2.3 and Figure 2.3). Pigment values for riverine and transitional zones in the Chattahoochee are not significantly different (at $p < 0.05$) (Figure 2.3). A significant increase in PPA of 49% occurs from the riverine to transitional zones in the Flint River and a 36% increase occurs in Spring Creek (Figure 2.3). Overall percent increases in PPA from the riverine to lacustrine zone are highest in Spring Creek and the Flint River with 64.2% and 62.7%, respectively (Figure 2.3). The Chattahoochee transect shows the smallest increase in PPA with 23.1% (Figure 2.3). Average pigment abundance is highest in months where *Hydrilla verticillata* is present in the reservoir with transitional stations experiencing the maximum increase of PPA by 67.42% when *Hydrilla* appears in the lake and riverine and lacustrine sites each increasing by 57% (Table 2.2, Figures 2.4 and 2.5). Principal component analysis (PCA) indicates that carotenoid and chlorophyll pigments both ordinate with months in which *Hydrilla verticillata* is present in the lake (Figure 2.6). All pigments with the exception of myxoxanthophyll are positive for principal component 1 (PC1). Chlorophyll-b, chlorophyll-a, and beta-carotene explain the majority of variation for PC1 at $\lambda_1 = 47.49$ with myxoxanthophyll and minor influences from fucoxanthin, and chlorophyll degradation products describing PC 2 at $\lambda_2 = 14.27$.

Average degradation abundance is composed of all chlorophyll degradation products which include chlorophyllide, pheophytin-a, pheophytin-b, pheophorbide, and pyropheophytin. Chlorophyllide comprises the majority of the degradation products and follows almost identical seasonal trends as total chlorophyll (TChl) abundance ($p < 0.05$) in which abundance increases in warmer months and when *Hydrilla verticillata* is present in the reservoir (Figure 2.5). Along the longitudinal gradient, degradation is highest in the lacustrine region and lowest in the riverine (Figure 2.7). Ratios of total degradation to chlorophyll abundance shows the transitional region containing the lowest ratio with the lacustrine exhibiting the highest (Table 2.5). Ratios of all regions increase significantly when *Hydrilla* is absent from the reservoir (Table 2.5). The riverine station in the Chattahoochee experiences the most degradation of the riverine zone and the transitional site of the Flint contains the most degradation in the transitional region of the reservoir. Pyropheophytin, indicative of zooplankton fecal pellets, is most abundant in lacustrine and transitional regions when *Hydrilla verticillata* is present in the lake (Figure 2.8). Pigment abundance generally increases from riverine to lacustrine, with the exception of the degradation products pheophytin-b and pheophorbide (Figure 2.8). Myxoxanthophyll only occurs in the transitional zone (Figure 2.8). December 2012 is excluded from analysis due to an algal bloom that appeared to be a unique event (see Chapter 3).

Spatial and Temporal Dynamics of Phytoplankton Community Structure and Abundance

Chlorophyll pigments appear to be highest in abundance however all pigments were normalized by their weight (µg/L) and not concentration (nmol/L) (Figure 2.8). Chlorophyll molecules weigh significantly more than carotenoids and as a result may exhibit very high abundance values when compared to carotenoids. Disregarding chlorophyll pigments, the most dominant photopigments are zeaxanthin + lutein (zea + lut), fucoxanthin (fuco), and alloxanthin (allo), comprising 62.36%, 15.12%, and 9.74% respectively of the composition of the carotenoids and are significantly higher ($p > 0.05$) in abundance during months that *Hydrilla verticillata* is present (Table 2.2, Figures 2.4, 2.5,and 2.8). Beta-carotene, neoxanthin, and diatoxanthin show little variability and relatively low abundance throughout the study although abundance did increase when *Hydrilla verticillata* was present. Myxoxanthophyll occurs in very small concentrations and is present only in the transitional region in Spring Creek and the Flint River. Chlorophyll-a (chl-a), chlorophyllide (chlphllide), and chlorophyll-b (chl-b) comprise a significantly higher abundance ($p > 0$ .05) than the other chlorophyll photopigments, contributing 48.79%, 34.13%, and 11.64%, respectively, to the total composition of chlorophylls observed in the study. The other chlorophyll photopigments present are the chlorophyll degradation products pheophytin-a, pheophytin-b, pheophorbide, and pyropheophytin, all contributing small amounts to the chlorophyll group among the sampling sites. The chlorophyll abundance is significantly higher during months that *Hydrilla verticillata* is present ($p > 0.05$, Table 2.2). PC1 and PC2 from the principal component analysis of all pigments were saved as variables and ordinated with the abiotic factors pH, temperature, and flow (Figure 2.9). The analysis reveals that PC1 (described by all pigments except myxoxanthophyll), highly ordinate with temperature and PC2 (mainly described by myxoxanthophyll) ordinates with pH, while both PC1 and PC2 negatively ordinate with flow (Figure 2.9).

Phytoplankton abundance and diversity estimated from pigment analyses (Table 2.1) show changes corresponding with seasonality, *Hydrilla* presence, and the longitudinal gradient in the reservoir. PPA increases step-wise down the longitudinal gradient with the highest abundance in the lacustrine zone of the reservoir and community structure diversity greatest in the transitional region when cyanobacteria is apparent in beds of *Hydrilla verticillata.*

Discussion

Hydrilla's Effects on Phytoplankton Abundance in Reservoir Zones

Phytoplankton abundance in Lake Seminole increases down a longitudinal gradient from riverine (up-reservoir), containing the least abundance of algae, to lacustrine (down-reservoir), containing the maximum abundance of the three zones (Table 2.2 and Figure 2.2). These results are unexpected as transitional zones are traditionally known to contain the highest abundance of phytoplankton (Thornton et al., 1990). However, regions of reservoirs can expand and contract in response to watershed runoff events, density flow characteristics, and reservoir operating schedules that can result in an overlapping of gradients (Thornton et al., 1990). In particular, shallow run-of-the-river reservoirs like Lake Seminole are more prone to riverine conditions persisting further down-reservoir (Thornton et al., 1990). As a result, the transitional region where samples were gathered can be periodically influenced by riverine conditions when flows were high and macrophytes are absent, resulting in lower than expected algal abundances at the transition. A prime example of this is reflected by the pigment concentrations in the Chattahoochee River. The Chattahoochee was missing beds of *Hydrilla* for the majority of the study and flows are the highest of the three rivers (Table 2.4). Subsequently, the transitional region of the Chattahoochee contains the highest algal abundance of all transition sites with the abundance values between riverine and transition zones being similar (Figure 2.3). This evidence suggests that Lake Seminole's gradients can oscillate in size and that *Hydrilla* can decrease flow rates. Additionally, the Flint River and Spring Creek seasonally contained *Hydrilla* and showed a significant increase in pigment abundance from riverine to transitional zones, further suggesting gradient oscillation in Lake Seminole and that *Hydrilla* affects flows (Figure 2.3). Furthermore, high flows in Lake Seminole potentially allow for partial merging of the transitional region with the dam region, thus increasing primary productivity further down reservoir (Table 2.2 and Figure 2.2).

The increased abundance of algae compared to the riverine zone in Lake Seminole's transitional region (Table 2.2, Figures 2.2 and 2.3) is expected, as such is normally the case in transitional zones because of decreased flow rates and increased availability of light and nutrients. However the presence of *Hydrilla* further decreases flow rates and increases nutrient sedimentation in the transitional region (Schulz et al., 2003; Sollie & Verhoeven 2008). These combined effects result in an enhanced environment for algal growth, supporting the conclusion that *Hydrilla* presence magnifies phytoplankton abundance in Lake Seminole (Table 2.2, Figures 2.4 and 2.5). In addition, the plunge point appears to be retained in the transition merely by the presence of *Hydrilla*. This is supported by the increased algal abundance seen when *Hydrilla* is present (Figure 2.4). Further support is derived from the Chattahoochee River where *Hydrilla* is primarily absent and shows no significant difference in abundance between riverine and transitional zones (Figure 2.3). This suggests that the plunge point for this inflow is further downstream in the lacustrine region. Furthermore, an overall decrease in algal abundance is seen when *Hydrilla* beds degrade (Figure 2.4). The transitional region of the reservoir shows the largest decrease in abundance when *Hydrilla* beds seasonally die-off (Figure 2.4), indicating *Hydrilla* positively impacts growth of phytoplankton.

The dam region of Lake Seminole contains the highest algal abundance of all regions which is not expected in reservoirs (Thornton et al., 1981) (Table 2.2, Figures 2.2, 2.3, and 2.4). *Hydrilla* provides multiple stressors that support the increased phytoplankton abundance seen in the lacustrine zone. First, when *Hydrilla* is present at the transition, it acts as a particulate filter and decreases turbidity which subsequently increases light availability further down-stream. Second, flows are decreased when *Hydrilla* is abundant at the transition, increasing the residence time of the reservoir. In addition, *Hydrilla* may moderate turbulent and stressed conditions into relatively calmer conditions, which retains lower flow rates than would normally be observed in turbulent conditions. PCA analysis supports an increase in algal abundance during decreased flows (Figure 2.9). Furthermore, chlorophyll-a values are relatively high but are globally mesotrophic, suggesting that *Hydrilla* is absorbing excess nutrients below eutrophic levels; a conclusion supported by the knowledge that *Hydrilla* absorbs the most phosphorus of any submerged macrophyte (Gu 2006; McEntire 2009).

When *Hydrilla* is absent, the plunge point is moved to the lacustrine region, supporting increased growth there. Flow data indicate multiple periods of increased flow rates during *Hydrilla* deficient periods (Table 2.4), adding support for a plunge point that extends past the transitional region and suggests a mechanism for the increased phytoplankton production in the lacustrine zone of Lake Seminole. Alternatively, the absence of *Hydrilla* may decrease algal abundance in the reservoir in multiple ways. First, influxes of dissolved organic carbon (DOC) are released upon the seasonal die-off of *Hydrilla* (Shivers 2010), which creates unfavorable conditions for algal growth such as increased turbidity and light attenuation. Second, flow rates increase, reducing the residence time which flushes algae at a faster rate. PCA analysis shows a decrease in algal abundance during high flows (Figure 2.9). Third, biotic factors such as the presence of the benthic organisms *Lyngbya* and *Corbicula* present in the transitional region of the Flint River absorb excess nutrients, limiting availability for phytoplankton (Waters et al., 2015, Patrick 2015).

Pigment abundance in the Flint River is lower than expected (Figure 2.3) for a river experiencing runoff from an agriculturally dominated watershed that should exert high nutrient loads into the reservoir. High nutrient loads have been shown in numerous studies to be highly correlated with increased phytoplankton growth (Reynolds 1984, Reynolds 1997; Lampert & Sommer 1997). The presence of seasonal *Hydrilla* beds and the benthic cyanobacteria, *Lyngbya,* in the Flint suggest that these biota are out-competing phytoplankton for nutrients. High algal abundances observed in the Chattahoochee are also unexpected since it traditionally contains lower nutrient loads than the Flint (Waters et al., 2015). The Chattahoochee is a highly regulated river with a high number of wastewater treatment plants and multiple "run-of-the-river" reservoirs that promote increased algal abundance. Additionally, *Hydrilla* was not present in the Chattahoochee to compete with phytoplankton for nutrients, further supporting the increased abundance observed in the Chattahoochee.

Hydrilla's Effects on Phytoplankton Community Structure

Zeaxanthin + lutein cannot be successfully separated in our HPLC with our methods. However, these pigments were found in high abundance throughout the study and are thought to primarily consist of lutein (green algae) due to the high abundance of chlorophyll-b and minimal abundance of cyanobacterium pigments. Phytoplankton communities varied down the longitudinal gradient in Lake Seminole with a culminating dominance of green algae for the entire reservoir. In Lake Seminole, the riverine region lacks *Hydrilla* and is used as a comparison to the transitional zone regarding the effects of the macrophyte on phytoplankton community structure. Nevertheless pigments in the riverine region indicate a community structure dominated by green algae, cryptophytes, and silicious algae (Figure 2.8). From riverine to transition zones, pigment analysis suggest that green algae dominate, but silicious algae increases in abundance while cryptophytes remain relatively stable suggesting that *Hydrilla* influences the growth of silicious algae (Figure 2.8). PCA analysis shows a negative ordination with flow suggesting that when flow rates decrease in the transitional and lacustrine region, algal pigments increase (Figure 2.9). Decreases in turbidity and light availability in *Hydrilla* beds support the similar abundance of cryptophytes seen in riverine and transitional zones. PCA also shows a strong positive ordination of algal growth with temperature, pH, and presence of *Hydrilla* (Figure 2.9), which is expected. pH is most likely ordinated with PC2 (composed of myxoxanthophyll and fucoxanthin) (Figure 2.6) because these pigments were in highest abundance when *Hydrilla* was present. As a result, absorption of CO_2 by *Hydrilla* and phytoplankton for photosynthesis decreases acidity (Shivers 2010) supporting the observed increased pH levels when PC2 pigments were measured. In addition, many diatoms are adapted to the low light conditions (Wetzel 1983) that *Hydrilla* provides, supporting the increase in silicious algae seen at the transition.

Cyanobacteria and silicious algae (PC2) are less ordinated with temperature than overall production and degradation (PC1) with PC2 being influenced almost equally by flow and temperature, suggesting that *Hydrilla* could play an indirect role in the growth of phytoplankton representing PC2. In addition, *Hydrilla* along with myxoxanthophyll is absent from the Chattahoochee river, further supporting the indication that *Hydrilla* influences cyanobacteria and diatom growth. Phytoplankton diversity throughout the study remained static, varying only during minute appearances of cyanobacteria at the transition (Figure 2.8). The Flint River and Spring Creek are both known to contain high levels of agriculture runoff (Waters et al., 2015) that are rich in nutrients to support the presence of organisms producing myxoxanthophyll during highly productive months. The dam region contains a community structure identical to the riverine zone with a dominance of green algae, cryptophytes, and silicious algae in which these pigments all peak in abundance here (Figure 2.8) due to changes in flow rates and turbidity from the presence or absence of *Hydrilla*.

Hydrilla verticillata Effects on Algal Degradation

Average degradation abundance in the transitional zone increased from riverine zones (Figure 2.4) most likely due to decreased flow rates, allowing for longer retention time of algae. Increased exposure to ultraviolet radiation due to less turbidity with the addition of degraded algae that have travelled from up-reservoir also support higher degradation down-reservoir (Figure 2.7). *Hydrilla* helps to increase degradation in the transition by further decreasing flow rates, providing increased light irradiance. In addition, zooplankton potentially increase in abundance within dense beds of *Hydrilla verticillata* (Schmitz & Osborne 1984). Zooplankton commonly feed on algae, leading to the increased abundance of zooplankton fecal pellets, and thus an increase in pyropheophorbide abundance (Figure 2.8), when *Hydrilla verticillata* is present in the lake. While degradation abundance increases down the longitudinal gradient (Figure 2.7), dead material to living material ratios oscillate without a corresponding steady increase as might be expected. The oscillation reveals that the transitional region contains the highest relative abundance of living material in the reservoir (Table 2.5 and Figure 2.2). This indicates that *Hydrilla*, rather than temperature, may influence degradation while simultaneously stimulating phytoplankton growth, further supporting the magnifying effect of *Hydrilla* on phytoplankton growth. Furthermore from dead/living ratios, the reservoir is mainly composed of degradation products when *Hydrilla* is absent from the lake (Table 2.5), indicating overall decreased productivity in the lake when temperatures are lower, which is expected, and when *Hydrilla* absent.

