TRANSITIONING FROM A RIVER TO A LAKE: HOW HYDROLOGY AND INVASIVE SPECIES ALTER NUTRIENT CYCLING AND RETENTION WITHIN A RESERVOIR

by

STEPHEN DERRILL SHIVERS

(Under the Direction of Alan Covich and Stephen Golladay)

ABSTRACT

Freshwater ecosystems, which include lakes and reservoirs, are important sites for biogeochemical cycling on both a regional and global scale. Reservoirs affect the storage and transformation of nutrients as water moves through a watershed transporting municipal and agricultural runoff. Water quality is often a major concern because reservoirs provide a reliable source of water for human consumption and are used for recreational fishing and boating; both can be threatened by the accumulation of excessive nutrients. Because reservoirs attract many different users, they can also facilitate the spread of invasive species. The goal of this research project was to investigate how abiotic and biotic factors affect nutrient processing within a reservoir. The study area features extensive coverage by the invasive plant *Hydrilla verticillata*, which affects water quality within the reservoir through nutrient uptake and storage. Therefore, this study quantified the spatial coverage of submerged aquatic vegetation (SAV) using annual vegetation surveys between 2012 and 2014. Coverage changed dramatically by decreasing from 35.6 km^2 to 18.3 km^2. High precipitation and flooding during early spring increased turbidity and reduced light availability needed for growth. These high flows through the reservoir resulted in decreased SAV coverage and changes in nutrient storage. This study also investigated how these changes in SAV coverage affected nutrient cycling and organic matter processing through a water quality monitoring program that quantified nutrient concentrations in the inflows and outflow of the lake. Concentrations of NO_3-N were lowest during the period of lowest SAV coverage. Consequently, flooding affected the coverage of SAV, which was driving nutrient cycling within the reservoir. To investigate the effects of *Hydrilla* and two other invasive species in the reservoir (*Corbicula fluminea* and *Pomacea maculata*), a mesocosm experiment was designed featuring different combinations of these species. The experiment demonstrated strong effects on nitrogenous compounds with *Hydrilla* reducing inorganic N, *Pomacea* converting stored N to available particulate N, and *Corbicula* mitigating the effects of *Pomacea* by reducing total N. Because *Pomacea* was recently introduced to the lake and the extent and rate of spread was unknown, snail egg mass surveys were completed during 2013 and 2014 to determine the spatial extent of the *Pomacea* population. Presence of *Pomacea* was found to be extensive in the reservoir and range expansion occurred in the second year of surveys. The expanding snail population has the potential to alter SAV coverage, which would affect overall nutrient processing of the reservoir.

INDEX WORDS: Biogeochemical Cycling, Nutrient Dynamics, Lake Seminole, ACF Basin, Submerged Aquatic Vegetation, *Hydrilla verticillata*, *Corbicula fluminea*, *Pomacea maculata*

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

Inland Waters

Although freshwater ecosystems comprise a small proportion of the Earth’s surface, inland waters are important for the biogeochemical cycling of nitrogen, phosphorus, and carbon (Cole et al. 2007; Harrison et al. 2009; Tranvik et al. 2009). Inland waters consist of rivers, streams, lakes, wetlands, and reservoirs. With an estimated global surface area of 1.5 million km^2, reservoirs play a crucial role in biogeochemical cycling (St Louis et al. 2000). This role may be enhanced as the number of reservoirs, particularly smaller reservoirs are predicted to increase (Downing et al. 2006). Because of their position in the landscape, lakes and reservoirs can function as integrators of the land within their watershed (Williamson et al. 2009). This function is especially true for reservoirs because the inflowing tributaries can flow over long distances with diverse land-use. Consequently, lakes and reservoirs can also function as sentinels for landscape change or for broader effects such as climate change (Williamson et al. 2008; Schindler 2009). Reservoirs can also facilitate the spread of invasive species because they are widely used for recreational boating and fishing which can accidently increase dispersal of many non-native species (Havel et al. 2005; Strayer 2010). These introductions can create novel ecosystems with unknown direct and indirect interactions as new biotic communities are formed (Hobbs et al. 2006; Williams and Jackson 2007). The growth of these non-native species can also alter the environment in ways that enhance the growth of additional invasive species while reducing the abundance of native species. The facilitation of one species by another following a series of non-native colonizations results in novel ecosystems that accelerate further environmental changes. This process of "invasional meltdown" is widely studied but has often lacked experimental analysis (Simberloff and von Holle 1999; Simberloff 2006). These interactions have the potential to produce deleterious effects, such as toxic cyanobacterial blooms or avian diseases, and reduce overall water quality (Wilde et al. 2005).

Shallow Lakes

Shallow lakes are classified and function differently from deeper lakes (Lewis 1983; Scheffer and van Nes 2007). Shallow lakes are usually polymictic, have greater effects from sediment-water interactions, and can have high spatial coverage by submerged aquatic vegetation (SAV) (Scheffer 2004; Scheffer et al. 2003). SAV can directly affect phytoplankton and biogeochemical cycling in freshwater ecosystems, and strongly influence physical and chemical parameters of water quality, such as: dissolved oxygen (DO), pH, dissolved organic carbon (DOC), and nutrient concentrations (Carpenter and Lodge 1986; Shivers et al. 2016). SAV can also indirectly affect biogeochemical cycling by slowing water flow which changes sedimentation rates (Sand-Jensen and Mebus 1996), or by releasing exudates into the water which can increase microbial metabolism and alter microbially mediated processes, such as denitrification (Wetzel 1969; Flindt et al. 1999; Ziegler and Benner 1999).

Shallow lakes can have two different states, a clear-water state dominated by SAV and a turbid state dominated by phytoplankton, and can shift between the two states due to increases in environmental drivers such as excess nutrients (Scheffer et al. 1993). These states represent alternative equilibria and it can be difficult to revert back to the alternate state because of internal feedback. In contrast, some lakes experience cyclical shifts between the two different states as a result of internal nutrient loading (Van Nes et al. 2007). Hydrology, lake size, and fish can also induce shifts between turbid and clear water states (Jeppesen et al. 1997; Scheffer and van Nes 2007; Loverde-Oliveira et al. 2009).

Hydrilla verticillata

Hydrilla verticillata is a rooted submerged macrophyte native to Asia and is found on all continents except Antarctica (Cook and Luond 1982). It was introduced in the United States at two locations in Florida in 1960 (Blackburn et al. 1969). Since 1960, *Hydrilla* has spread west through the Gulf Coast states to Texas, and northward into the mid-Atlantic states of Maryland and Delaware (Langeland 1996). *Hydrilla* currently extends north to Maine and west into California and Washington (Barnes et al. 2014). There have been at least two introductions based on the observation that two different forms of *Hydrilla* are present in the US. It is likely that a third introduction brought *Hydrilla* to the western states. *Hydrilla* exists as two different biotypes either monoecious, having pistils and stamens on the same plant, or dioecious, having pistils and stamens on separate plants. *Hydrilla* plants in the southeastern US are all dioecious female, whereas the plants north of South Carolina are monoecious. Genetic analyses confirm that the two varieties are from different locations within Asia (Madeira et al. 1997).

Hydrilla has been called "the perfect aquatic weed" and is capable of rapid colonization because of high vegetative reproductive success through fragmentation and production of turions, tubers, and seeds (Langeland 1996). *Hydrilla* fragments produce more shoots and roots than native plants and recover faster from desiccation, which potentially leads to competitive displacement (Umetsu et al. 2012). In addition to fragmentation, *Hydrilla* can also regrow from both tubers (buried turions) and turions. Tubers can remain viable for several years in temperate areas and are important overwintering energy sources, but they are viable for a much shorter period in warmer tropical waters. Growth from tubers is faster than from fragments or by plants native to the Neotropics and yields a competitive advantage over native plants (Bianchini et al. 2010). Because the *Hydrilla* plants of the southeastern US are all dioecious female, sexual reproduction and seed production do not occur, however seed production does occur in the monoecious variety (Langeland 1996).

Hydrilla is an adaptable plant that is capable of growing in a variety of water conditions. For example, *Hydrilla* is found in conditions ranging from acidic to alkaline, oligotrophic to eutrophic and fresh to brackish (Cook and Luond 1982). It is not typically found in swift or deep waters but studies have shown that *Hydrilla* is capable of growing and thriving in flowing water (Hofstra et al. 2010). *Hydrilla* is most commonly found in shallow water (< 3 m) but is reported to have occurred as deep as 15 m in the Crystal River, Florida (Langeland 1996). *Hydrilla* is a superior competitor for light in most water conditions and can grow up to one inch per day eventually forming a canopy and shading out other SAV. *Hydrilla* has a lower light compensation point than other similar native or invasive plants, which offers a competitive advantage in aquatic environments (Van et al. 1976; Holaday and Bowes 1980). Light limitation caused by either depth, high densities of phytoplankton or benthic algae, or inorganic solids can limit where *Hydrilla* can grow, but these conditions do not alone control growth (Havens 2003).