Conclusion

The differing land-uses surrounding the river inflows and seasonally dense coverage of *Hydrilla verticillata* presents Lake Seminole as a prime site for natural experimental study. In the current experiments algal photopigments collected over a 2-year period were analyzed to determine the effects that the invasive macrophyte, *Hydrilla* *verticillata,* has on phytoplankton abundance and community structure along a longitudinal gradient in Lake Seminole. *Hydrilla* is concluded to magnify phytoplankton abundance by slowing flow rates and increasing nutrient sedimentation. With *Hydrilla* slowing flow rates, the plunge point is retained in the transitional zone, supporting algal productivity by increasing light availability and decrease of flow rates. During *Hydrilla* deficient periods, the plunge point is extended to the lacustrine region (as seen in the Chattahoochee River), supporting primary productivity further downstream. High productivity at the dam when *Hydrilla* is present is supported by the combined effects of autochthonous nutrient loads from DOM remineralization at the benthos and from the top water withdrawal mechanism from the dam that preserves nutrients at the dam. *Hydrilla* also increases diversity as observed by the minor growth of cyanbacterium in Spring Creek and Flint River that is maximized in *Hydrilla* beds.

As global temperatures continue to rise, invasive macrophytes like *Hydrilla* have the potential to spread further north and ultimately impact more waterways than is usually observed. This implication can have significant impacts on ecosystems and the economy due to increased efforts for management. The mere presence of *Hydrilla* appears to change the region of the reservoir in which primary productivity is highest. This implies that other reservoir systems could be altered significantly and possibly permanently upon occupation of an invasive macrophyte species such as *Hydrilla.* Long term research is required on reservoirs that have been occupied by invasive species such as *Hydrilla.* Although no cyanobacterium blooms were observed in this study, cyanobacteria abundance increased in *Hydrilla* beds, raising concern over potential toxic blooms in other systems that are affected by *Hydrilla*. Further research is required on the effects of *Hydrilla* on cyanobacterium growth.

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Chapter III

SPATIO-TEMPORAL EFFECTS OF LAND-USE PRACTICES ON PHYTOPLANKTON DYNAMICS IN A SHALLOW RESERVOIR

Abstract

Differing land-use practices deposit nutrients and other materials, either directly or indirectly, into the catchments of nearby rivers or lakes. As a result, reservoirs typically receive larger influxes of nutrients into their watershed than natural lakes due to their larger watersheds. Biotic and abiotic factors can alter the dynamics of these nutrient loads within aquatic systems, resulting in dynamic phytoplankton responses to the nutrient inputs. Photosynthetic pigments were measured in this study within the differing inflow rivers of Lake Seminole, GA, a large reservoir receiving inflows from two watersheds representing differing land uses (agriculture and urban/industrial) and flow regulation (run-of-the-river and highly fragmented). Comparisons of phytoplankton abundance and community structure were made that correlate with the differing land-use practices and nutrient loads. Results indicate that phytoplankton diversity remained stable while abundance varied between the two land-uses, with the urban/industrial watershed containing the highest abundance of pigments from phytoplankton, which is unexpected. In addition, two unique, episodic algal blooms are analyzed in response to nutrient loads and land-use. It is inferred that the dynamic input observed raises concern for other rivers experiencing inputs from highly urban or agricultural watersheds.

Introduction

Past research has convincingly demonstrated that alterations by humans to landscapes can seriously impact the trophic status, health, and benefits of the once unaltered land (Knight et al., 2003). The Environmental Protection Agency (EPA) reported in 2004 that approximately 44% of the streams, 64% of the lakes and 30% of the estuaries around the nation were impaired due to excessive nutrient loading, hydrologic modifications, urban and agricultural runoff and sewage input (EPA 2009). Examples of anthropogenic land-use changes include urbanization and agriculture in which the effluent and materials are either directly or indirectly deposited into rivers. Furthermore, watersheds dominated by agricultural or urban lands typically export nutrients at higher rates than undisturbed watersheds (Puckett 1995).

Nutrient composition in most rivers and lakes now reflects some degree of influence from urban and agricultural change (Ngoye & Machiwa 2004). These nutrient inputs increase the growth of primary producers thus altering the physical and chemical characteristics of the aquatic ecosystems. Abiotic dynamics such as hydrology and physical charactersistics of the catchment can also influence nutrient loads (Li et al., 2008 and Migliaccio et al., 2007). Additionally, shifts in hydrologic regimes, such as a change from drought to flood conditions, result in a change in the primary transport mechanism for nutrient input into the receiving water (Meixner et al., 2007). Runoff and drainage often become the dominant mechanism for nutrient input during high flows (Burns et al., 2003).

Reservoirs receive larger amounts of nutrients compared to natural lakes as their watersheds are typically much larger (Wetzel 1990). Because of the influence of stream inflows, reservoirs exhibit pronounced gradients in light and nutrients, resulting in rapid changes in the distribution of photosynthetic organisms (Kimmel et al., 1990). Reservoirs usually contain a wide array of nutrients which directly influence phytoplankton community structure (Happey-Wood, 1988). Consequently, phytoplankton are frequently utilized to assess water quality because each group exhibits characteristics that may reflect the current condition of the ecosystem (Paerl et al., 2003). Examining temporal phytoplankton dynamics in reservoirs lends insight into the water quality as well as the influences that river inflows have on abundance and community structure.

Biotic stressors can incur profound effects on nutrient dynamics. For example, trophic cascading and nutrient loading models are complementary wherein productivity at all trophic levels is set by nutrient supply and is dependent on the recycling of nutrients (Carpenter et al., 1985). Additionally, the presence or absence of top predators can alter the primary production in lakes due to top-down trophic cascade events (Carpenter et al., 1985). Invasive macrophytes, like *Hydrilla verticillata*, can sequester large amounts of phosphorus from the water column thus altering biogeochemical dynamics in a system (Gu 2006; McEntire 2009; Waters et al., 2015). Bivalves, both native and invasive, can filter organic matter, algae and other seston changing water clarity and provide a connection between benthic and pelagic areas (Patrick 2015; Scheffer 2004). Benthic algae and cyanobacteria can also fix nitrogen and stabilize sediments (Waters et al., 2015).

Few studies exist on the effects of watershed land-use and phytoplankton dynamics in reservoirs of the southeastern United States. Due to the numerous biotic and abiotic factors in reservoirs that can affect phytoplankton, there is a need for investigations where phytoplankton dynamics can be placed in context to land use, hydrologic change, and biota. This study was conducted to analyze spatial and temporal phytoplankton dynamics in response to differing land use practices of a reservoir in southwestern Georgia, United States. To complete this study, three objectives were investigated:

1) What is the effect of watershed land-use on phytoplankton abundance?
2) What is the effect of watershed land-use on phytoplankton community structure?
3) What are the environmental or anthropogenic drivers of two episodic algal blooms observed in Lake Seminole?

Methods

Study Site

Lake Seminole (Figure 3.1) is a large and shallow reservoir in southwestern Georgia with a surface area of 152 km^2, mean depth of 3m and a maximum depth of 10m (Sammons & Maceina 2005). Uses for the reservoir consist of navigation, hydroelectric power generation, and recreation. Large beds of the submerged aquatic macrophyte *Hydrilla verticillata,* which can account for over 50% of the reservoir's area are seasonally abundant (Gholson 1984). The reservoir is part of the Apalachicola-Flint-Chattahoochee (ACF) River Basin, which spans through Georgia, Florida, and Alabama and drains an area of 51,800 km^2 (Frick et al., 1998). Lake Seminole is at the confluence of the three rivers making up the ACF (Figure 3.1) with the Chattahoochee River and Flint River joining to form the Apalachicola River. The Flint River and Chattahoochee

River headwaters begin in the upper ACF basin south of Atlanta and in north Georgia, respectively.

Although the two rivers are similar regarding geologic position, they differ in land use and human populations, as well as the number of dams, sewage treatment discharges and hydrological variability (McEntire 2009). The Chattahoochee is known for its higher density of urbanization from Atlanta and Columbus, Georgia, and contains 169 wastewater treatment plants, four large reservoirs, and nine low storage "run-of-the-river" reservoirs (Table 3.1). The Flint River has only two "run-of-the-river" reservoirs and Spring Creek's (a former tributary of the Flint) flow is unimpeded (Frick et al., 1996; Abbott 2005) (Table 3.1). Agricultural practices account for 49% of the land use in the lower ACF and are predominantly located around the Flint River and Spring Creek corridors (Frick et al., 1996). The Flint/SC watershed contains significantly higher loads of nitrate and, while not significant, the Chattahoochee contained higher phosphate loads (Table 3.2). pH varies more in the Chattahoochee although average pH is not significantly different from the Flint/SC watershed (Table 3.2). Average nutrient loads measured in the summer seasons for the 2 inflow watersheds are given in Table 2.2.

For Spring Creek and the Flint River, base flows are provided by the Upper Floridan aquifer whereas the Chattahoochee River's base flow is determined by the Army Corps of Engineers operation of reservoir release at dams. Average flow rates for each inflow and year are given in Table 3.3. Lake Seminole discharges at the Jim Woodruff Lock and Dam forming the Apalachicola River, which runs unimpeded into the Gulf of Mexico at Apalachicola Bay. Apalachicola Bay is a crucial fishery for the state of

Florida and the United States containing 90% of Florida's and 10% of the United States' oyster industry (Oczkowski et al., 2011).

Field Collection

Samples from 277 water column locations from various depths were collected usually monthly over the course of 2 years from seven different sampling sites (Figure 2.1) on Lake Seminole as part of the monthly water quality monitoring plan by the Joseph Jones Ecological Research Center; June 2012 – August 2014. Only surficial and mid depth samples (up to 2m) were included in the study since deeper samples were compromised by the beds of *Hydrilla verticillata* which increase light attenuation. Sample stations that included more than one sample were averaged to generate a single value. The stations included are four riverine stations, three transitional, and one lacustrine station (Figure 3.1). Figure 3.1 shows only three riverine sites however the fourth is located at the beginning of the Apalachicola River at the dam. Therefore, this riverine site is analyzed as a dam site. Months where no samples were collected are July and November of 2012, along with January and December 2013 and February 2014, and are excluded from analysis. Whole water samples were filtered at the Joseph Jones Ecological Research Center immediately after sampling, and the filters containing all seston material were placed in aluminum foil to prevent UV decay of pigments, and stored in a freezer at -20° C. The samples were analyzed for pigment type and concentration via High Performance Liquid Chromatography (HPLC). Nutrient data was collected on site via YSI meter and from www.waterwatch.usgs.gov from gauge 02356000 in Georgia. No nutrient data were collected for the dam site, therefore only data measured from USGS gauges at the dam were used which only consist of flow rate (m^3s^{-1}), rain (cm), and temperature (C^o).

Photosynthetic Pigment Analysis

Photosynthetic pigments (carotenoids and chlorophylls) were measured by an HPLC system using the methods of Leavitt and Hodgson (2001) and Waters et al., (2012). The filter samples were extracted using a solvent mixture (80% acetone, 15% methanol, and 5% HPLC grade H_2O) and injected into a Shimadzu HPLC system using the mobile phase and time sequence of Leavitt and Hodgson (2001). Chlorophylls and carotenoids were separated by passing through a Phenomenex Luna C18 column and measured using a photodiode array detector set at 435 nm for carotenoids and a fluorescence detector for chlorophylls. Pigment identification was made using retention times of known standards and pigment specific spectra recorded by the detectors (Waters et al., 2012). Pigment associations with various algal and cyanobacteria groups were based on pigment measurements from known plankton cultures (Leavitt & Hodgson 2001) (Table 3.4). The pigments scytonemin and peridinin are used qualitatively due to a lack of standard for these pigments.

Statistical Analysis

Statistical analysis includes regression and multivariate analyses to determine any spatial and temporal variances of phytoplankton dynamics via the different land-use practices specific to each region of Lake Seminole. In terms of calculating algal abundances, the stations that compose each arm or region were averaged. For example, the Flint/Spring Creek (SC) arm is composed of four sampling stations in which the pigment values of all four stations are averaged to calculate pigment abundance values for this arm of Lake Seminole. The Chattahoochee arm and dam site each contain two sampling stations. Outliers due to algal blooms were determined by the Thompson tau outlier test resulting in two samples being removed from analysis: December 2012 of the transitional site on the Flint River and March 2014 of the riverine site of Spring Creek.

Results

Spatial Dynamics of Phytoplankton Abundance

Average primary producer abundance (PPA) is highest in the Chattahoochee arm and a *t* test reveals no significant difference in values from the dam region ($p < 0.05$). The Flint/SC arms contained the lowest PPA (Table 3.5 and Figure 3.2) which is significantly different from the Chattahoochee and Dam sites ($p > 0.05$). Average chlorophyll values are highest in the Chattahoochee although not significantly different in all regions measured (Table 3.5). Ratios of average total degradation to chlorophyll pigments show that the Flint/SC arms contain the lowest ratio with 0.47 and the dam region holding the highest living/dead ratio at 0.73 (Table 3.5). The dam region contains the highest average total degradation in which the *t* test reveals no significant difference in values with the Chattahoochee ($p < 0.05$) (Table 3.5 and Figure 3.2). The Flint/SC arms experience the least degradation (Table 3.5 and Figure 3.2).

Temporal Dynamics of Phytoplankton Abundance

Temporally, the three arms experienced similar oscillations in PPA, increasing in warmer months and decreasing in cooler months (Figure 3.3). For 2012, the Chattahoochee contained the highest PPA in summer and fall with the Flint/SC arms surpassing the Chattahoochee in winter (Figure 3.3). In 2013, the dam site contained the highest PPA in all seasons. The Chattahoochee contained higher average PPA than

Flint/SC within each season in 2013 except for fall. Although PPA is higher in Flint/SC than Chattahoochee for fall 2013, *t* test confirms no significant difference in values between the two arms ($p < 0.05$). The Chattahoochee arm had the highest PPA in 2014 with the Flint/SC arms containing the least PPA (Figure 3.3). The most productive seasons in the study were summer 2012 and summer 2014 which showed no significant difference in PPA for each season ($p < 0.05$) (Figure 3.4). The least productive season of the study is winter 2012.

Comparing the summer season of each year in the study, PPA was variable for each region of the reservoir over the course of the study, however no significant difference in value is seen between Flint/SC and the dam region in summer 2012 (Figure 3.4). The Chattahoochee contained the highest PPA for the summers of 2012 and 2014 and the dam region was highest in 2013 (Figure 3.4). Dead to living material ratios show stable ratios for the Flint and SC regions throughout the study with the Chattahoochee and dam regions varying significantly (Table 3.6). The Chattahoochee had the highest dead/living ratio in summer 2012 with the dam at the highest in summer 2013 and 2014 (Table 3.6). The Flint and SC's dead/living ratio is the lowest of the three regions throughout the study and showed no significant difference from the dam in summer 2012 (Table 3.6).

Phytoplankton Community Structure: The Chattahoochee Arm

The majority of the Chattahoochee arm's community structure is comprised of chlorophyll-a and its degradation product chlorophyllide, contributing 39.89% and 30.12% to the total algal abundance of the Chattahoochee arm. Carotenoids that comprise a smaller portion of the community structure are zeaxanthin + lutein, alloxanthin, and neoxanthin with 15.94 %, 3.042%, and 1.75% respectively. Chlorophyll-b is highest in the Chattahoochee contributing 8.62% to the abundance of the arm. The degradation product pheophorbide contributes minimal amounts to the community structure of the Chattahoochee although it is highest in this arm. PCA analysis was conducted ordinating pigments to sampling sites, and the principal components were saved as variables (Chatt PC1 and Chatt PC2) (Figures 3.6a and 3.6b). PC1 is composed mainly of zeaxanthin + lutein, neoxanthin, chlorophyll-b, and beta-carotene with PC2 comprising degradation products and minor influences from fucoxanthin. PC1 positively ordinates with temperature and PC2 positively ordinates with pH. Both principal components negatively ordinate with rain, flow, and organic nitrogen (Figure 3.6b).

Phytoplankton Community Structure: The Flint River and Spring Creek Arms

Pigments measured from Flint/SC resulted in the most diverse community structure of the three regions (Figure 3.5). Chlorophyll-a and chlorophyllide contributed the most in terms of abundance to the Flint/SC arms with 41.62% and 19.86%, respectively. Zeaxanthin + lutein comprises 15.15% of the arms with chlorophyll-b and fucoxanthin contributing 10.62% and 2.84%, respectively. The rest of the pigments contribute minimal amounts to community structure (2% or less). Pigment values for Flint/SC are not significantly different from the other two regions except for alloxanthin, zeaxanthin + lutein, and chlorophyllide. Scytonemin and peridinin were in highest abundance in these arms. PCA analysis was conducted on the pigment values for the Flint/SC arms and saved as variables (FSC PC1 and FSC PC2) (Figures 3.7a and 3.7b). PC1 is composed mainly of chlorophyll-a, chlorophyll-b, beta-carotene, and chlorophyllide with minor influences from fucoxanthin and pheophytin-a and strongly ordinates with temperature (Figures 3.7a and 3.7b). PC2 is explained by myxoxanthophyll and diatoxanthin with minor influences from degradation pigments and weakly ordinates with ammonia, organic nitrogen, and organic carbon (Figures 3.7a and 3.7b).

Phytoplankton Community Structure: The Dam Region

The dominant pigments in the dam region are pheophytin-a and fucoxanthin, contributing 39.70% and 30.53%, respectively, to the total pigment abundance in the dam region (Figure 3.5). Other carotenoids that are highest in the dam zone are beta-carotene and diatoxanthin, comprising 15.05% and 2.36% of the total abundance. Three degradation pigments were highest in the dam zone: pheophytin-b, pheophytin-a, and pyropheophorbide. *T* tests show no significant difference in values ($p < 0.05$) between all pigments in the dam region and Chattahoochee arm except for pyropheophorbide, highest in the dam zone. Pigments were ordinated on their respective sampling sites and the principal components were saved as variables (Dam PC1 and Dam PC2) (Figures 3.8a and 3.8b), then ordinated against abiotic factors measured for the dam region. Dam PC1 is comprised of mainly carotenoids and chlorophyll-a with Dam PC2 composed mainly of fucoxanthin and minor influences from degradation products (Figure 3.8a). PC1 strongly ordinates with temperature and PC2 strongly ordinates with flow with minor influences from rain (Figure3.8b).

Algal Blooms in the Flint and Spring Creek Arms

The statistical outliers December 2012 from the Flint River's transitional region (FlintH) and March 2014 from the riverine region of Spring Creek (Spring253) both exhibit a significant increase in abundance of all pigments except myxoxanthophyll during the bloom months (Tables 6.1 and 6.2). Table 3.7 shows the FlintH bloom values in December 2012 correlated with ammonia loads. Fucoxanthin, chlorophyllide, and diatoxanthin showed the most significant increases in abundance during the December 2012 bloom (at $p < 0.05$). Table 3.8 shows the algal bloom that occurred in Spring253. Large increases in fucoxanthin, diatoxanthin, and zeaxanthin + lutein were observed. No nutrient data gathered shows any significant correlation with the values for the March 2014 bloom.

Discussion

This study utilized a large shallow reservoir as a natural experiment to analyze the differences of watershed land-use on phytoplankton abundance and community structure. The data show differences in the algal abundance and community structure of each arm in Lake Seminole accompanied by the biotic and abiotic drivers that correlate with increased productivity. The decreased abundance in the Flint/SC arms is intriguing as Waters et al. (2015) shows this arm of the reservoir to contain high sedimentary phosphorus capable of internal loading. The two algal blooms in the Flint/SC arms suggest episodic internal nutrient loading and allochthonous nutrient inputs from surrounding agricultural practices as the drivers of blooms.

Biotic and Abiotic Factors Influencing Algal Abundance and Degradation

Overall phytoplankton abundance in the Flint/SC region is lower than the Chattahoochee (Figure 3.2) which is the opposite from what is expected since agricultural watersheds are expected to promote higher algal abundance due to higher nutrient loads (Waters et al., 2015; Carpenter et al., 1998; and Allan 2004). The Chattahoochee appears to be primarily affected by various abiotic stressors such as river/watershed management practices and turbidity while the Flint/SC is mainly influenced by biotic stressors such as the presence of benthic cyanobacteria, macrophytes, and invasive clams.

The industrially fragmented Chattahoochee contains higher PO_4 loads and phytoplankton abundance that can be attributed to several abiotic mechanisms. First, the Chattahoochee contains 13 up-stream reservoirs promoting increased algal productivity in these lacustrine conditions (Thornton et al., 1990) that act as an algal seeding mechanism into Lake Seminole upon dam release. The release of water from these upstream reservoirs can also resuspend nutrients that increase availability to algae and increase turbidity (Waters et al., 2015). PCA analysis supports this conclusion as phosphorus loads are highly ordinated with TSS (Figure 3.6b), an influx of materials during productive periods. In addition, material input from industrial and municipal installations deposit large quantities of silt (Waters et al., 2015), supporting increased turbidity in the Chattahoochee. As a result, increased turbidity can favor phytoplankton species capable of living in the water column over benthic primary producers (Dzialowski et al., 2008). Second, the lack of biotic competitors such as *Hydrilla verticillata* and *Lyngbya* in the Chattahoochee supports the increased PO_4 loads measured due to the lack of nutrient absorption by these biota. Additionally, *Corbicula* is present in the macrophyte-free Chattahoochee further supporting increased nutrient loads due to sediment resuspension via bioturbation by the clam. Third, the Chattahoochee receives large amounts of treated sewage water from over 160 wastewater treatment plants that promote algal growth in the river and support allochthonous nutrient loading in the reservoir.

The decreased PO_4 loads and algal abundance measured in the agriculturally dominated Flint River and Spring Creek are supported by multiple mechanisms. First, the nutrients available here are primarily utilized by benthic and macro biota as these rivers contained dense, seasonal beds of *Hydrilla* and *Lyngbya* along with populations of *Corbicula* in macrophyte free areas year round. Subsequently, all of these biota are known to sequester large amounts of nutrients. Second, the Flint River and Spring Creek lack large numbers of dams and as a result experience decreased water retention. This free flowing nature allows for more deposition of materials, an oxygenated environment, and increased benthic primary productivity.

Pigment abundance values between the Chattahoochee and dam site are not significantly different which is expected since the dam mixes the two sites and flow is dominated by the Chattahoochee. Ratios of total degradation to chlorophyll pigments show that the Flint/SC has a lower ratio of dead to living seston material than the Chattahoochee and dam region. This indicates a higher relative abundance of living seston in Flint/SC than the Chattahoochee and dam. Degradation in the Chattahoochee and dam can also be attributed to the presence/absence of *Hydrilla* (see Chapter 2) in which its presence in the Flint/SC region provides a sanctuary for phytoplankton from intense UV radiation and zooplankton predation. Since the Chattahoochee did not contain significant macrophyte coverage for most of the study, materials accumulated faster in the dam site than the *Hydrilla* occupied Flint/SC arms which is expected. This is consistent with the data as the ratio of total degradation to chlorophyll is highest in the dam region and PCA analysis strongly ordinates principal component 2 (comprised of degradation products) with flow (Table 3.5 and Figure 3.8b).

Effects of River Flow on Algal Abundance in Lake Seminole

Flow rates are continually higher in the Chattahoochee than Flint/SC unless under drought conditions in which the Flint dominates (Couch et al 1996). Nutrient resuspension events are likely to occur in the Chattahoochee arm as flow rates increase because of the shallow depths (Waters et al., 2015). Linear regression models indicate a negative correlation between summer pigment abundance and summer flow rates within each arm which is expected since these inflows are characteristic of high flushing rates. However a significant positive relationship occurs in the dam area with $r^2 = 0.51$ and $p = 0.03$, indicating that algal abundance increases at the dam during increased flows (Figures 3.3 and 3.8b). Flows are typically slowest at the dam region, supporting a condensed algal population collected from the mixing of each arm comprising the reservoir. Biotic factors such as *Hydrilla* in the Flint/SC arms may decrease flow (Schulz et al., 2003; Sollie & Verhoeven 2008), suggesting that material from these arms are reaching the dam area less rapidly than the Chattahoochee. Linear regression analysis indicates opposing correlations of summer nutrient loads with summer flow rates for each arm with a strong positive correlation in the Chattahoochee with NO_3 loads and a negative weak correlation with PO_4 loads with $r^2 = 0.90$ and $p = 0.21$ and $r^2 = 0.25$ and $p = 0.66$ respectively. Conversely, the Flint/SC arms show opposite flow to nutrient correlations as the Chattahoochee, with a strong positive correlation with summer PO_4 loads and a weak negative correlation with summer NO_3 at $R^2 = 0.96$ and $p = .12$ and $R^2 = 0.35$ and $p = 0.60$ respectively. PCA analysis also reflects these correlations (Figures 3.6b and 3.7b). This is expected as increased flow rates are thought to deliver large amounts of nutrients from upstream (Waters et al., 2015). However measurements here show P loads in

Flint/SC increasing and N loads decreasing with flow and vice versa for the Chattahoochee suggesting differing nutrient limitations for each arm.

Phytoplankton Community Structure: The Chattahoochee Arm

Separating zeaxanthin + lutein in the methods used was not possible and due to the presence of chlorophyll-b and very low abundance of cyanobacteria measured, zeaxanthin + lutein is assumed to be primarily comprised of lutein indicating green algae. Based on pigment concentrations, the community structure for the Chattahoochee arm of Lake Seminole consists of green algae and cryptophytes. In a previous paleolimnology study, diatoms and cryptophytes were found to be the dominant algal producers in sediment cores collected from the Chattahoochee arm (Waters et al., 2015). Cryptophytes are tolerant to turbid conditions (Reynolds 2006) and PCA analysis shows P loads strongly ordinated with increases in total suspended solids (Figure 3.6b), supporting the presence of cryptophytes. Waters et al., (2015) conducted supplemental testing for alloxanthin and diatoxanthin from *Hydrilla,* finding the community structure to be the same as to what was currently living in the lake. *Hydrilla* in this region was absent for most of the present study, suggesting the presence of *Hydrilla* to promote diatom growth and the absence to promote chlorophyte growth in the Chattahoochee.

The Flint River and Spring Creek Arms

The prominence of zeaxanthin + lutein, chlorophyll-b, and fucoxanthin indicates the main algal producers in the Flint/SC arms to be green algae and diatoms. Diatoms are particularly sensitive to fluctuations in nutrients (Hockin et al., 2012) and were found to be associated with *Hydrilla verticillata* (Waters et al., 2015) which was seasonally abundant in these arms during the study. Since these arms are surrounded by mainly agricultural practices, large influxes of nutrients are expected and reflected in our nutrient data. Phytoplankton diversity in Lake Seminole remained static except for very small concentrations of myxoxanthophyll found only in Flint/SC arms which is weakly correlated with influxes of nutrients (Figure 3.7b, FSC PC2). The Flint/SC arm is known to contain extensive communities of benthic primary producers consisting of Lyngbya and a few other species (Waters et al., 2015). My data support this inference with lower phytoplankton pigments measured in the water column and the presence of scytonemin in my samples indicating the presence of benthic cyanobacteria (Waters et al., 2013). As a result, the lower levels of phytoplankton in the Flint/SC do not indicate a lack of productivity in the arm, but support the primary productivity to be driven by benthic primary producers and macrophytes instead of phytoplankton.

The Dam Region

Diatoms are the dominant algal group present in the dam region which most likely originates from up-stream. Degradation is also prominent in this zone and could be related to flow based on the strong ordination of flow with Dam PC2, which is composed of diatoms and degradation. Temperature explains the majority of variation in algal productivity in the dam region (Dam PC1, Figure 3.8b), which is expected as the lacustrine conditions of the dam region provide more light availability and decreased flows for phytoplankton growth and reproduction (Thornton et al., 1990).

The Flint River Algal Bloom

Pigment concentrations indicate that the algal bloom occurring in December 2012 is mainly composed of diatoms due to the significant increase in fucoxanthin and diatoxanthin. Diatoms require nitrogen for growth (Gilpin 2003) and respond rapidly to influxes of nitrogen (Hockin et al., 2012). Multiple mechanisms are potentially supporting this episodic bloom. First, ammonia is inferred to be the source of the bloom as loads increase substantially on the bloom date and highly correlate with fucoxanthin ($R^2 = 0.98$ and $p = 1.19E-18$). Sources of ammonia loads could occur from internal loading in the Flint arm as the presence of *Hydrilla verticillata* decreases flow rates and increases sedimentation of nutrients (Waters et al., 2015). Second, precipitation data show that the area received significant rainfall (~2.5 cm) just a few days before the bloom. As a result, the intense rainfall can stir sediments and resuspend nutrients. Furthermore, the Flint watershed was experiencing a drought prior to the bloom. Also, the rainfall could have flushed nutrients that have accumulated during the drought from surrounding agriculture fields resulting in the large influx of nutrients that were observed in the Flint. Third, migratory waterfowl also arrived in this area at this time and nitrogenous wastes could account for the increased loads.

The Spring Creek Algal Bloom

Diatoms and green algae compose the algal bloom observed in Spring Creek March 2014. No nutrient data measured *in situ* shows any correlation with the bloom. Additionally, biotic and abiotic data collection was limited for Spring Creek. For example, supplemental parameters that were measured in other arms such as TSS, ammonia, organic carbon, total nitrogen, and turbidity were not measured in Spring Creek. This lack of nutrient data leaves the cause of this unique bloom to be unexplained, but it does show that blooms in the Flint/SC arms are more episodic than cyclical.

Conclusion

Lake Seminole provides a unique natural experiment due to the dynamic variation in the land-use practices of each river inflow combined with the biotic and abiotic dynamics within the reservoir. Algal photopigments were collected over a 2-year period to investigate the effects of differing land–use practices on phytoplankton abundance and community structure in a large, shallow reservoir, Lake Seminole. Lake Seminole is concluded to utilize both biotic and abiotic drivers to stimulate algal growth. In the urban/industrially fragmented Chattahoochee River, abiotic factors such as high flow and turbidity provide influxes of nutrients via up – stream sources and internal loading from sediments. Alternatively, biotic stressors such as the presence of invasive macrophytes, clams, and large mats of benthic cyanobacteria in the Flint River and Spring Creek promote algal growth through various mechanisms. The inferences that arise from this study are pertinent to other watersheds that may undergo urbanization or increased agricultural practices around the world.

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Chapter IV

CONCLUSION: A CONCEPTUAL MODEL OF LAKE SEMINOLE PHYTOPLANKTON

In Lake Seminole, phytoplankton communities respond to both anthropogenic and environmental stressors which are composed of either abiotic or biotic constituents. As a result, the major conclusions drawn from the previous chapters are diagrammed as conceptual models to help visualize the abiotic and biotic drivers of phytoplankton production in Lake Seminole (Figures 4.1 and 4.2). Changes in both external and internal processes can alter phytoplankton dynamics (Figures 4.1 and 4.2). In the Chattahoochee, abiotic factors are primarily driving phytoplankton production. These abiotic factors are composed of changes in flow regimes and land use reflecting urban/industrial effluent that ultimately results in changes in turbidity via silt loads (Figure 4.1). Changes in flow regimes result from climate changes in precipitation and anthropogenic dam release, driving flows and material delivery in the Chattahoochee River Basin. Furthermore, the varying flows alter the location of the plunge point, resulting in nutrient sedimentation that varies spatially along the longitudinal gradients of the three rivers contributing to the reservoir. In the Chattahoochee, the plunge point is directly influenced by flows due to the absence of dense stands of *Hydrilla* since 2012. Turbidity is increased from the abundant silt deposits delivered from urban/industrial land use practices, resulting in changes in the internal processes of the lake. Alterations to the internal processes of the lake directly impact other dynamics of the reservoir such as changes in nutrient loads and phytoplankton abundance. Increased turbidity results in decreased light availability for phytoplankton production. As result, cryptophytes, which are tolerant to low light conditions, grow in abundance in the Chattahoochee.