A variety of factors, both physical and chemical, affect the growth and distribution of *Hydrilla*. Warmer early growing season temperatures cause an increase in SAV biomass, but higher overall temperatures result in less turion and tuber production in *Hydrilla*, which can delay regrowth in subsequent growing seasons (McFarland and Barko 1999; Rooney and Kalff 2000). *Hydrilla* plants possess the unique ability to shift between C_4 and C_3 photosynthesis depending on CO_2 concentration within the water (Bowes et al. 2002), although increasing production has not been observed with increasing CO_2 concentrations (Chen and Coughenour 1996). Increased sediment and water column nutrient concentrations also stimulate the growth and abundance of *Hydrilla* (Barko et al. 1988; Kennedy et al. 2009; Jiang et al. 2010).

Hydrilla can cover large areas of lakes and reservoirs and because of this spatial coverage it can alter biogeochemical cycling and nutrient transformation (Sousa 2011). *Hydrilla* can affect the physical parameters of water by increasing sedimentation rates and stabilizing sediments (Posey et al. 1993; Madsen et al. 2001). Hydrilla alters water quality by decreasing N and P concentrations in both the sediment and the water column (White 2006; Gu 2006; James et al. 2011). Because of the high uptake, *Hydrilla* is used to reduce nutrients in eutrophic aquatic systems in its native range and can also remove organic pesticides and heavy metals (Hinman and Klaine 1992; Xiao et al. 2007). *Hydrilla* also releases allelopathic phenolic compounds that inhibit the growth of cyanobacteria (Wu et al. 2009; Gao et al. 2011; Wang et al. 2015) and are toxic to fungi (Hipskind et al. 1992).

Hydrilla can affect other biota by providing habitat for a variety of macroinvertebrates in the following orders: Hemiptera, Amphipoda, Gastropoda, Coleoptera, and Diptera (Colon-Gaud et al. 2004; Copeland et al. 2012; Stratman et al. 2013) and by providing habitat for assemblages of juveniles fishes (Cunha et al. 2011). For larger fish, an intermediate level of *Hydrilla* coverage is considered optimal for growth and recruitment of largemouth bass, whereas high spatial coverage causes larger fish to grow slower (Brown and Maceina 2002). *Hydrilla* increased the number and diversity of waterfowl in the Chesapeake Bay after native SAV declined (Rybicki and Landwehr 2007). However, *Hydrilla* can also harbor a novel cyanobacteria that causes a neurologic, potentially fatal, disease (avian vacuolar myelinopathy) in some waterfowl and avian predators (Birrenkott et al. 2004; Wilde et al. 2005; Wiley et al. 2007).

Thus, *Hydrilla* is a superior competitor to many native and non-native plants and, once established, can reduce biodiversity because of competitive displacement (Mony et al. 2007; Wang et al. 2008; Sousa et al. 2010). As a result, physical, biological, and chemical methods are employed to combat *Hydrilla* spread. However, recent studies suggest that control measures to prevent spread to new areas and to preserve intact native communities should continue although the ecological functions provided by *Hydrilla* might outweigh the negative consequences produced from control measures in areas where it is established (Evans et al. 2007; Hershner and Havens 2008).

Pomacea

Snails of the genus *Pomacea* (order Ampullariidae) are large-bodied snails commonly called apple snails. Their large size enables some species to feed on SAV and they are noted as voracious herbivores (Baker et al. 2003; Morrison and Hay 2011). They have a calcareous shell and lay calcareous-encased egg masses on hard structures out of the water (Brown 2009; Kyle et al. 2013; Marzolf 2015). *Pomacea paludosa* (Florida apple snail) is the only species native to the United States and is found in the southeastern US. Other *Pomacea* species are native to South and Central America and the Caribbean (Rawlings et al. 2007). Invasive apple snails were introduced into both Asia and the United States and can cause major changes to ecosystem structure and function. Because of their sensitivity to temperature and pH the potential range is predicted based on these environmental factors (Byers et al. 2013).

Apple snail investigations can be problematic because adults are difficult to detect and their brightly colored egg masses are not reliable estimators of abundance (Darby et al. 1999). According to Hayes et al (2012), *P. maculata*, *P. canaliculata*, and *P. insularum* have not been characterized taxonomically. Clarification of the *P. canaliculata* group is necessary in order to understand their effects. Based on the research by Hayes et al (2012), the snails in Lake Seminole were identified as *P. maculata*. A second species, *P. paludosa,* an apple snail native to Florida is also found in Lake Seminole.

Apple snails feed on a variety of native and non-native vegetation, including *Hydrilla* (Baker et al. 2010). Feeding and growth rates for *P. maculata* were higher than for *P. paludosa*. This relatively high growth rate may influence the high invasibility by *P. maculata* (Morrison and Hay 2011). Another factor is the high fecundity of some invasive apple snails. For example, a single individual *P. insularum* can lay numerous egg masses and each egg mass can have more than 4000 eggs (Barnes et al. 2008). However, habitat type exerts control on apple snail reproductive dynamics with permanent habitats maintaining stable populations and ephemeral, agricultural habitats having high population densities (Burlakova et al. 2009). Interspecific competition can also affect both *P. maculata* and *P. paludosa*. The presence of *P. maculata* negatively affects the growth of *P. paludosa* which could increase the expansion potential of *P. maculata* (Conner et al. 2008). The combination of high feeding rates and high fecundity can lead to apple snails exerting a strong influence on ecosystem function.

P. canaliculata can severely degrade aquatic ecosystems. For example, herbivory by exotic apple snails destroyed the native aquatic plant community in a tropical wetland ecosystem, which led to more available nutrients and caused a shift to a algae-dominated state (Carlsson et al. 2004). In addition to affecting the SAV community, apple snails can also affect populations of their avian predators. Cattau et al. (2010) found that handling times and consumption rates of invasive apple snails by the endangered snail kite were lower compared to their predation on native Florida apple snails, so that juvenile snail kite survival decreased (Cattau et al. 2010). Invasive apple snails may also represent a vector for avian vacuolar myelinopathy (AVM) transmission because the snails transferred AVM to chickens (Robertson 2012). *P. maculata* might also pose a threat to human health because the rat lungworm parasite, *Angiostrongylus*, has been found in snails in the southeastern US (Teem et al. 2013).

Corbicula

Corbicula fluminea are freshwater clams, native to Asia, that have invaded aquatic ecosystems throughout Europe and the Americas. These filter-feeders are capable of rapidly reproducing and are effective at dispersing into new habitats (Darrigran 2002). *Corbicula* have high filtration rates and have been recorded as having the highest assimilation efficiency among freshwater bivalves (McMahon and Bogan 2009). Because of these characteristics, *Corbicula* can affect whole ecosystems. This impact is of particular concern in northern latitudes, such as the Great Lakes, where range expansion could occur if winters become warmer (Pagnucco et al. 2015).

Corbicula are currently found on all continents except Antarctica. Their range is limited by cold winter temperatures and oligotrophic conditions (shortage of Ca^{2+})(Crespo et al. 2015).

Corbicula have a variety of methods for dispersal both within invaded habitats and into new areas. These clams are frequently spread by people, especially fishermen who accidently transport the microscopic larvae in bait buckets. Ship and boat traffic also play major roles for long-distance movements (Kappes and Haase 2011). Fish and birds can transport *Corbicula* upstream and larvae can drift passively downstream. They produce mucous threads which facilitate flotation of juvenile and adult clams (Prezant and Chalermwat 1984). On smaller scales, strong winds can move larvae throughout a water body (Hoyer et al. 2015).

Corbicula use cilia lined siphons to move water through the mantle where suspended particles are collected, sorted, and ingested (McMahon and Bogan 2009). Filtration rates of invertebrates can be affected by a variety of factors, such as temperature and particle size, and *Corbicula* can adjust its filtration rate to optimize efficiency (Vaughn and Hakenkamp 2001). This increased efficiency is demonstrated by *C. fluminea* having higher clearance rates of organic and inorganic materials per body mass when compared to native mussels (Atkinson et al. 2011). Rapid filtration rates can cause phytoplankton decreases in areas where *Corbicula* are present (Cohen et al. 1984). *Corbicula* feed on a wider range of particles than native mussels and can concentrate pollutants, such as pesticides and heavy metals, in aquatic systems (Pereira and Domagalski 1996; Atkinson et al. 2010; Shoults-Wilson et al. 2010).