Biotic factors primarily drive phytoplankton production in the Flint River and Spring Creek (Figure 4.2). Organisms such as *Hydrilla, Lyngbya,* and *Corbicula* are present in these rivers and can absorb significant nutrient loads delivered from the agricultural watersheds. The presence of *Hydrilla* in these rivers allows for flows to decrease and alter the location of the plunge point. *Hydrilla* also prevents sediment resuspension and ultimately magnifies phytoplankton abundance at the transition of the reservoir. Alternatively when *Hydrilla* is absent, the plunge point extends further down–reservoir. When *Hydrilla* seasonally dies, increased DOC loads are released, decreasing light availability for phytoplankton. Furthermore, the prominent absence of dams in these rivers allows for the climate to manage flows (Figure 4.2), resulting in slow flows when compared to the Chattahoochee. It is apparent that the Flint arm has significant primary productivity due to the presence of *Hydrilla* and *Lyngbya.* Therefore while algal productivity is lower in the Flint than the Chattahoochee, overall primary productivity could easily be higher in the Flint.

This study aimed to understand the environmental and anthropogenic stressors that influence phytoplankton abundance and community structure in a large, shallow reservoir in southeastern Georgia, USA. Abiotic and biotic factors are shown to be drivers of phytoplankton production within varying degrees of environmental and anthropogenic stressors in Lake Seminole. As the climate continues to warm, northern reservoirs and lakes that are not affected by invasive macrophytes may soon become occupied by them. As a result, the flow regimes and nutrient dynamics of susceptible aquatic ecosystems are subject to change, raising concern over the ecological, economic, and municipal management of lakes and reservoirs. Each reservoir is different from the other, but current management methods are commonly focused on analyzing nutrient concentrations from grab samples and ignore other drivers of productivity such as turbidity or biotic factors. This research exhibits the need for management programs to consider other drivers of productivity. In addition, this study analyzed phytoplankton dynamics in a reservoir, however, further long term studies in large lakes are required to analyze differences between lakes and reservoirs regarding phytoplankton responses to environmental and anthropogenic stressors. Furthermore, this research shows that reservoir dynamics could be more complex and variable depending on a multitude of abiotic and biotic factors.

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Chapter III

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APPENDIX A:

Figures for Chapters 1 - 4

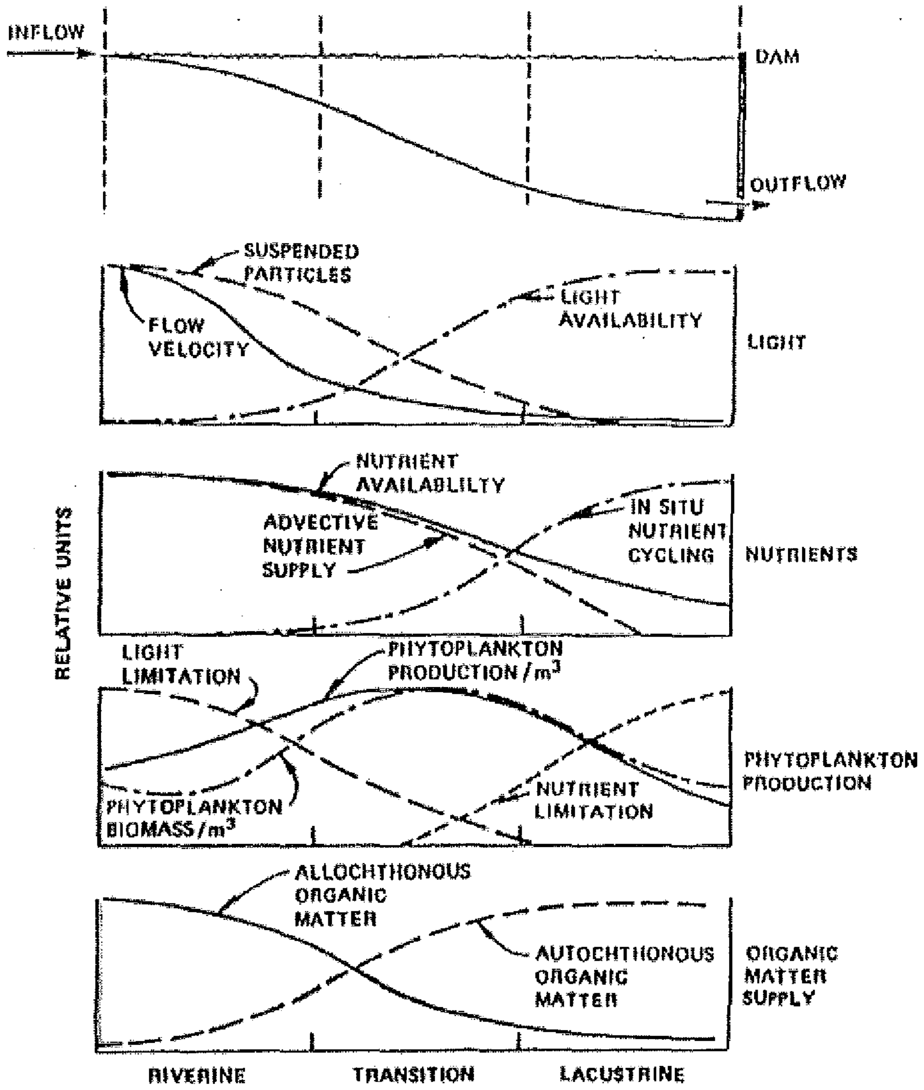

Figure 1.1: Typical longitudinal gradient dynamics in reservoirs. (From Thornton et al., 1990).

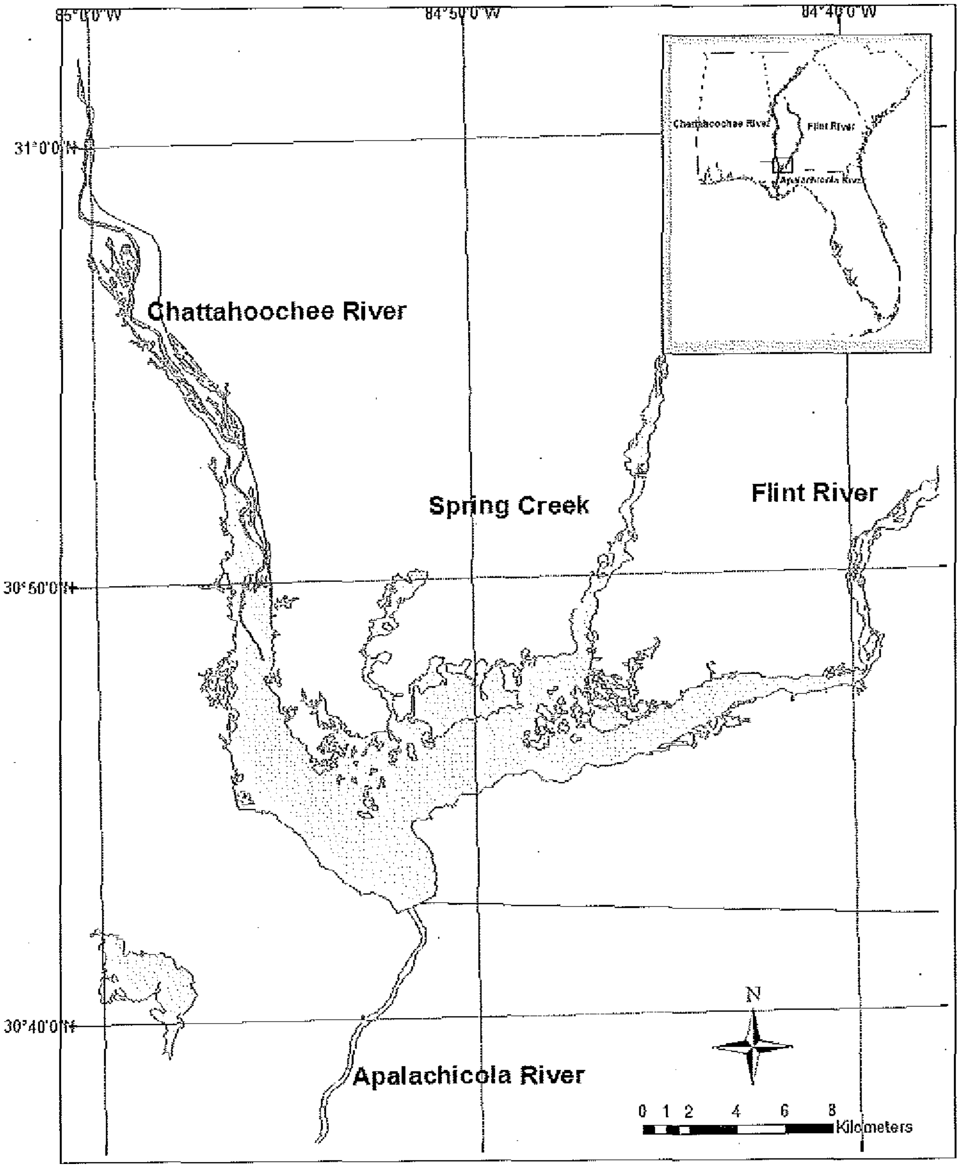

Figure 1.2: A map of Lake Seminole, GA, USA with corresponding river inflow and outflow rivers. (From Patrick 2015).

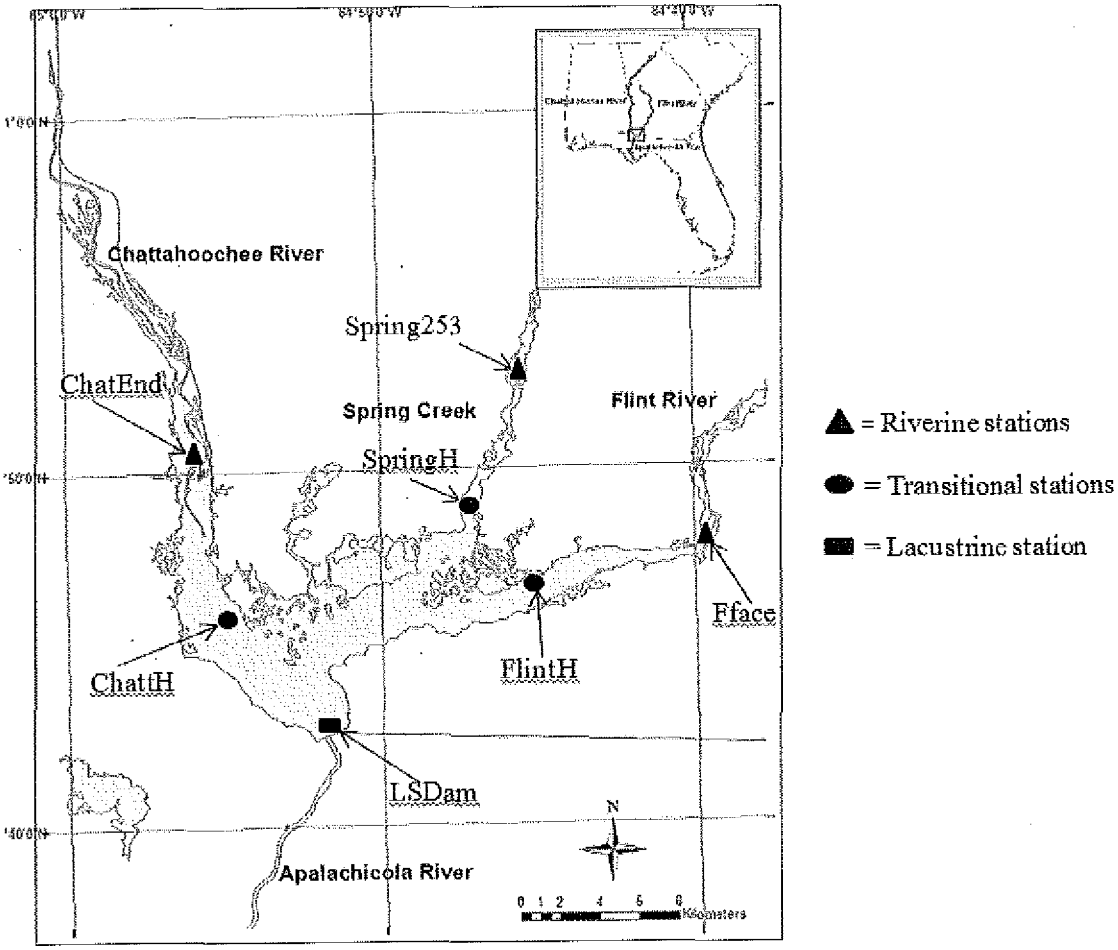

Figure 2.1: Lake Seminole with corresponding river inflows, single outflow at the Apalachicola River (From Patrick 2015), and sampling stations.

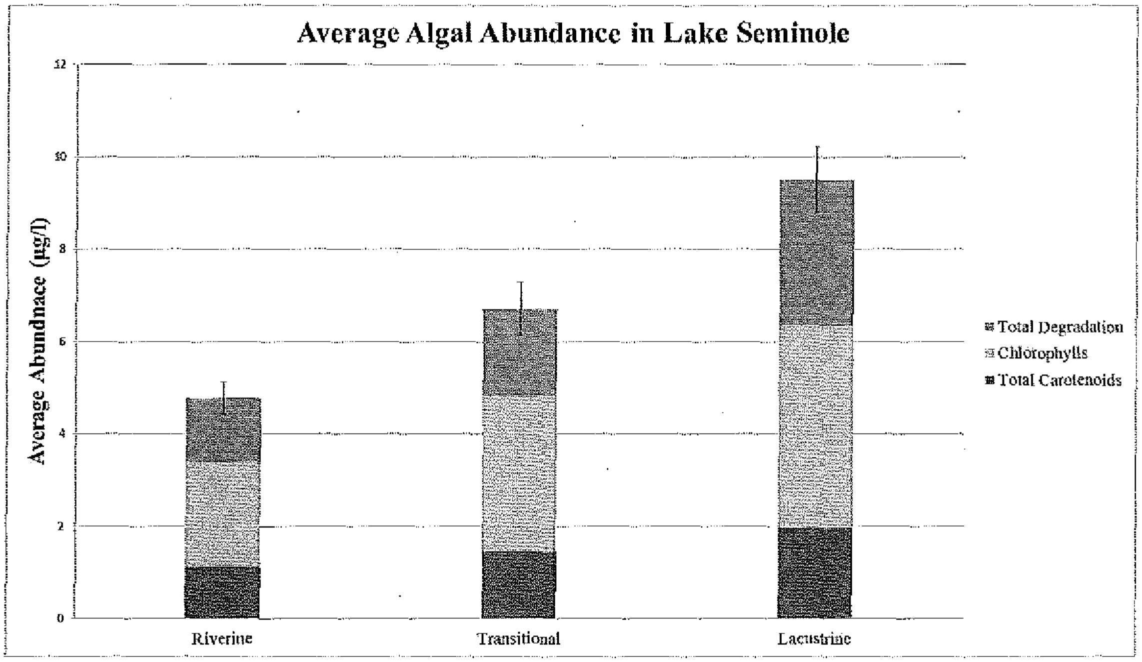

Figure 2.2: Average algal abundance in Lake Seminole by average abundances of total degradation, total carotenoids, and the total chlorophyll of the lake.