Corbicula can burrow into soft sediments, combine filter and pedal feeding, and alter the microbial community present in the sediment, while serving as a link between the benthos and the water column (Hakenkamp et al. 2001). A combination of filtering suspended particles, excreting waste, and bioturbation of the sediment can affect biogeochemical cycling (Vaughn and Hakenkamp 2001). *Corbicula* mediated changes on nutrient cycling include direct uptake of suspended particles or indirect impacts on the biotic community (Pigneur et al. 2013). Because of the high densities at which *Corbicula* can occur and the resulting decrease in phytoplankton, soluble reactive phosphorus (SRP) can increase as producers decline. Conversely, decreases in phytoplankton can decrease turbidity, which can result in a shift to a macrophyte-dominance as was seen in the Potomac River (Phelps 1994). Nutrients filtered from the water can move through the food web. *Corbicula* are eaten by crayfish (Covich et al. 1981) and by fishes with shell-breaking pharyngeal teeth (Robinson and Wellborn 1988). *Corbicula* can also serve as a terrestrial nutrient subsidy when a decrease in water levels exposes large concentrations of clams to both mammal and avian predators (Bódis et al. 2013).

Lake Seminole and the ACF Basin

The Apalachicola-Chattahoochee-Flint (ACF) Basin is located in the southeastern US and drains 51,300 km^2 of land (Feldman 2008). Lake Seminole, a 152 km^2 impoundment, is the most downstream reservoir in the ACF Basin (Torak et al. 2006). Lake Seminole is operated by the US Army Corps of Engineers as a run-of-the-river reservoir for the primary purposes of providing hydroelectric power and to aid in navigation. The mean depth of the lake is 3 m and the maximum depth is 10.7 m (Sammons and Maceina 2005). The major surface water inflows are the Chattahoochee River, the Flint River, and Spring Creek with groundwater also contributing a component of flow into the lake (Torak et al. 2006). These inflows traverse very different landscapes and provide a contrast in both land use and hydrology. The Flint River and Spring Creek are unregulated and have a greater agricultural influence, whereas the Chattahoochee River is largely regulated with a greater urban influence (Frick et al. 1998). Both the Flint River and Spring Creek have higher NO_3 concentrations likely due to agricultural fertilizer use (McEntire 2010). Sediment concentrations of P are high within the lake (Waters et al. 2015). Lake Seminole is dominated by the invasive plant *Hydrilla verticillata* during the summer growing season, and *Hydrilla* can cover 40% to 70% of the lake surface area (Maceina and Slipke 2004). The Apalachicola River begins as water exits the Jim Woodruff Lock and Dam and flows south emptying into the Gulf of Mexico at the Apalachicola Bay.

Since 1989, the states of Georgia, Florida, and Alabama have disputed over water allocation within the ACF Basin (Carter et al 2008). Their disagreements revolve around balancing municipal withdrawals for metropolitan demands in the northern part of the ACF, industrial withdrawals to support manufacturing and power generation, agricultural withdrawals to support crop production, and maintaining enough freshwater to support native biotic communities. In particular, the multimillion dollar oyster and finfish fisheries of Apalachicola Bay are dependent upon sufficient high-quality freshwater input from the Apalachicola River to maintain salinity requirements for the fisheries and wildlife (Corn et al. 2008b). There are also four listed species, Gulf Sturgeon (*Acipenser oxyrinchus*), fat three-ridge mussels (*Amblema neislerii*), Chipola slabshell mussels (*Elliptio chipolaensis*), and purple bankclimber mussels (*Elliptoideus sloatianus*), which are dependent on sufficient flow volume (Corn et al. 2008a). Multi-year droughts have exacerbated these tri-state disputes (Carter et al 2008). According to recent climate models, the southeastern US might experience stronger seasonal rainfall and more variable rainfall events, which could further complicate the tri-state water disputes (Diffenbaugh et al. 2005; Dore 2005). Because Lake Seminole is the most downstream reservoir in the ACF Basin, its outflow determines the quantity and quality of the Apalachicola River. The water quality of the Apalachicola River is primarily dependent on the ecosystem functions within Lake

Seminole. Consequently, biogeochemical cycling and the effects of invasive species in Lake Seminole are important for sustaining downstream water quality in the Apalachicola River and Bay.

Project Objectives

The overarching goal of this dissertation research is to investigate the direct effects and interaction effects of multiple invasive species on water quality at a lake-wide scale. Previous studies on Lake Seminole have identified that the lake can function as both a source and a sink for nutrients and carbon (McEntire 2009), and that invasive SAV has strong effects on the physical and chemical characteristics of water column carbon and nutrients (Shivers 2010). This project utilized these previous studies to build a framework for a whole lake study on how invasive species affect nutrient cycling and transformation in a subtropical reservoir. This project is focused on the following objectives:

Objective 1: To investigate the abiotic factors that control the distribution of *Hydrilla verticillata* over different hydrological conditions (drought versus wet years).

Objective 2: Use a mesocosm experiment to determine how different combinations of three invasive species, *Hydrilla verticillata*, *Corbicula fluminea*, and *Pomacea maculata*, affect nutrient cycling.

Objective 3: Elucidate how a subtropical reservoir shifts from functioning as a lake to a river during floods and the overall effects of these shifts.

Objective 4: Assess the distribution of two species of apple snails, one introduced from South America (*P. maculata)* and a second that is native to Florida (*P. paludosa*).

Objective 1 utilized monthly data collection and a series of visual plant surveys during the peak of the growing season during 2012, 2013, and 2014. An in-lake mesocosm experiment was designed and implemented to investigate objective 2. Objective 3 consisted of monthly surveys on all surface inflows and outflows between 2012 and 2014. Visual surveys of snail egg masses laid above the water line during 2012 and 2013 were used to complete objective 4.

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CHAPTER 2

CHANGES IN SAV COVERAGE AFFECT THE FUNCTION OF A SHALLOW SUBTROPICAL LAKE[1]

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[1] Shivers, S.D., S.W. Golladay, M.N. Waters, S.B. Wilde, and A.P. Covich. To be submitted to *Hydrobiologia*.

Abstract

Submerged aquatic vegetation (SAV) affects productivity and biogeochemical cycling within freshwater ecosystems. Changes in abiotic and biotic factors, driven by hydrological variation, that alter water clarity affect the spatial area covered by SAV. To evaluate variation in SAV coverage, annual whole-lake vegetation surveys were conducted during the peak of the growing season over a three-year period. Physical parameters were directly measured (PAR) or obtained from USGS river gages (river discharge and turbidity) to investigate the relationship between hydrology and SAV coverage. Precipitation was 62% lower in the first year of the study compared to the following two years causing the lowest river discharge observed over the three-year study. SAV coverage, particularly of *Hydrilla verticillata*, was the greatest during the reduced flow period (35.5 km^2). With increasing precipitation and river discharge, SAV coverage was reduced during subsequent years (22.9 km^2 and 18.3 km^2, respectively). Increased discharge caused turbidity to increase, which reduced light availability during the early growing season and caused a delay in germination and subsequent reduction in SAV coverage. Because of the large areas that SAV is capable of covering, large magnitude coverage changes can alter ecosystem functionality in freshwater systems.

Introduction

Freshwater ecosystems, i.e., rivers, streams, lakes, and reservoirs, comprise a small proportion of the Earth's surface but are important for the biogeochemical cycling of nitrogen, phosphorus, and carbon (Cole et al. 2007; Harrison et al. 2009; Tranvik et al. 2009). With an estimated global surface area of 1.5 million km^2, reservoirs play a crucial role in biogeochemical cycling that is expected to expand as the number of reservoirs increases (St Louis et al. 2000; Downing et al. 2006). Reservoirs function as integrators within landscapes and as sentinels for change (Williamson et al. 2008; Schindler 2009; Williamson et al. 2009). Reservoirs also facilitate the spread of invasive species through intense human activities, such as boating or fishing (Havel et al. 2005; Strayer 2010).

Several species of invasive submerged aquatic vegetation (SAV) are spread by human activities in addition to natural vectors. SAV affects overall productivity and biogeochemical cycling of freshwater ecosystems by directly altering variables such as concentrations of dissolved oxygen (DO) and nutrients, as well as pH (Carpenter and Lodge 1986). SAV also indirectly affects biogeochemical cycling by slowing water flow, which increases sedimentation rates (Sand-Jensen and Mebus 1996), or by releasing exudates into the water. These exudates increase microbial metabolism and alter microbially mediated processes, such as denitrification (Flindt et al. 1999; Ziegler and Benner 1999; Shivers et al. 2016).

SAV spatial coverage changes in response to either abiotic factors or biotic factors that alter water clarity (Depew et al. 2011; Ginn 2011; Bakker et al. 2012). Changes in coverage can either be positive or negative as a result of increasing or decreasing water clarity (Findlay et al. 2014; Gurbisz and Kemp 2014). Different types of SAV have varying physiological requirements and have different magnitudes of response to environmental changes (Chambers et al. 2008; Bornette and Puijalon 2011). In order to assess the effects of SAV on water quality and overall lake function, the spatial coverage of SAV must first be assessed. The objective of this project was to determine the area of lake surface covered by SAV and to investigate interannual changes in SAV spatial coverage. Previous studies have demonstrated the correlation between water conditions and vegetation coverage, but few have looked at how an aggressive invader (*Hydrilla verticillata*) responds to differing hydrological conditions and related water clarity on a lake-wide scale.

Methods

Site Description

Lake Seminole is a 152 km^2 impoundment located in southwestern Georgia and is the most downstream reservoir within the Apalachicola-Chattahoochee-Flint (ACF) Basin (Figure 2.1). Lake Seminole is shallow with a mean depth of 3 m and a maximum depth of 10.7 m. The Chattahoochee River, the Flint River, and Spring Creek are the major surface inflows and drain a combined land area of 46,141 km^2. The outflow from Lake Seminole is the Apalachicola River, which discharges into the Apalachicola Bay at the Gulf of Mexico. Groundwater also contributes a small component of inflow and outflow of the lake (Torak et al. 2006). Submerged aquatic vegetation (SAV) can cover large areas of the lake during the growing season and the SAV community is dominated by *Hydrilla verticillata*. *Hydrilla*, native to Asia, was introduced into the lake in the 1960s and can cover extensive areas (up to 76% within Spring Creek) if conditions are appropriate (Brown and Maceina 2002). *Hydrilla* exhibits seasonal growth patterns on Lake Seminole with a pre-growing season (January-March), early growing season

(April-June), peak growing season (July-September), and late growing season (October-December).

Vegetation Surveys

A visual survey by boat was conducted during the peak of the annual growing season (August-September) during 2012, 2013, and 2014. Beds of submerged and floating leaf vegetation were identified and delineated by collecting continuous data points using a Nomad GPS unit. SAV beds were classified into the following categories: hydrilla only, native only, hydrilla mixed, native mixed, and floating leaf only. Polygons were created from the field data using ArcMap 10.2.2 and zones free of vegetation were removed. Aerial photographic images from the 2009 and 2010 National Agriculture Imagery Program (NAIP) were used to remove emergent vegetation, such as *Typha* spp., from the polygon areas. Control points were used to assess the accuracy of removal.

Physical Measurements

Precipitation data from 18 locations extending across the ACF Basin were requested from the National Centers for Environmental Information division of NOAA. These data were averaged annually and for the pre and early growing season to represent rainfall between 2012-2014. Data from the closest stream gages to Lake Seminole, maintained by the United States Geological Survey (USGS), were used for calculating inflow into the lake for the Flint River (USGS 02356000), the Chattahoochee River (USGS 0234805), and Spring Creek (USGS 02357150). Average annual discharge was calculated using data from USGS gages at 15-minute intervals.

Physical parameters were measured within the reservoir (3 sites upstream representing the three surface inflows and 1 site below the dam to capture outflow) monthly or bimonthly between 2012 and 2014 (quarterly during the first quarter of 2012). Photosynthetically active radiation (PAR) was measured using a spherical quantum sensor (LICOR, LI – 193) mounted on a lowering frame. Measurements were taken at the surface to the sediment at 2 m intervals in the deeper water of the stream channel. The light extinction coefficient was calculated using the following formula: $I_z = I_o e^{-kz}$, where I_z = light at depth z, I_o= light at surface, k = extinction coefficient, and z = euphotic zone (m). Turbidity data from the Flint River stream gage were used from the National Water Information System provided by the United States Geological Survey.

Statistical Analysis

Statistical tests and graphics were created using GraphPad Prism 6. Analysis of variance (one-way ANOVA) with a post-hoc Tukey's HSD test was utilized for significance testing of hypotheses.

Results

Hydrology

Average annual precipitation was significantly different between 2012 and 2014 (F=56.7, $p<0.0001$). The 2012 precipitation was 62% lower than 2013 and 19% lower than 2014. A similar, but stronger, pattern was observed for pre and early growing season precipitation with 2012 being 82% lower than 2013 and 34% lower than 2014 (Table 2.1). Combined average annual discharge, calculated from 15-minute gage data, of the Flint River, the Chattahoochee River, and Spring Creek into Lake Seminole was significantly different between 2012 and 2014

(F=10422, $p<0.0001$) with 2012 (74 m^3/s) lower than 2013 or 2014 (208 m^3/s and 192 m^3/s)(Table 2.1). Average annual discharge for each inflow followed the same pattern with 2013 and 2014 discharges higher than 2012. Mean pre-growing season (January-June) discharge during 2013 and 2014 was also significantly higher for both the Flint and the Chattahoochee when compared to 2012 (F=9107, $p<0.0001$). In July and August 2013 there were higher than normal flows in both the Flint (301 m^3/s) and the Chattahoochee (427 m^3/s) rivers.

Physical Measurements

Mean annual turbidity was greater in 2013 (9.51 NTU) and 2014 (10.0 NTU) compared to 2012 (3.66 NTU) (Table 2.2). The same pattern of greater turbidity during pre- and early growing season 2013 and 2014 was also observed during the pre- and early growing season of 2012. The maximum turbidity was also greater during 2013 (48 NTU) and 2014 (33 NTU) than during 2012 (8.5 NTU). The mean light extinction coefficient was smaller in 2012 than either 2013 or 2104. The maximum light extinction coefficient was also smaller in 2012 than 2013 or 2014 (Table 2.2).

SAV Spatial Coverage

The greatest spatial extent of SAV occurred in 2012 (35.5 km^2) followed by decreases in 2013 (22.9 km^2) and in 2014 (18.3 km^2) (Table 2.3). The Flint River arm had the greatest spatial coverage of SAV in 2012 (15.9 km^2), followed by the Chattahoochee River arm (12.2 km^2), and Spring Creek had the least coverage (7.6 km^2). The Chattahoochee River exhibited the greatest decrease in SAV in 2013 but coverage rebounded somewhat in 2014 (Table 2.4). Conversely, SAV coverage decreased in both 2013 and 2014 in the Flint River and Spring Creek.

SAV beds composed solely of hydrilla exhibited large reductions of coverage decreasing from 20.4 km^2 to 8.0 km^2 between 2012 and 2013 and to 2.6 km^2 in 2014 (Figures 2.2, 2.3, and 2.4). Beds composed of mixed SAV including hydrilla also exhibited reductions in coverage decreasing from 14.7 km^2 to 11.3 km^2 between 2012 and 2014 (Table 2.3). In contrast, beds of mixed SAV without hydrilla increased from 0.1 km^2 to 0.5 km^2 between 2012 and 2013, and beds of native SAV also increased from 0.05 km^2 to 0.3 km^2 during the same time period (Figure 2.5). The largest increases in spatial coverage occurred for floating leaf SAV which increased from 0.4 km^2 to 3.6 km^2 between 2012 and 2014 (Table 2.3).

Discussion

Hydrology and Light

Hydrological variability in the ACF Basin is influenced by a suite of factors including diverse geology, climatic cycles and gradients, and a variety of human land- and water uses (LaFontaine et al. 2015). The Chattahoochee River begins in the Appalachian Mountains of northern Georgia, flows through several metropolitan areas, including Atlanta, and has 13 dams (4 creating large reservoirs) before reaching Lake Seminole. The lower Flint River and Spring Creek flow through predominately agricultural areas and are relatively unimpeded (two run of the river dams on the Flint). Thus, each river responds differently to precipitation events. Lower precipitation across the entire ACF Basin in 2012 led to lower flow into Lake Seminole. The lower ACF Basin consists of karst geology and groundwater dominates baseflow during low flow periods (Golladay and Battle 2002). This type of baseflow exhibits low suspended sediments and low turbidity. Thus, turbidity decreased with low flows and PAR, measured by light penetration, increased. Extraction of water, both from surface and ground sources, particularly in the Flint River and Spring Creek basins, to support irrigated agriculture further reduced flow with reduced precipitation during the growing season in 2012, but these effects were more prevalent in the agriculturally dominant Flint River and Spring Creek basins (Rugel et al. 2012). In contrast, higher precipitation in 2013 and 2014 caused increased surface flow into Lake Seminole. During high flow periods, surface water flow paths dominate differing from low flow periods (Golladay and Battle 2002). These surface flows are turbid and have more suspended sediment because of wetlands and swamps discharging into the creeks and rivers. Increased flows caused greater turbidity and decreased PAR. More importantly, changes in turbidity and PAR were pronounced during the pre and early growing season during both 2013 and 2014. This response of SAV to turbidity is similar to results reported in a large lake in Florida (Havens et al. 2004).