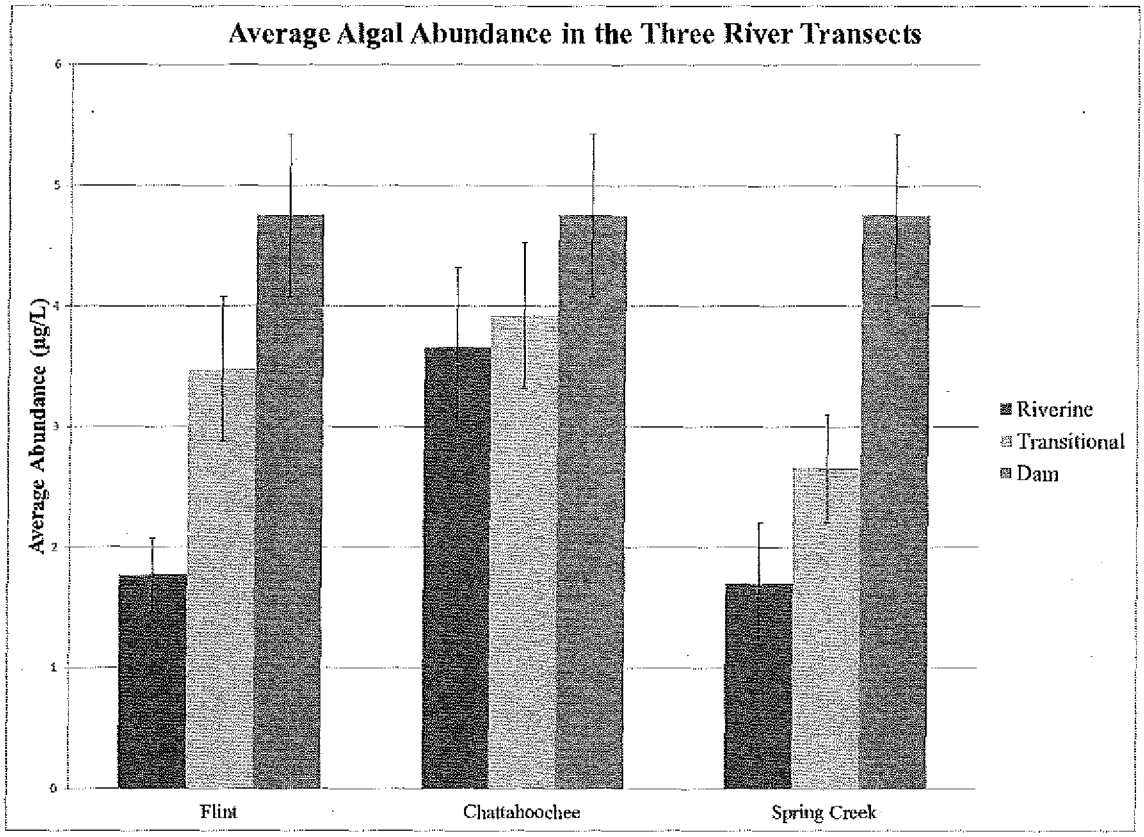

Figure 2.3: Average abundance of algae for the three transects of rivers that form Lake Seminole. PPA percent increase from riverine to transitional: Flint = 49.10%, Chattahoochee = 6.76%, and Spring Creek = 36.00%. PPA percent increase from riverine to lacustrine: Flint = 62.74%, Chattahoochee = 23.06%, Spring Creek = 64.22%.

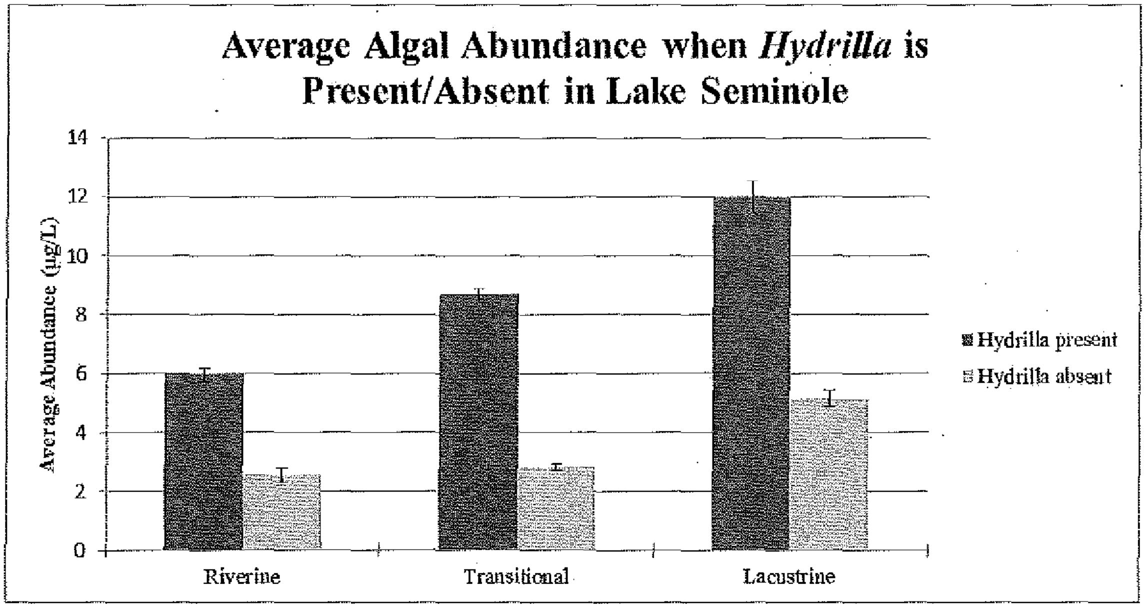

Figure 2.4: Average algal abundance in each region of the reservoir when *Hydrilla* is present/absent. Decreases in average abundance from when *Hydrilla* is present/absent: Riverine = 57%, Transitional = 67%, Lacustrine = 57%.

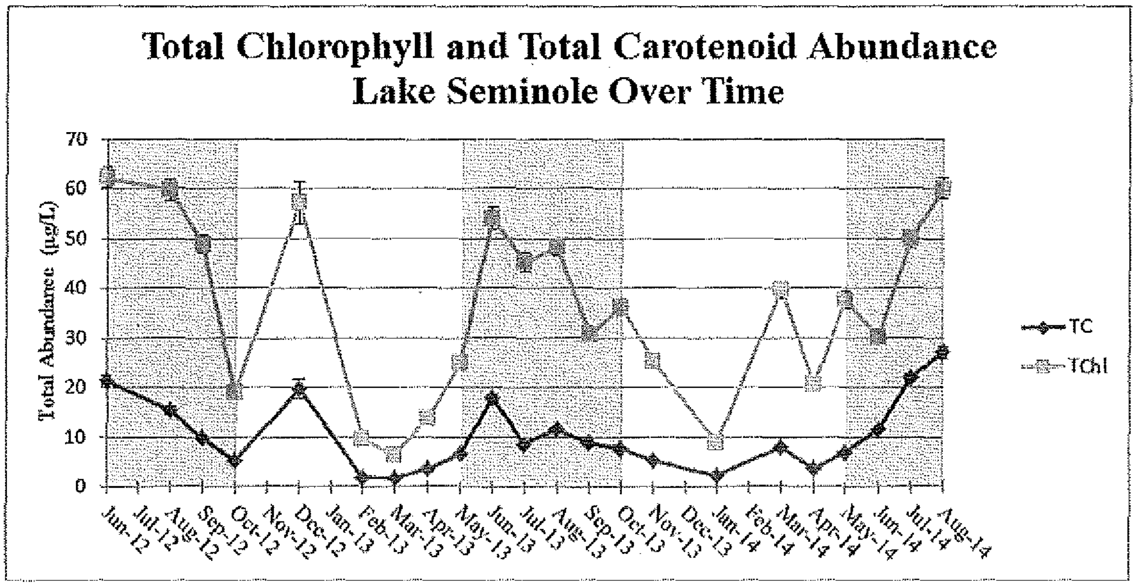

Figure 2.5: Sum of total chlorophyll and total carotenoid of all stations. Shaded areas represent temporal intervals in which *Hydrilla verticillata* is present in the lake. The Flint December 2012 algal bloom is included here.

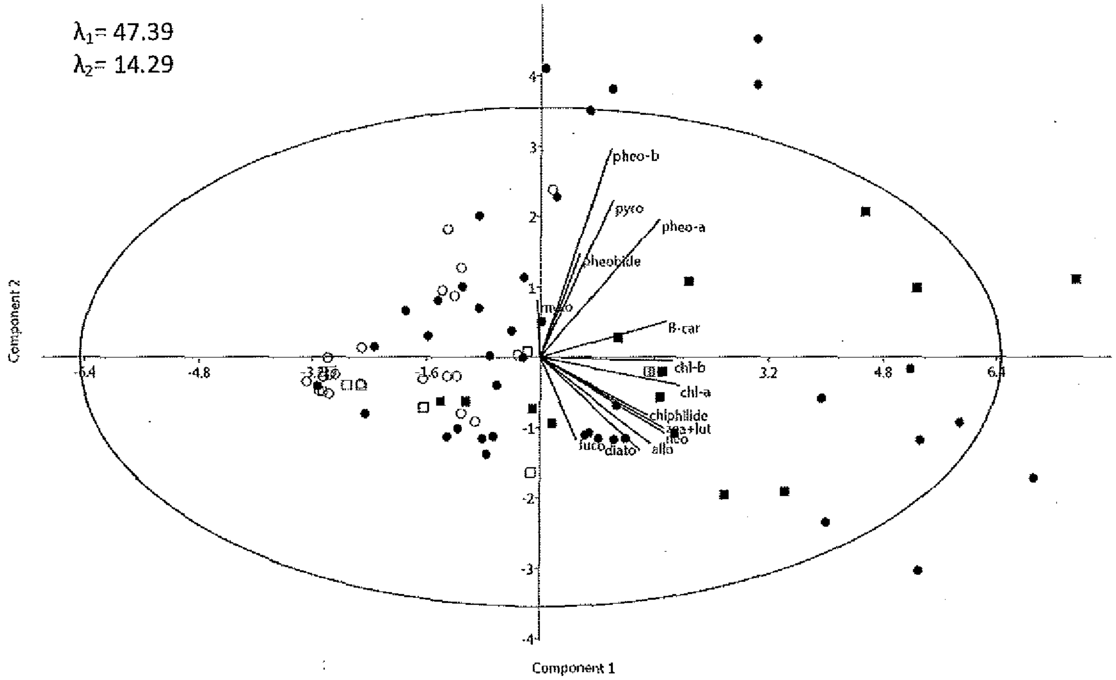

Figure 2.6: PCA plot of carotenoids and chlorophylls detected in the study among the transitional and lacustrine sites (riverine sites were not included due to the assumption that *Hydrilla* has no influence among them). December 2012 and August of 2012 and 2014 of FlintH are outliers and are excluded from this PCA. Circles are transitional samples and squares are lacustrine samples. Open shapes denote months that *Hydrilla* is absent from the lake, whereas filled shapes indicate months that *Hydrilla* was present in the lake.

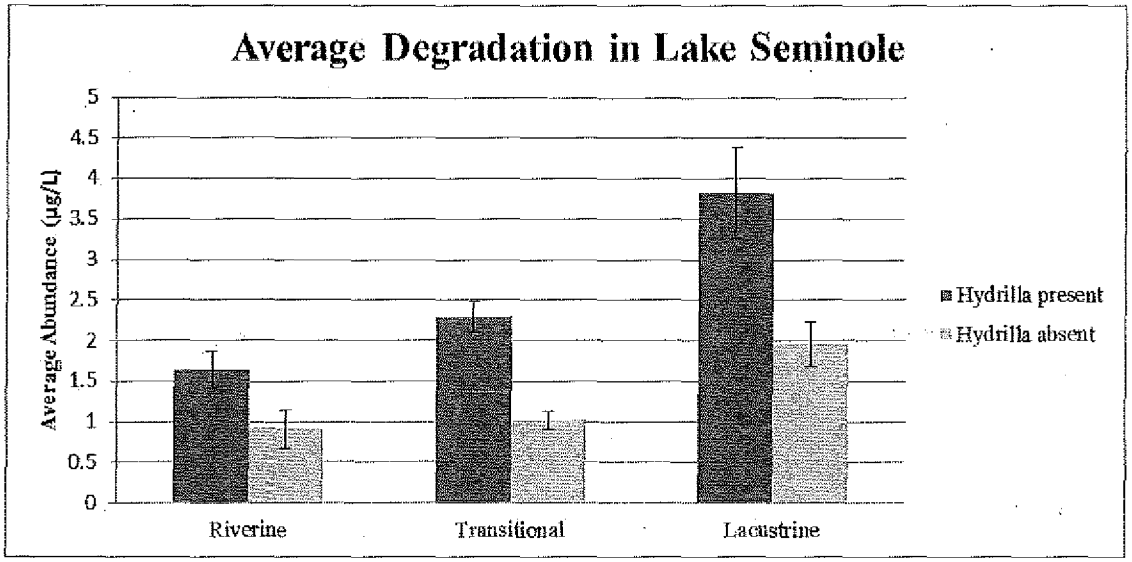

Figure 2.7: Average abundance of degradation pigments in Lake Seminole by all months analyzed and presence/absence of *Hydrilla*. Percent decrease from *Hydrilla* presence to absence: Riverine = 44%, Transitional = 55%, Dam = 49%.

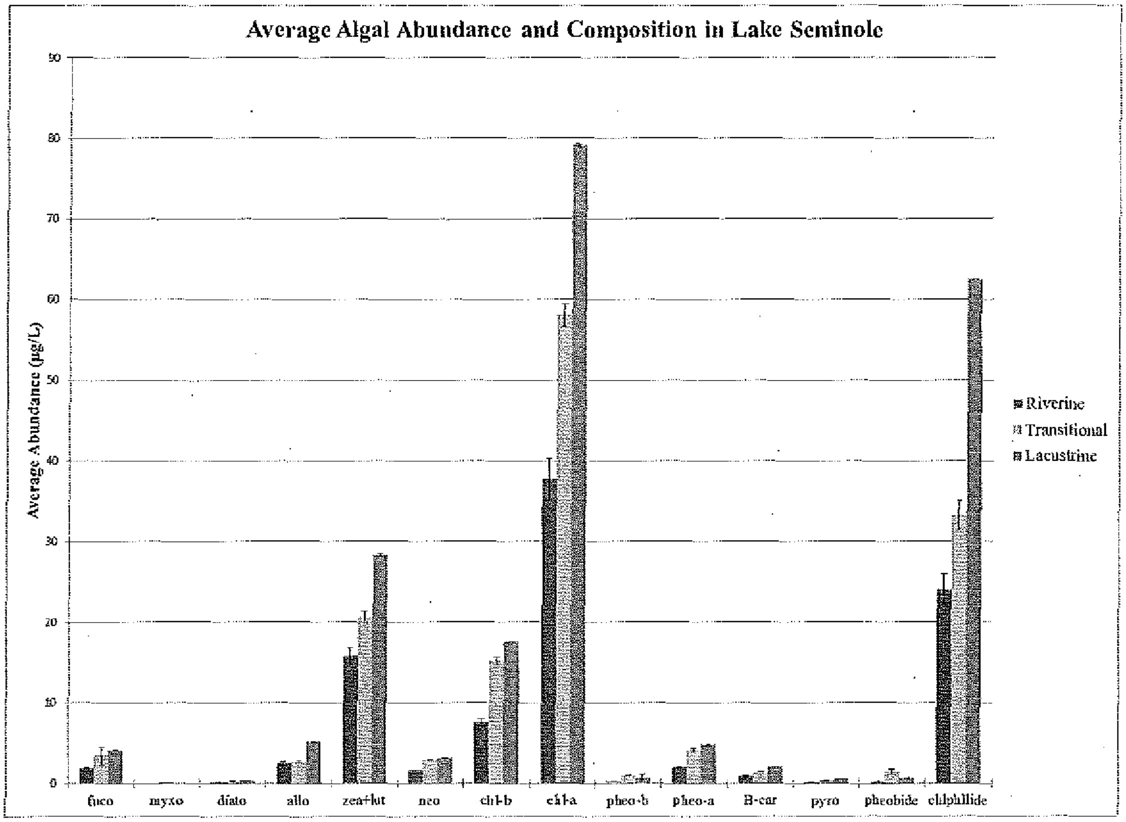

Figure 2.8: Pigment composition and average abundance for each station in Lake Seminole.