Overall SAV Spatial Changes

The high spatial coverage of overall SAV within the lake in 2012 was primarily the result of previous hydrological conditions (low rainfall and low discharge) and was attributable to extensive coverage by *Hydrilla*. The 2012 growing season was the last year of a multi-year drought in the southeastern U.S. and drought conditions favored *Hydrilla* growth by promoting good water clarity in the pre and early growing season. *Hydrilla* can propagate through a variety of methods including fragmentation, seeds, turions, and tubers (Langeland 1996). Tubers are subterranean reproductive structures that can remain viable for several years in the sediment. *Hydrilla* growth from tubers is fast with biomass doubling time ranging from 2 to 11 days under good growing conditions (Bianchini et al. 2010). These tubers provide *Hydrilla* with a fast growth response following winter conditions once sufficient light is available for sprouting. This offers *Hydrilla* a competitive advantage over other types of SAV (Fleming and Dibble 2015). The lower turbidity and increased water clarity prior to and during the 2012 growing season likely allowed *Hydrilla* coverage to be close to the theoretical maximum based on lake bathymetry in all three river arms (Figure 2.6).

The significant reduction of overall changes in SAV coverage after 2012 was largely driven by reduction in the coverage of *Hydrilla*. The PAR decreased in 2013 and 2014 as a result of increased turbidity, particularly in the pre and early growing season. Previous studies have demonstrated that *Hydrilla* is adapted to low light conditions (Langeland 1996), however a minimum light threshold (10-20 $\mu\text{mol}\backslash\text{s}^{-1}\text{m}^{-2}$ or $k_d < 2.5$) limits *Hydrilla* growth (Sousa 2011). During the early growing season in 2013 and 2014 as well as late July/early August 2013, water conditions in Lake Seminole approached the minimum thresholds resulting in inhibition of *Hydrilla* growth and reduced coverage. Because *Hydrilla* dominates the SAV community in Lake Seminole, its inhibition caused reduced overall SAV coverage in 2013 and 2014. The majority of the coverage loss was from decreases in beds composed solely of *Hydrilla*, whereas smaller changes were observed in beds of mixed *Hydrilla*. The presence of other SAV within mixed beds likely slowed water flow and increased deposition of suspended sediments, thus creating suitable condition for *Hydrilla* to grow (Rybicki and Landwehr 2007).

The response of vegetation to increased flow and turbidity was also different among the different inflows. SAV coverage on the Flint River arm decreased consistently between 2012 and 2014. However, the SAV on the Chattahoochee River arm responded with a large decrease in 2013 and followed by expansion in 2014. Declines on both arms in 2013 were likely the result of the unusual summer flood pulse. This flood pulse extended turbid conditions on the main body of the lake well into the 2013 growing season.

Response by other SAV

Native SAV responded to the decline in *Hydrilla* coverage with a small increase in coverage in 2013. Previous studies have shown that this is a common response by native vegetation to decreasing invasive coverage (Smart et al. 1998; Hofstra and Clayton 2014). Further increases were not observed in 2014. The persistence and duration of *Hydrilla* would likely slow the spread of native vegetation, but if *Hydrilla* regrowth were prevented for an extended period of time, the native community might undergo further expansion (Smart et al. 1998).

A greater response was observed for floating leaf plants compared to submerged plants, however the apparent increases may be misleading. In 2013, most of the increase in floating leaf coverage was the result of *Hydrilla* not returning to areas of mixed vegetation while floating leaf plants did return. The ability of floating leaf vegetation to grow in turbid water is consistent with previous studies (Bornette and Puijalon 2011). This vegetation shift might be utilized in the overall management of *Hydrilla* by establishing, in areas where possible, an environmental flow regime. Preserving late spring runoff would reduce *Hydrilla* coverage while allowing other types of vegetation to grow and would be more cost effective and environmentally sound compared to chemical control.

Changes in Lake Function

The substantial decrease in SAV coverage, particularly of *Hydrilla*, caused the reservoir to change how it functions at the SAV bed level and overall. The shift from submerged vegetation to floating leaf vegetation altered physical processes and changed how these SAV beds function. A combination of *Hydrilla* not returning and the structural nature of floating leaf plants results in water flow being less impeded. This can result in significant changes to nutrient transformations and sedimentation. Without impeded flow, sedimentation rates would decrease resulting in increased turbidity. Thus, the transition from thick beds of SAV to thin beds of floating leaf plants could produce a positive feedback loop further reducing SAV from returning (Madsen et al. 2001; Rovira et al. 2016).

Hydrilla is a highly productive plant that can utilize nutrients from both the sediment and the water column (Barko and Smart 1986). In addition to affecting physical processes within SAV beds, changes in *Hydrilla* coverage may also affect the water quality of the reservoir. *Hydrilla* affects nutrient cycling through direct uptake, and indirectly by creating appropriate conditions (i.e. increased sedimentation and low benthic DO) for microbial processing of nutrients. *Hydrilla* also stabilizes the sediment preventing sediment resuspension, which can reduce internal loading of nutrients. This reduction is important in Lake Seminole because of the high sediment P concentrations that reach levels observed in eutrophic lakes (Waters et al. 2015). Conversely, increased sedimentation caused by *Hydrilla* might have contributed to the high P concentrations as P is sequestered within the sediment. Because *Hydrilla* can cover large spatial areas, localized physical and chemical effects can be translated to the reservoir scale, thus the lake may serve as a source or a sink for nutrients depending on the level of SAV coverage. Reducing nutrient concentrations in the outflowing Apalachicola River is an important function of the reservoir in order to prevent damage to the fragile ecosystem within Apalachicola Bay, which is a productive oyster and finfish fishery. Therefore, management strategies ought to consider the useful ecosystem services provided by *Hydrilla* and might be adjusted to maximize the overall ecosystem function of the lake (Evans et al. 2007; Hershner and Havens 2008).

Overall, the response of vegetation, particularly *Hydrilla*, was surprising as the large magnitude of change was not expected over a short time scale. However, hydrological conditions were more appropriate for SAV growth in 2015 and *Hydrilla* regained much of the lost coverage from the previous two years (personal observation). It is clear that SAV, especially invasive SAV, influences on a lake-wide scale and that SAV coverage can vary significantly over short time scales. Combining these qualities results in altering how a lake or reservoir functions and can change the water quality both within and downstream of the lake. As the quality of water, not only the quantity, becomes more important for management and regulation of freshwater resources, entities within lakes that might alter lake function must be addressed. Future research should investigate the contributions of in lake processes to overall water quality within a drainage basin.

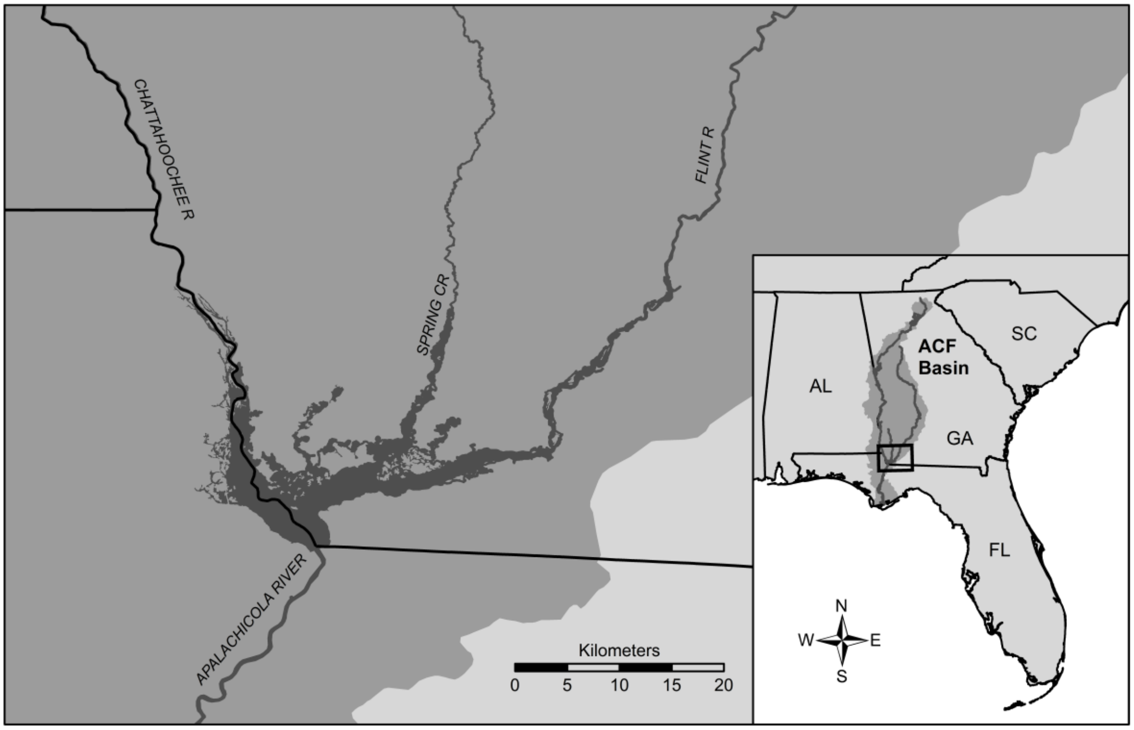

Figure 2.1: Lake Seminole is located in southwestern Georgia and is formed by the confluence of the Chattahoochee River, the Flint River, and Spring Creek; the outflow is the Apalachicola River.

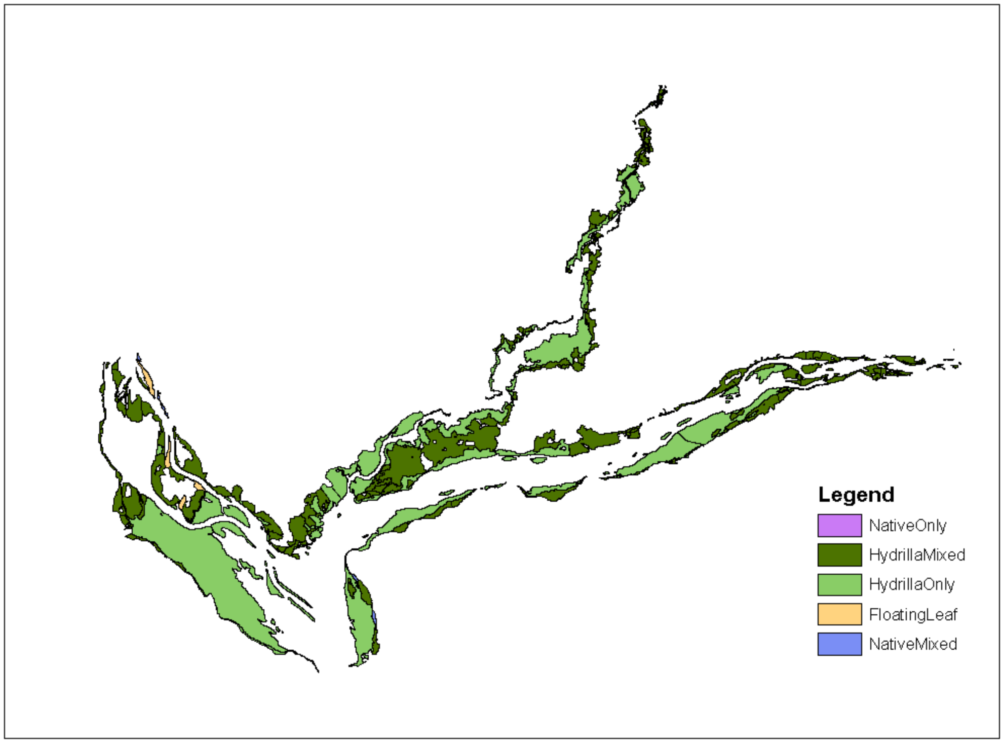

Figure 2.2: The spatial coverage of SAV in 2012.

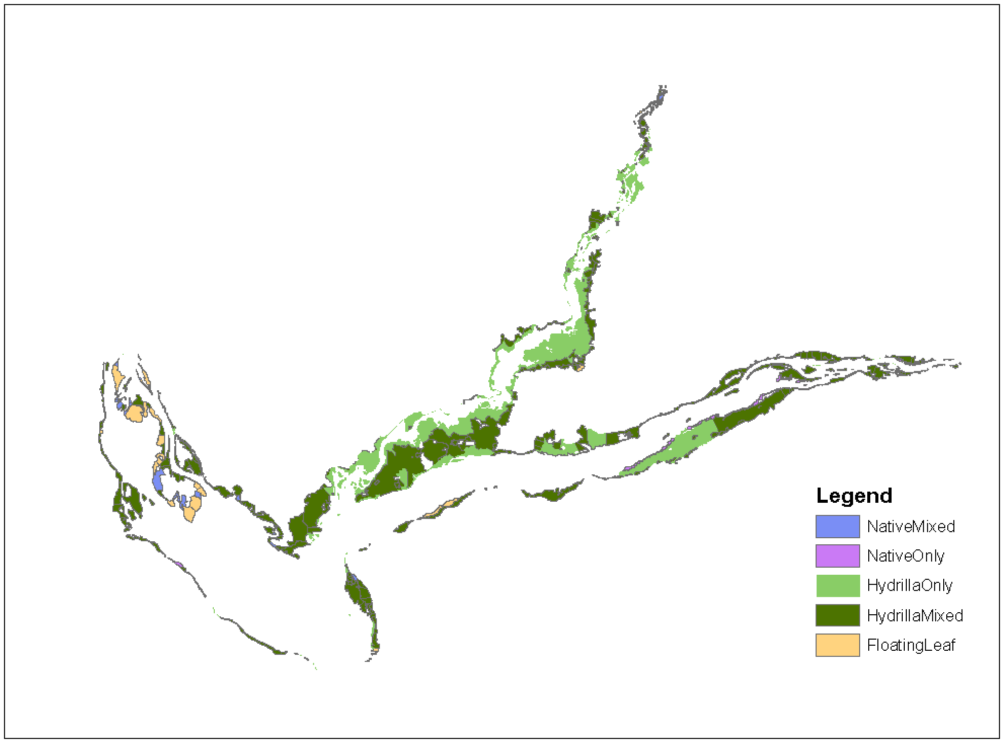

Figure 2.3: The spatial coverage of SAV in 2013.

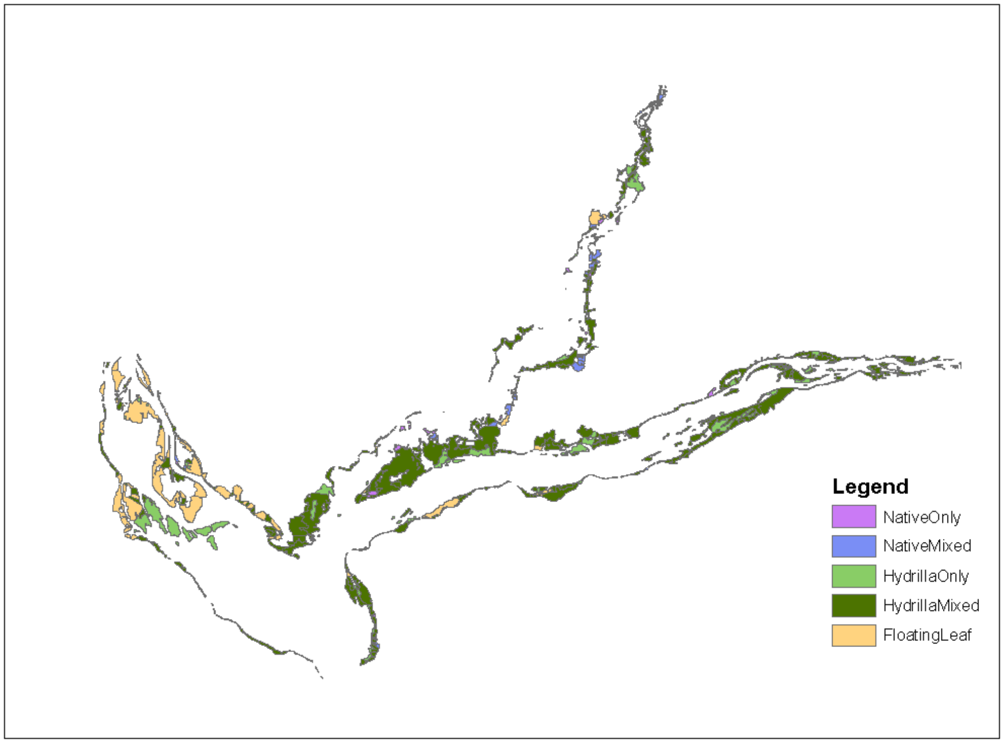

Figure 2.4: The spatial coverage of SAV in 2014.