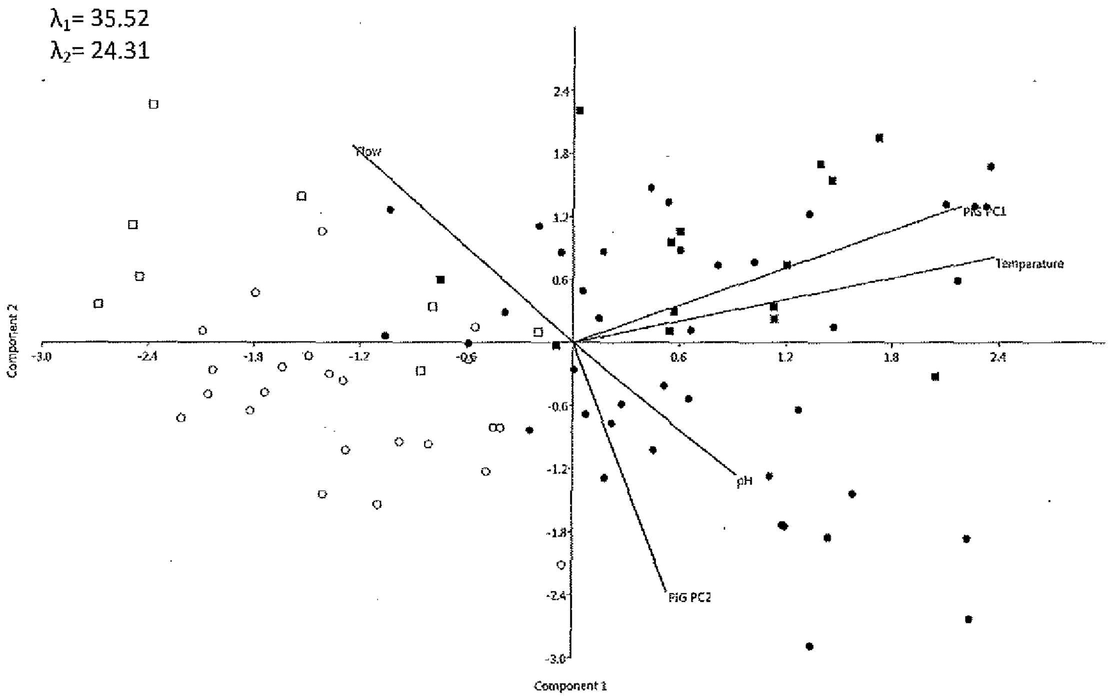

Figure 2.9: PCA plot showing pigment and flow correlation. Square shapes are lacustrine sites and circles are transitional sites with open shapes representing months in which *Hydrilla* is absent and filled shapes indicating months in which *Hydrilla* is present in the lake.

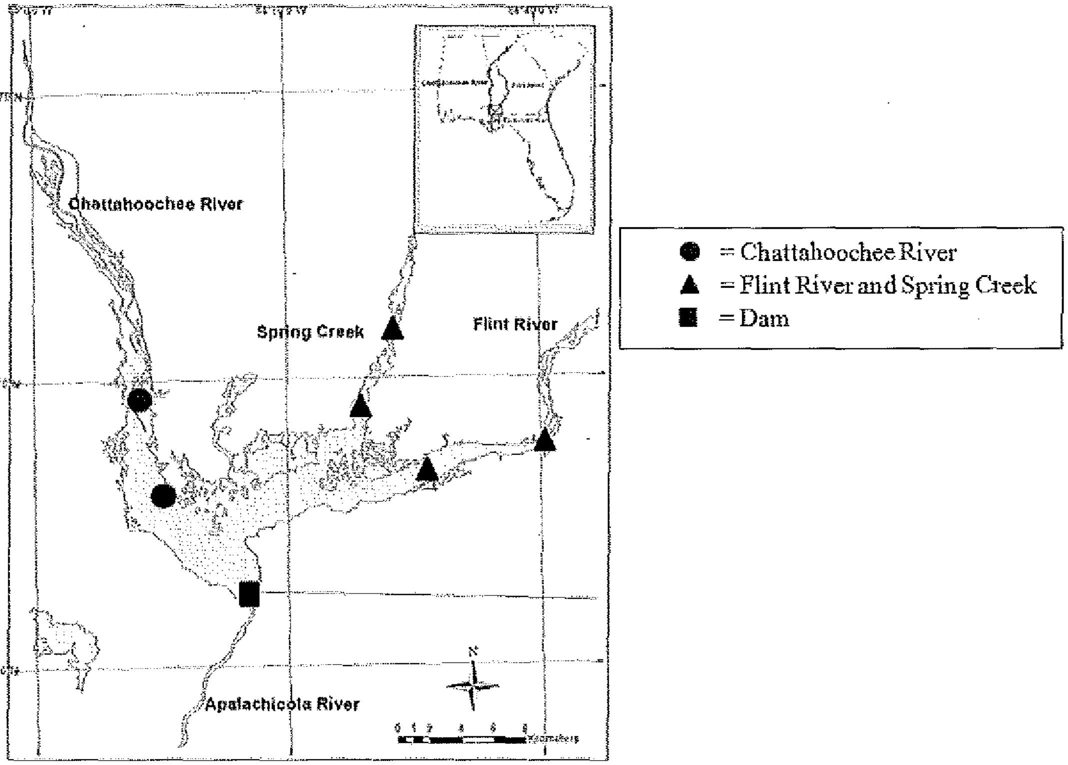

Figure 3.1: Lake Seminole showing the 3 arms of the lake with the different effluent types. Circles represent urban/industrial effluent, triangles indicate agricultural runoff, and the rectangle represents a mixture of the previous two at the dam.

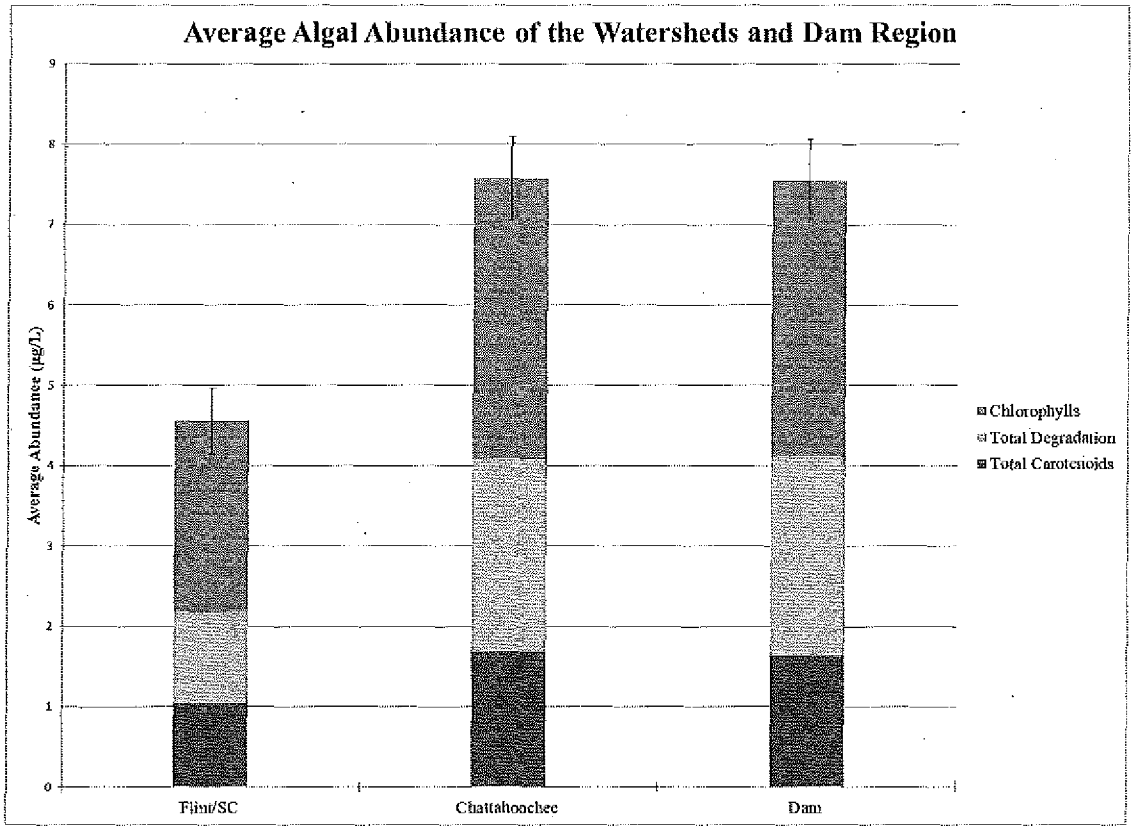

Figure 3.2: Bar graph displaying the average algal abundances of the different watersheds in Lake Seminole.

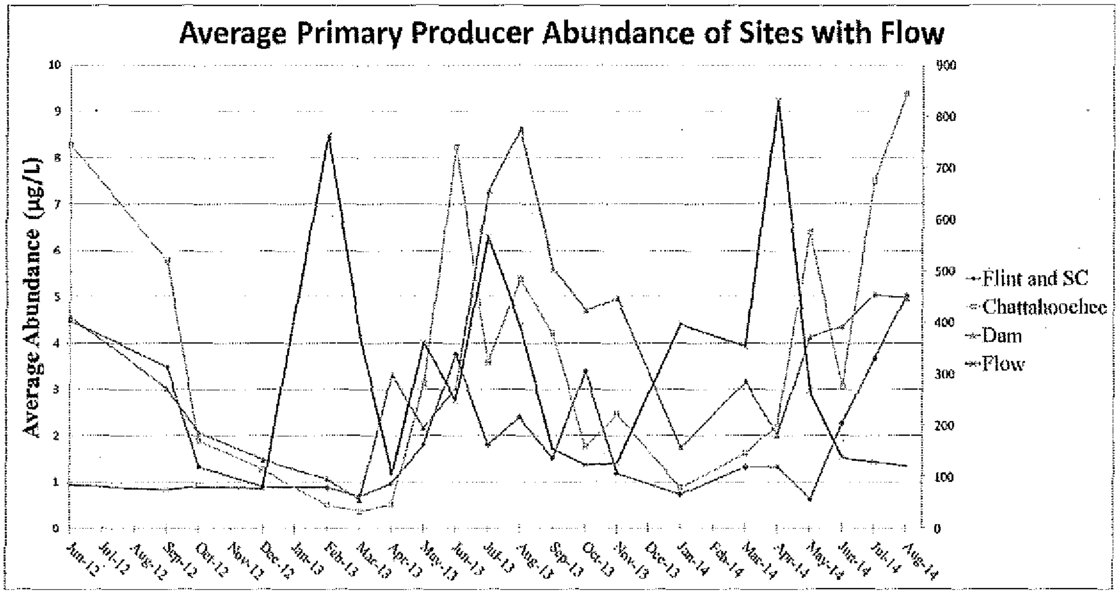

Figure 3.3: Total average algal abundance in each region with flow rates (m^3s^{-1}).

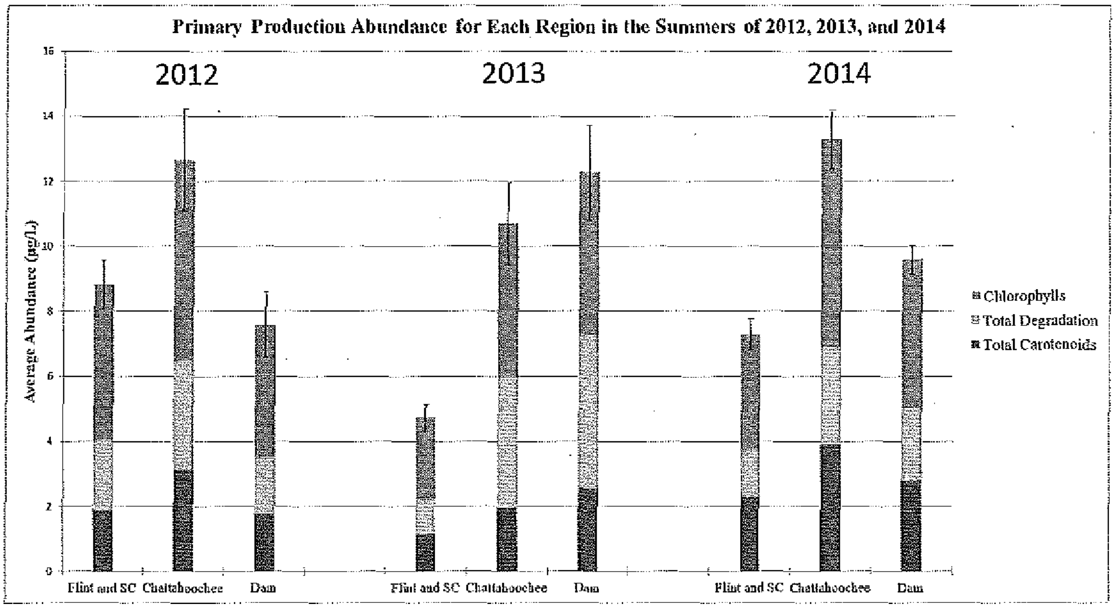

Figure 3.4: Total average primary producer abundance for the summer season of each year in the study.

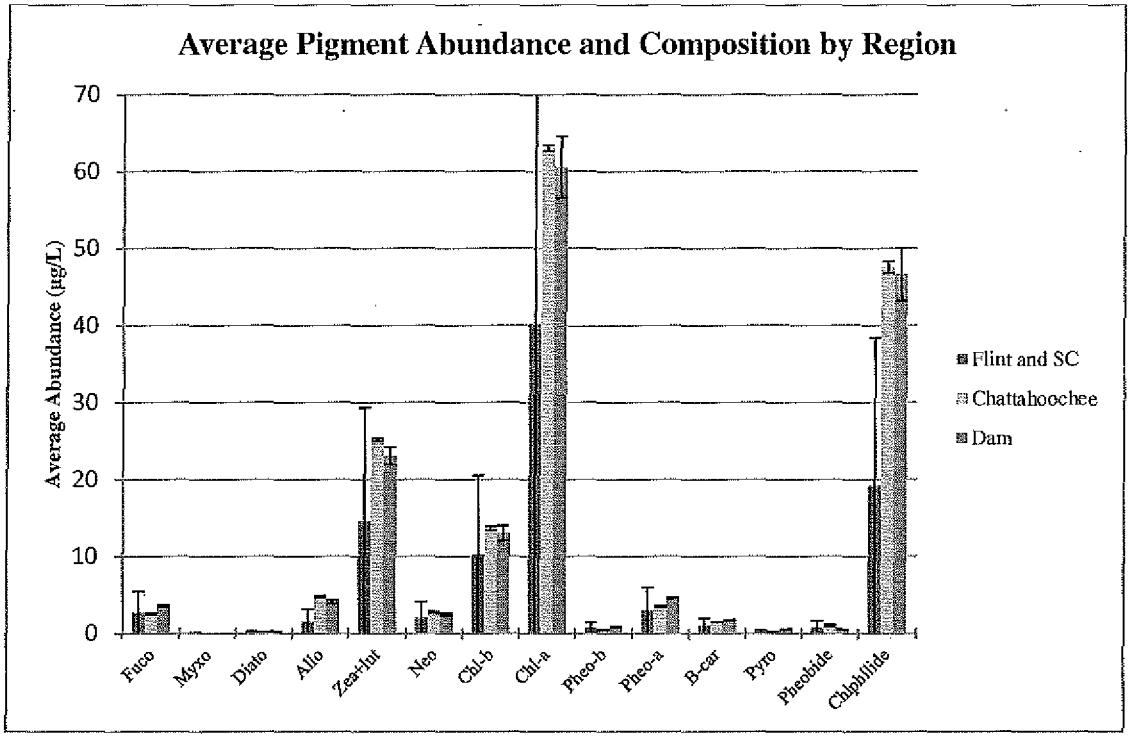

Figure 3.5: Pigment composition and average abundance in each watershed.