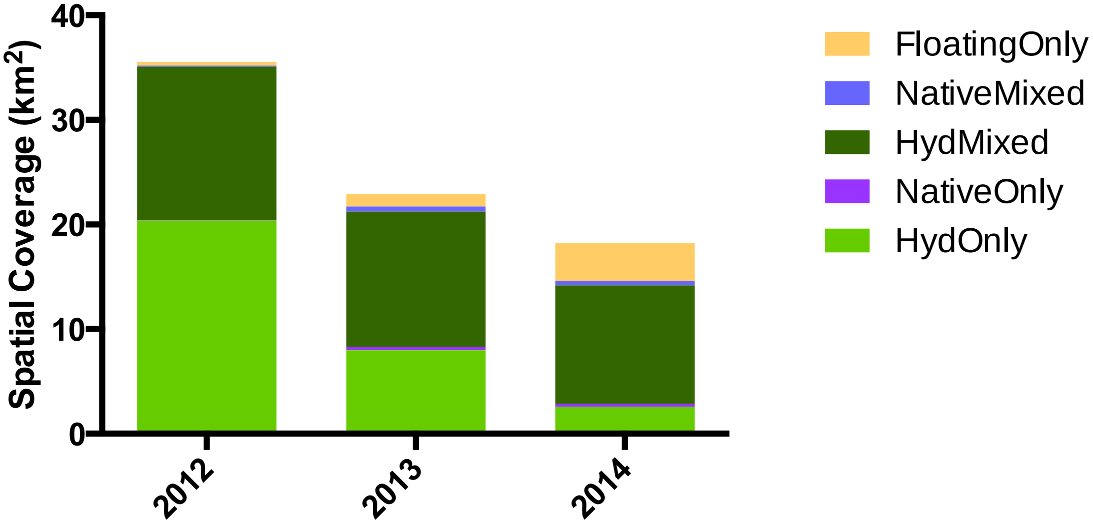

Figure 2.5: Categorical breakdown of SAV in 2012, 2013, and 2014.

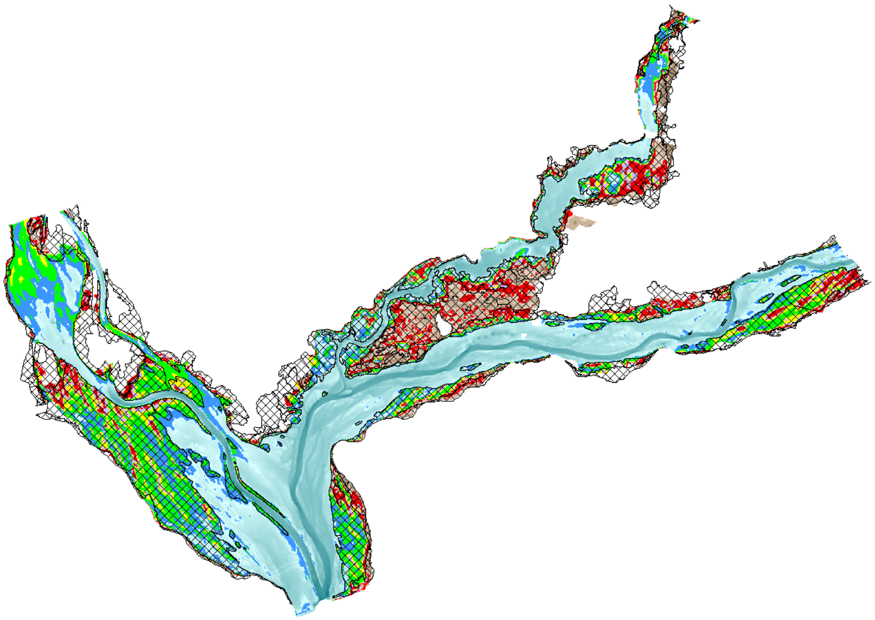

Figure 2.6: In 2012, SAV coverage (represented by crosshatched pattern) was near the theoretical maximum based on lake bathymetry. The warmer colors represent shallow areas where SAV growth is possible, and the cooler colors are deeper waters where SAV is limited by depth.

Table 2.1: Total precipitation (mm) and average discharge (m^3/s) for all inflows on annual and seasonal basis.

	Annual			**Pre/Early**		
	2012	**2013**	**2014**	**2012**	**2013**	**2014**
Precipitation	1114	1808	1324	525	956	702
Flint River Discharge	74±42	235±169	256±207	98±45	264±195	399±201
Chattahoochee River Discharge	129±174	334±347	270±335	175±209	362±360	408±404
Spring Creek Discharge	7±5	13±7	12±8	8±6	12±8	21±6
Combined Discharge	74±117	208±264	192±261	95±141	223±280	314±322

Table 2.2: Mean and maximum turbidity (NTU) and light extinction coefficient (k) both annually and seasonally.

	Annual			**Pre/Early**		
	2012	**2013**	**2014**	**2012**	**2013**	**2014**
Mean Turbidity	3.66	9.51	10	5.3	14.9	17.5
Max Turbidity	8.5	48	33	8.5	48	33
Mean k	1.2	1.3	1.58	1.2	1.4	1.7
Max k	1.89	2.57	3.1	1.89	2.57	3.1

Table 2.3: SAV coverage (km^2) of Lake Seminole between 2012 and 2014.

	Hyd Only	**Native Only**	**Hyd Mixed**	**Native Mixed**	**Floating Only**	**Total**
2012	20.4	0.05	14.7	0.1	0.4	35.5
2013	8.0	0.3	13.0	0.5	1.2	22.9
2014	2.6	0.3	11.3	0.4	3.6	18.3

Table 2.4: SAV coverage (km^2) in each river arm of Lake Seminole between 2012 and 2014.

	Flint River	**Chattahoochee River**	**Spring Creek**
2012	15.9	12.2	7.6
2013	12.1	3.7	7.2
2014	9.1	5.2	4.0

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CHAPTER 3

RIVERS TO LAKES: HYDROLOGICAL DRIVERS CONTROL LAKE FUNCTION BY AFFECTING THE ABUNDANCE OF SUBMERGED AND FLOATING MACROPHYTES[1]

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[1] Shivers, S.D., S.W. Golladay, M.N. Waters, S.B. Wilde, and A.P. Covich. To be submitted to *Limnology and Oceanography*.

Abstract

Lakes and reservoirs are important sites for biogeochemical cycling on both a regional and global scale. Shallow lakes can have higher coverage of submerged aquatic vegetation (SAV) and greater interactions between the sediment and the water column compared to deeper lakes. These biotic and abiotic interactions can alter nutrient cycling. This study evaluated how hydrologically driven changes in SAV coverage affected nutrient processing within a reservoir. To assess these effects, a comprehensive water quality monitoring program was established that quantified nutrient concentrations in the inflows and outflow of the lake. Annual vegetation surveys were completed to quantify the spatial coverage of SAV. Annual inflow was significantly lower in the first year of the study (74 m^3/s) compared to the following two years (208 m^3/s and 192 m^3/s). Consequently, SAV coverage was also highest during the lowest flows during the first year (35.5 km^2) and was lower the following two years (22.9 km^2 and 18.3 km^2). NO_3-N concentrations were also lowest during the growing season of the first year. Therefore, hydrological variation was driving the coverage of SAV, and SAV coverage altered nutrient processing at the reservoir scale.

Introduction

Although inland freshwater ecosystems comprise a small proportion of the Earth, these ecosystems are important for the biogeochemical cycling of nitrogen, phosphorus, and carbon (Harrison et al. 2009; Finlay et al. 2013; Hanson et al. 2015). These processes have functional links among streams, rivers, wetlands, lakes, and reservoirs. With an estimated global surface area of 1.5 million km^2, reservoirs are integral in biogeochemical processes, and these effects may be enhanced given that the number of reservoirs is predicted to increase in many parts of the world (St Louis et al. 2000; Downing et al. 2006). Because of their position within a watershed, reservoirs are integrators of the landscape and can function as sentinels for change (Schindler 2009; Williamson et al. 2009). Reservoirs internally affect the storage and transformations of sediments, nutrients, and organic matter that can alter water quality of downstream habitats. These processes are affected by regional differences in land use, hydrology, and climate (Powers et al. 2013).

Reservoir size and shape is dependent on the geography of the underlying valley in which the dam was constructed resulting in many reservoirs being shallow (Hutchinson 1975, Morris and Fan 1998). Shallow and deep basins function differently because of distinct attributes such as longer residence times of nutrients that can accumulate in deep, density-stratified lakes and reservoirs (Lewis 1983). Shallow waters have greater effects from sediment-water interactions, such as wind-driven mixing, and can have high spatial coverage by submerged aquatic vegetation (SAV) (Scheffer and Nes 2007). In shallow lakes that are subject to seasonal flooding some submerged plants can be transported downstream by high flows that affect nutrient budgets and dominance relationships (e.g., Franklin et al. 2008, Hilt et al. 2011, Zhu et al. 2012). The increased abundance of SAV can cause a persistent shift from primary production by phytoplankton to SAV once a tipping point is reached in available nutrients or other drivers (Scheffer 2004, 2009, de Tezanos Pinto and O'Farrell 2014).