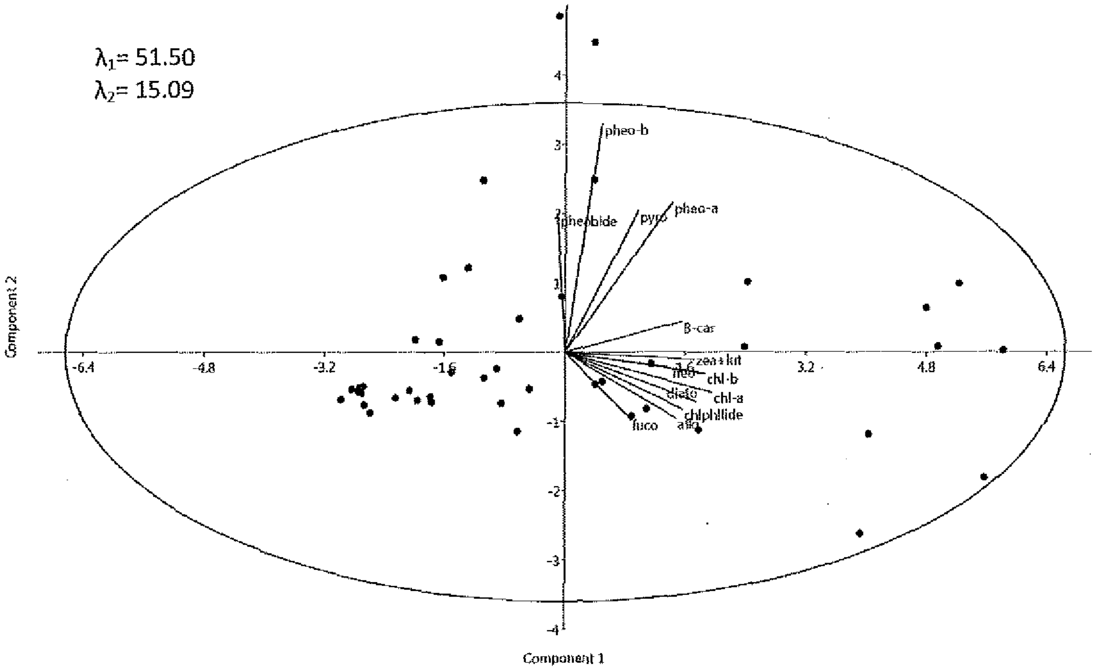

Figure 3.6a: PCA plot of the pigments in the Chattahoochee watershed against their corresponding sampling dates.

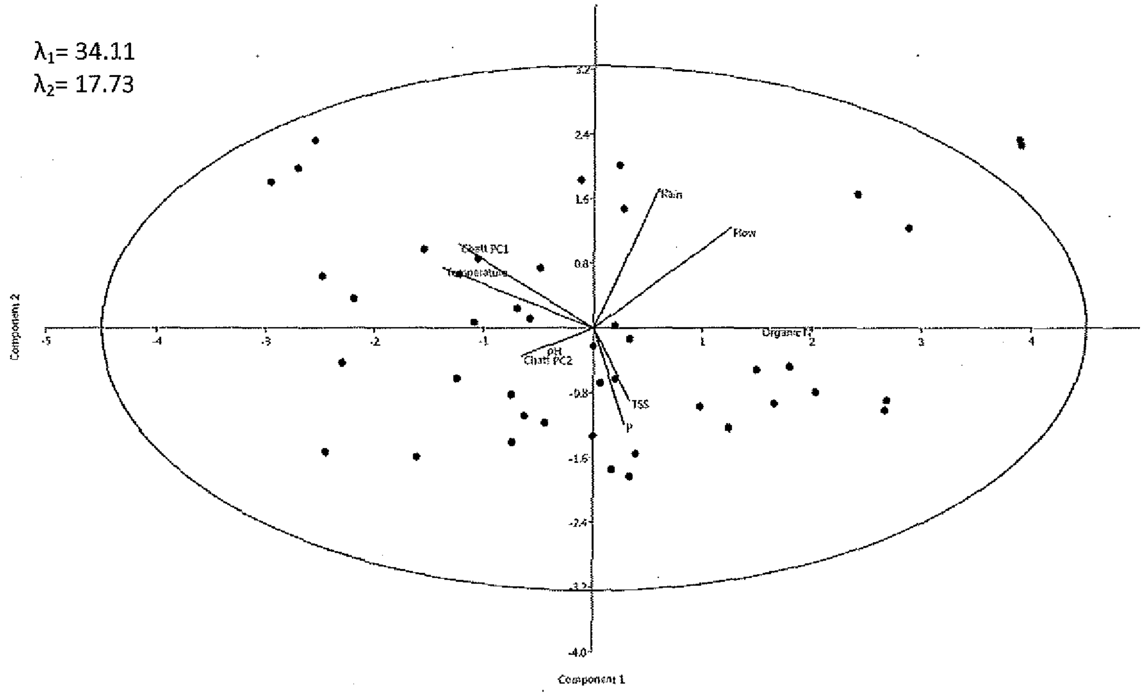

Figure 3.6b: PCA plot of the pigments of the Chattahoochee watershed saved as variables (From Figure 3.5a, Chatt PC1 and Chatt PC2) ordinated against biotic and abiotic factors measured in Lake Seminole during the study.

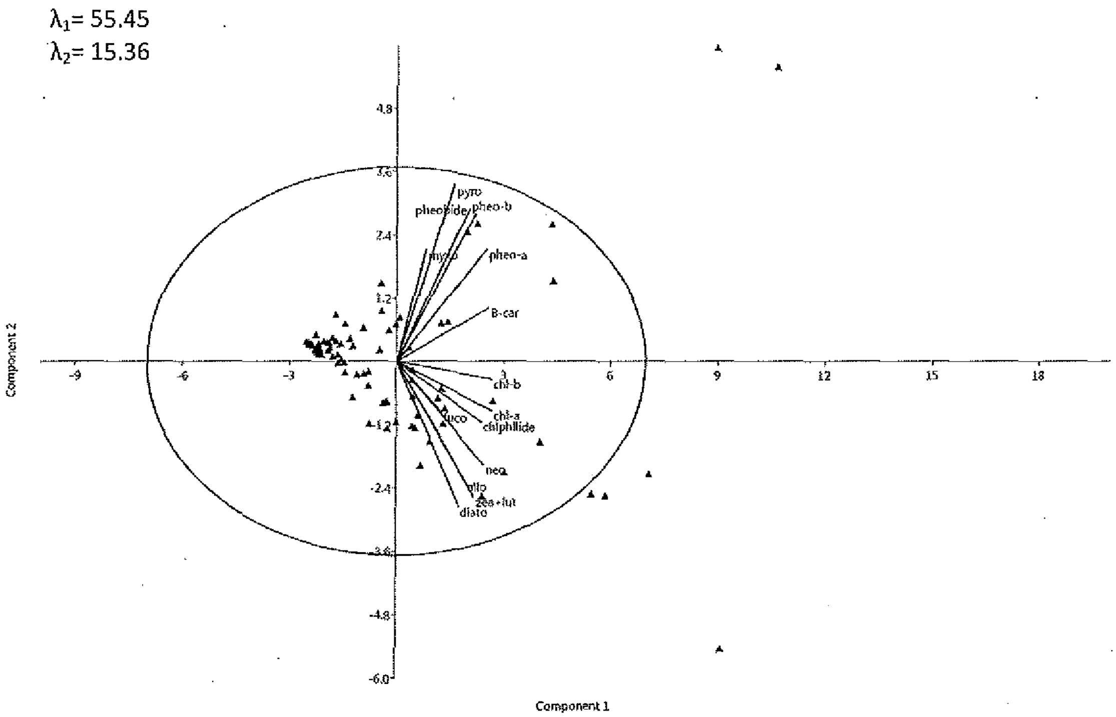

Figure 3.7a: PCA plot of the Flint River and Spring Creek pigments ordinated against their corresponding sampling dates.

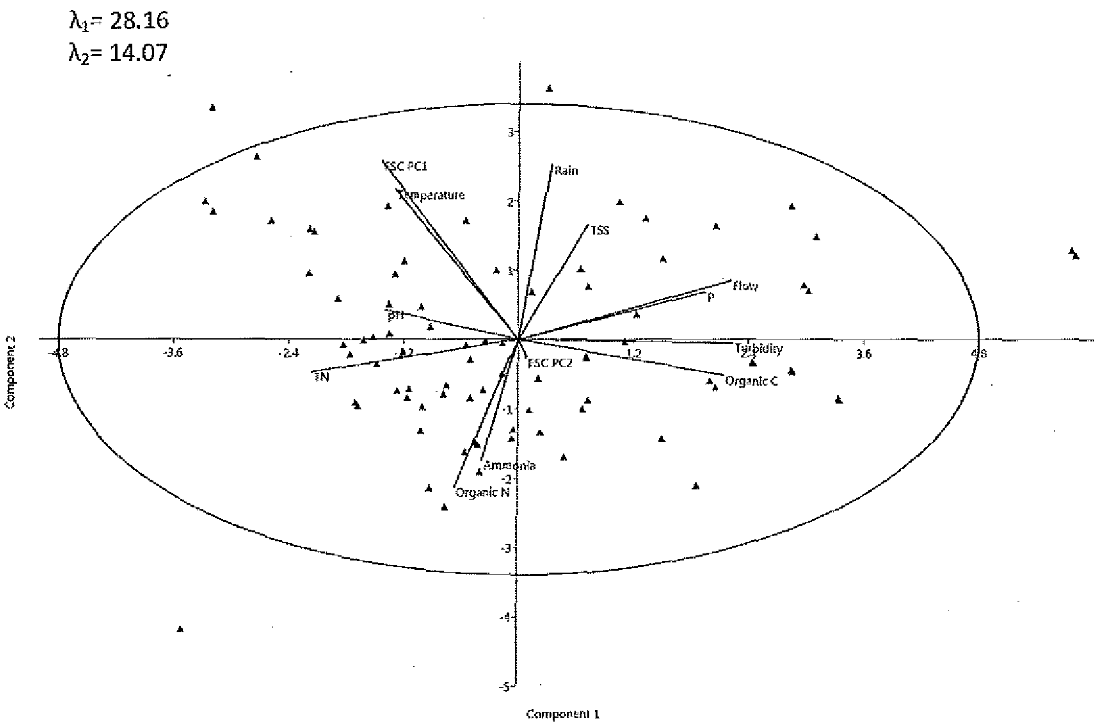

Figure 3.7b: PCA plot of the pigments of the Flint and SC watershed saved as variables (From Figure 3.7a, FSC PC1 and FSC PC2) ordinated against biotic and abiotic factors measured in Lake Seminole during the study.

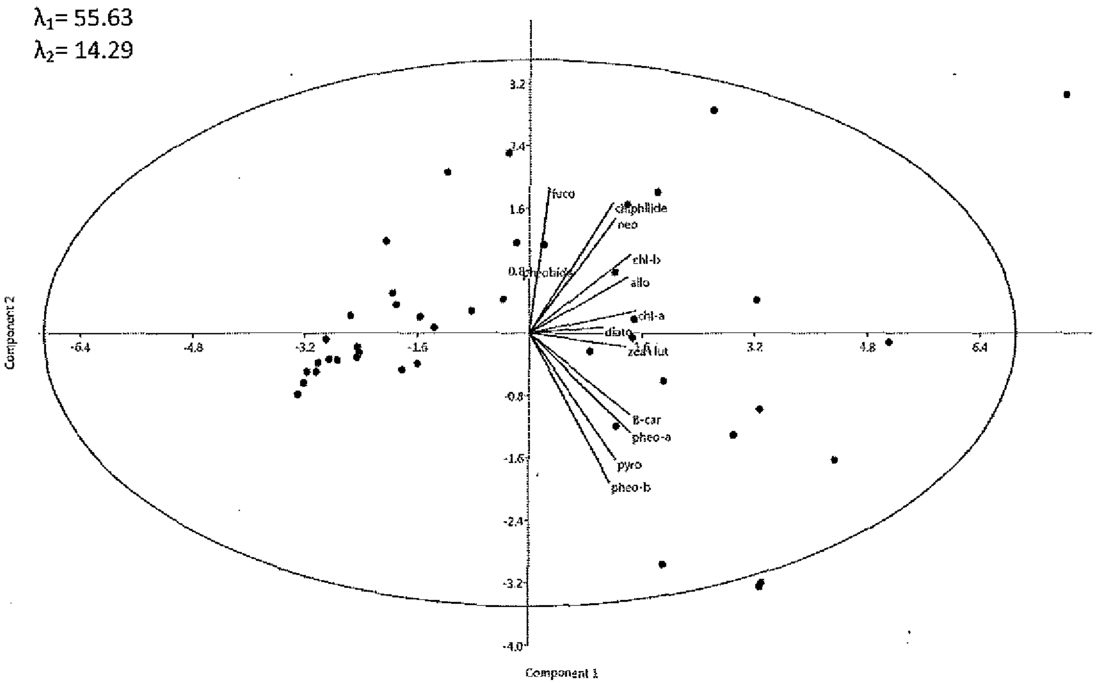

Figure 3.8a: PCA plot of the dam region's pigments ordinated against their corresponding sampling dates.

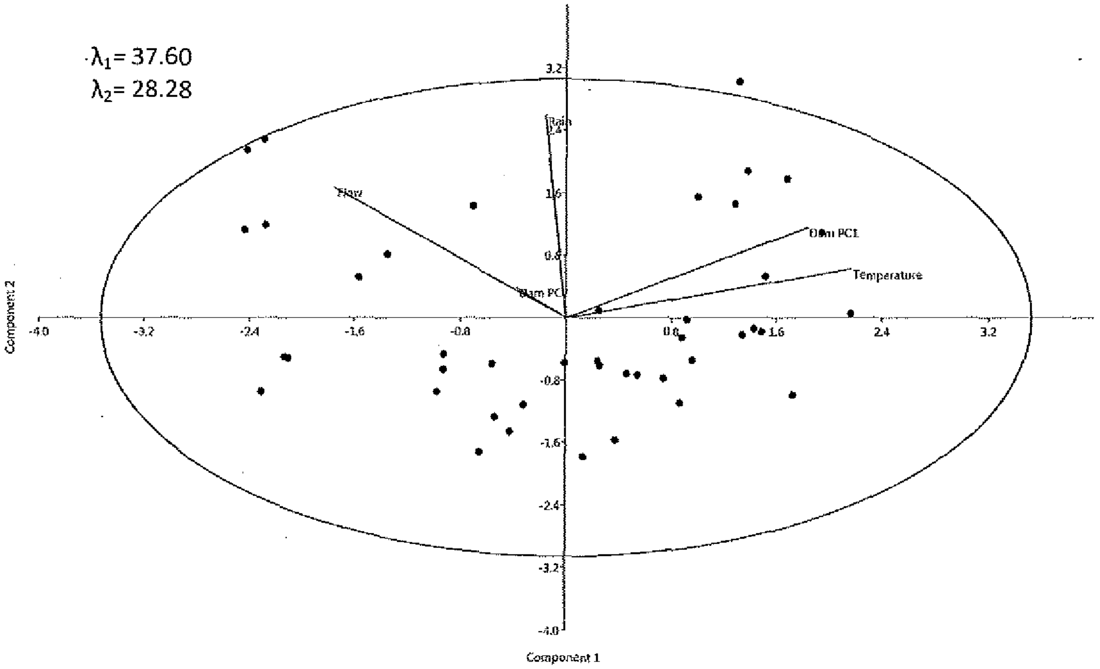

Figure 3.8b: PCA plot of the pigments of the dam sites saved as variables (from Figure 3.7a, Dam PC1 and Dam PC2) ordinated against abiotic factors measured in Lake Seminole during the study.

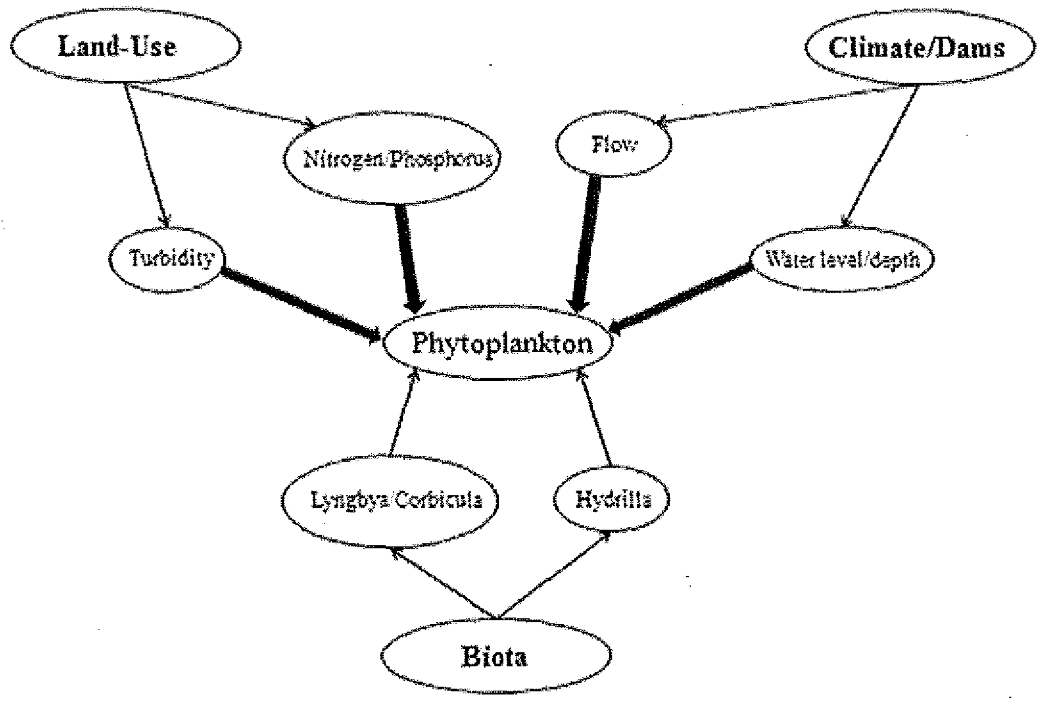

Figure 4.1: Conceptual model of the abiotic processes that drive phytoplankton production in Lake Seminole. Bold arrows indicate abiotic drivers of algal production in the reservoir.

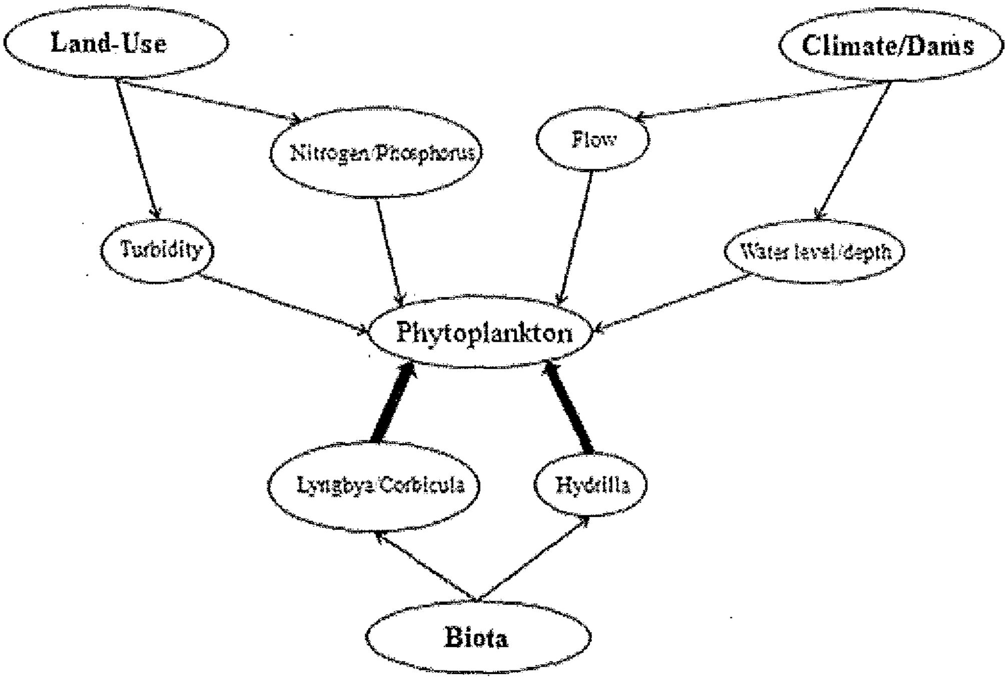

Figure 4.2: Conceptual model of the biotic processes that drive phytoplankton production in Lake Seminole. Bold arrows indicate biotic drivers of algal production in the reservoir.

APPENDIX B:

Tables for Chapter 1 - 4

Table 2.1: A List of phytoplankton photopigments identified in the study and their corresponding algal groups or use in analysis of total abundance or total degradation.

Photopigments	**Algal group(s) or use in study**
Fucoxanthin	Silicious algae
Neoxanthin	Chlorophytes
Myxoxanthophyll	Colonial cyanobacteria
Diatoxanthin	Diatoms
Alloxanthin	Cryptophytes
Zeaxanthin+Lutein	Cyanobacteria + chlorophytes
Chlorophyll-b	Chlorophytes
Chlorophyll-a	Total abundance
Pheophytin-b	Chlorophytes
Pheophytin-a	Total abundance and total degradation
Beta carotene	Total abundance
Pyropheophytin	Total abundance and total degradation
Pheophorbide	Total abundance and total degradation
Chlorophyllide	Total abundance and total degradation

Table 2.2: Table of total carotenoid and total chlorophyll average abundance of all months sampled and months when *Hydrilla* is present/absent in the lake (μg/L).

	All Months			**Hydrilla present**			**Hydrilla absent**		
	Total	**TC**	**TChl**	**Total**	**TC**	**TChl**	**Total**	**TC**	**TChl**
Riverine	4.76 ± 0.15	1.12 ± 0.17	3.65 ± 0.55	5.97 ± 0.19	1.47 ± 0.19	4.50 ± 0.54	2.58 ± 0.10	0.47 ± 0.10	2.10 ± 0.52
Transitional	7.54 ± 0.23	1.70 ± 0.30	5.85 ± 0.80	8.68 ± 0.30	1.94 ± 0.19	6.74 ± 0.55	2.83 ± 0.11	0.50 ± 0.43	2.32 ± 0.22
Lacustrine	9.5 ± 0.59	1.96 ± 0.18	7.54 ± 0.72	11.98 ± 0.72	2.60 ± 0.14	9.40 ± 0.71	5.16 ± 0.37	0.84 ± 0.09	4.32 ± 0.45

Table 2.3: Table of total average abundance for the three transects that compose Lake Seminole (μg/L).

	Flint River	**Chattahoochee River**	**Spring Creek**
Average total pigments	10.00 ± 0.86	12.33 ± 0.33	9.11 ± 0.90

Table 2.4: Average monthly flows for each inflow into Lake Seminole (m^3s^{-1}). Shaded areas represent periods in which *Hydrilla* was present in the reservoir.

Month Sampled	**Chattahoochee**	**Flint**	**Spring Creek**
June-2012	84.81	57.85	1.53
July-2012	105.96	39.92	0.068
August-2012	70.45	46.94	0.009
September-2012	75.26	47.65	0.15
October-2012	81.46	53.09	0.24
November-2012	91.54	46.86	0.000595
December-2012	78.15	59.21	0.583
January-2013	156.42	98.06	1.563
February-2013	763.13	386.80	69.15
March-2013	373.78	470.34	39.84
April-2013	105.81	265.35	15.02
May-2013	361.03	208.77	5.824
June-2013	249.49	164.23	1.934
July-2013	566.90	301.57	62.32
August-2013	395.58	336.12	61.19
September-2013	154.75	162.79	20.52
October-2013	122.81	95.20	7.220
November-2013	127.76	93.95	4.355
December-2013	503.75	213.28	11.21
January-2014	397	380.89	22.55
February-2014	467.79	401.52	32.28
March-2014	353.67	372.39	33.38
April-2014	831.38	681.58	67.05
May-2014	267.84	380.81	42.33
June-2014	137.87	175.64	5.255
July-2014	129.57	120.68	1.843
August-2014	121.19	76.45	0.515

Table 2.5: Ratio of total degradation to chlorophyll abundance in each region of Lake Seminole.

	Hydrilla present	**Hydrilla absent**
Riverine	0.58	0.77
Transitional	0.52	0.78
Lacustrine	0.69	0.83

Table 3.1: Physical characteristics of the three river inflows into Lake Seminole and the outflow river, The Apalachicola (From McEntire 2009 and Waters et al., 2015).

River	**Chattahoochee**	**Flint**	**Spring Creek**
Length (km)	692	563	56
Area Drained (km^2)	8,770	8,460	585
% Forested	61.8	43.1	32
% Urban	10.9	3.6	1.2
% Agricultural	12.6	35.3	61
Population	1.9 million	600,000	22,300
Waste water plants	169	60	1
Reservoirs	13	2	0
Mean Flow (m^3s^{-1})	247	204	18

Table 3.2: Total average nutrient loads for each watershed (µg/L).

Watershed	**NO_3**	**PO_4**	**pH**
Flint and SC	1053.30 ± 93.73	4.36 ± 1.54	7.77 ± 0.81
Chattahoochee	528.83± 46.17	6.18 ± 1.15	7.69 ± 1.13

Table 3.3: Average flow rates (m^3s^{-2}) by year for each inflow of Lake Seminole. Average values are calculated from the months of sampling and are not representative of the entire year.

Year	**Chattahoochee**	**Flint**	**Spring Creek**
2012	83.95 ± 2.28	50.22 ± 1.32	0.37 ± 0.11
2013	323.44 ± 40.28	233.04 ± 23.47	25.01 ± 5.00
2014	338.29 ± 46.00	323.75 ± 37.61	25.65 ± 4.44

Table 3.4. List of phytoplankton photopigments identified in the study, their corresponding algal groups or use in analysis of total abundance or total degradation.

Photopigments (Abbreviation)	Algal group(s) or use in study
Fucoxanthin (fuco)	Silicious algae
Neoxanthin (neo)	Chlorophytes
Myxoxanthophyll (myxo)	Colonial cyanobacteria
Diatoxanthin (diato)	Diatoms
Alloxanthin (allo)	Cryptophytes
Zeaxanthin+Lutein (zea+lut)	Cyanobacteria + chlorophytes
Chlorophyll-b (chl-b)	Chlorophytes
Chlorophyll-a (chl-a)	Total abundance
Pheophytin-b (pheo-b)	Chlorophytes
Pheophytin-a (pheo-b)	Total abundance and total degradation
Beta carotene (b-car)	Total abundance
Pyropheophytin (pyro)	Total abundance and total degradation
Pheophorbide (pheobide)	Total abundance and total degradation
Chlorophyllide (chlpllide)	Total abundance and total degradation

Table 3.5: Table with total average algal abundance (PPA), total carotenoids (TC), total chlorophyll (TChl), total degradation (TD), and chlorophyll average by watershed in Lake Seminole. PPA is calculated by adding TC and TChl. TChl is calculated by adding TD and chlorophyll.

Watershed	Total Pigments	TC	TChl	TD	TD/Chlorophyll
Flint/SC	4.80 ± 0.55	1.08 ± 0.13	3.71 ± 0.42	1.12 ± 0.14	0.47
Chattahoochee	7.58 ± 1.00	1.69 ± 0.26	5.89 ± 0.73	2.40 ± 0.32	0.68
Dam	7.54 ± 0.82	1.64 ± 0.16	5.90 ± 0.65	2.48 ± 0.31	0.73

Table 3.6: Total degradation to chlorophyll pigment ratios for the summer season of each year in the study.

Region	2012	2013	2014
Flint and SC	0.41	0.45	0.4
Chattahoochee	0.54	0.84	0.47
Dam	0.43	0.94	0.5

Table 3.7: Abundance table of fucoxanthin, diatoxanthin, ammonia loads, and total chlorophyll pigments in Flint/SC over the course of the study. *Statistical outlier (Thompson tau test).

Date	Fucoxanthin (µg/L)	Diatoxanthin (µg/L)	NH_3 (mg/L)	TChl (µg/L)
June-2012	0.09	0.001	30	6.26
August-2012	0.24	0.005	30	12.75
September-2012	0.02	0.006	30	9.91
October-2012	0.10	0.004	30	3.61
December-2012*	12.95*	0.080*	200*	45.06*
February-2013	0.12	0	30	1.37
March-2013	0.07	0.002	30	1.09
April-2013	0.09	0	30	1.31
May-2013	1.29	0.007	50	5.21
June-2013	0.23	0.048	30	14.02
July-2013	0.31	0.014	30	4.80
August-2013	0.85	0.056	30	7.10
September-2013	0.22	0.013	30	4.41
October-2013	0.60	0.024	30	13.70
November-2013	0.10	0	30	1.88
January-2014	0.03	0	40	0.36
March-2014	0.08	0	40	0.71
April-2014	0.09	0	40	0.70
May-2014	0.04	0	30	0.70
June-2014	0.17	0.007	30	4.15
July-2014	0.08	0.043	30	5.60
August-2014	0.46	0.014	30	13.20

Table 3.8: Abundance table total carotenoids and total chlorophyll in Spring 253 over the course of the study. *Statistical outlier (Thompson tau test).

Date	Total Carotenoids (µg/L)	Total Chlorophyll (µg/L)
June-2012	1.71	7.5
September-2012	0.97	3.46
October-2012	0.18	0.50
December-2012	0.08	0.43
Feburary-2013	0.18	1.10
March-2013	0.23	0.70
April-2013	0.15	0.63
May-2013	0.31	0.79
June-2013	0.31	1.11
July-2013	0.26	1.21
August-2013	0.76	3.00
September-2013	0.20	1.04
October-2013	0.47	2.43
November-2013	0.17	0.62
January-2014	0.33	1.36
March-2014	4.20*	20.94*
April-2014	0.41	1.81
May-2014	0.19	0.72
June-2014	0.29	1.38
July-2014	1.25	3.16
August-2014	1.72	3.21