SAV can directly affect productivity and biogeochemical cycling in freshwater ecosystems, and these effects can result in changes in the physical and chemical parameters of water quality, such as: dissolved oxygen (DO), pH, dissolved organic carbon (DOC) concentrations and nutrient concentrations (Carpenter and Lodge 1986). SAV can also indirectly affect biogeochemical cycling by slowing water flow, which changes sedimentation rates (Sand-Jensen and Mebus 1996) or by releasing exudates into the water which can increase microbial metabolism and alter microbially mediated processes, such as denitrification (Wetzel 1969; Flindt et al. 1999; Ziegler and Benner 1999). Large amounts of diverse SAV also increase the surface area by several orders of magnitude that affect the growth of periphyton and biofilm aggregates of microbes. These macrophyte structures and associated food resources are important for growth of invertebrates and small fishes, as well as for sustaining populations of adult fish (e.g., Chambers et al. 2008, Bornette and Puijalon 2011).

The objective of this study was to determine how variation in SAV spatial coverage, caused by different hydrological patterns, affects nutrient processing within a shallow reservoir, Lake Seminole, GA, USA. We investigated local effects of SAV on water quality as well as effects on the reservoir scale. We compared the effects of different annual and seasonal discharges on biogeochemical processes from three inflows relative to their effects on SAV. We determined that some reservoirs can function differently than the alternate stable state theory predicts relative to the dominance of SAV (Scheffer 2004, 2009, de Tezanos Pinto and O'Farrell

2014). This study suggests that a different characterization from that used for lakes is needed for shallow run-of-river reservoirs such as Lake Seminole where residence times of inflowing nutrients and internal recycling from sediments vary seasonally and annually.

Methods

Site Description

Lake Seminole is a 152 km^2 impoundment located in southwestern Georgia and is the most downstream reservoir within the Apalachicola-Chattahoochee-Flint (ACF) Basin (Figure 3.1). Lake Seminole is shallow with a mean depth of 3 m and a maximum depth of 10.7 m (Brown and Maceina 2002). The Chattahoochee River, the Flint River, and Spring Creek are the major surface inflows and drain a combined land area of 46,141 km^2. The outflow from Lake Seminole is the Apalachicola River, which discharges into the Apalachicola Bay in the Gulf of Mexico. The landscape through which these rivers flow is different for each river. The Chattahoochee River begins in the Appalachian Mountains and flows through several metropolitan areas, including Atlanta, and is impounded at 13 locations (four creating large reservoirs) before reaching Lake Seminole. In contrast, the Flint River and Spring Creek flow through an agricultural landscape and are relatively unimpeded. These diverse landscapes result in different physical and chemical qualities of the three surface inflows. Groundwater contributes a smaller component of inflow and outflow (Torak et al. 2006).

Submerged aquatic vegetation (SAV) can cover large areas of the lake during the growing season and the SAV community is dominated by *Hydrilla verticillata*. *Hydrilla*, native to Asia, was introduced into the lake in the 1960s and can cover extensive areas (up to 76% within Spring Creek) if conditions are appropriate (Brown and Maceina 2002). *Hydrilla* exhibits seasonal growth patterns on Lake Seminole with a pre-growing season (January-March), early growing season (April-June), peak growing season (July-September), and late growing season (October-December).

Vegetation Surveys

A visual survey by boat was conducted during the peak of the annual growing season (August-September) during 2012, 2013, and 2014. Beds of submerged and floating leaf vegetation were identified and delineated by collecting continuous data points using a Nomad GPS unit. The survey focused on the main body of the lake and excluded the upper reaches of all three rivers as well as backwater areas (74 km^2 surveyed). Polygons were created from the field data using ArcMap 10.2.2 and zones free of vegetation were removed. Aerial photographic images from the 2009 and 2010 National Agriculture Imagery Program (NAIP) were used to remove emergent vegetation from the polygon areas. Control points were used to assess the accuracy of removal.

Physical and Chemical Measurements

Field data was collected from 10 sites with six representing inflow (two in each river arm) and one below the dam representing outflow. The remaining three sites were located within areas that are historically covered by *Hydrilla* (one in each river arm), although coverage was variable during this study. Temperature, dissolved oxygen (DO), pH, and conductivity were measured in situ using a Hydrolab Quanta System (Hach Laboratories). Physical measurements were taken from the surface to the sediment at 2 m intervals at all locations except the *Hydrilla* sites. *Hydrilla* site measurements were taken at three depths (surface, middle, and sediment surface). Water samples were collected at all sites in 1 L Nalgene polycarbonate bottles and placed on ice until returned to the lab. Water samples were filtered through pre-ashed 0.7 μm glass fiber filters within 24 hours of collection and stored either below 0°C (NO_3 and PO_4) or between 0°C and 5°C (DOC) until analysis. DOC was measured using a Shimadzu TOC-V total organic carbon analyzer. NO_3-N and PO_4-P were measured using a Lachat QuikChem 8500 series 2 flow injection analyzer and the corresponding appropriate method.

Statistical Analyses

Statistical tests and graphics were created using GraphPad Prism 6. T-tests with Welch's correction, in order to account for unequal variances, were used to determine significance of pH and % DO between presence and absence of SAV. Analysis of variance (one-way ANOVA) with a post-hoc Tukey's HSD test was utilized to assess the significance of differences in river flow and nutrient concentrations.

Results

Combined average annual discharge of the Flint River, the Chattahoochee River, and Spring Creek into Lake Seminole was significantly different between 2012 and 2014 ($F=10422$, $p<0.0001$) with 2012 (74 m^3/s) lower than 2013 or 2014 (208 m^3/s and 192 m^3/s). Average annual discharge for each inflow followed the same pattern with 2013 and 2014 discharges higher than 2012. Cumulative inflow from the tributaries was the lowest during the growing season of *Hydrilla* (44.3 m^3/s) and post-growing season (46.8 m^3/s) of 2012. Mean inflow increased in the pre-growing season of 2013 (260.8 m^3/s) and remained high until the growing season in 2014 (Figure 3.2). Inflow to the lake by the three rivers as well as outflow out of the lake via the Apalachicola River followed the same pattern.

SAV covered 48% of the lake surface area (35.5 km^2) in 2012 with *Hydrilla*, either in monoculture or mixed beds, covering 47% (35.0 km^2) of the lake's surface (Table 3.1). In 2013, overall SAV coverage was 31% of the lake and *Hydrilla* only was 28% coverage. Further reductions in both overall SAV (25%) and *Hydrilla* (19%) were observed in 2014. Even though overall SAV decreased each year, SAV responded differently in each river arm. SAV in the Flint River decreased steadily each year, while in Spring Creek a small decrease occurred in 2013 followed by a large decrease in 2014. In contrast, SAV in the Chattahoochee River arm decreased dramatically in 2013 while increasing in 2014.

Physical conditions at the *Hydrilla* bed sites varied among years and lake depths (Table 3.2). The combined average % DO and pH was highest in 2012 and lowest in 2013. In addition to annual variation, % DO and pH were different depending on whether or not SAV was present. Three-year average % DO at the surface was significantly higher when SAV was present (129%) compared to when SAV was absent (91%) ($t=4.7$, $p<0.001$). pH was also significantly higher at the surface during SAV presence (8.57) compared to SAV absence (7.77)($t=5.4$, $p<0.001$). A similar, but opposite, pattern was observed by sampling near the sediments where significantly lower % DO occurred when SAV was present (42%) versus when SAV was absent (85%)($t=7.0$, $p<0.001$). Similarly, pH was also significantly lower when SAV was present (7.59) compared to SAV absence (7.84)($t=3.3$, $p=0.002$).

NO_3-N concentrations followed dissimilar patterns among the Flint River, the Chattahoochee River, and Spring Creek (Table 3.3). The Flint River NO_3-N concentrations were intermediate compared to the Chattahoochee River or Spring Creek and were highest on average and less variable during 2012 but were not significantly different than 2013 or 2014. NO_3-N concentrations in the Chattahoochee River were lower than the other inflows and demonstrated seasonal fluctuations with higher concentrations during the pre growing season and lower concentrations throughout the rest of the year. NO_3-N concentrations were significantly lower in 2012 compared to 2013 or 2014 ($F=5.3$, $p<0.01$). Spring Creek had the highest overall concentrations of NO_3-N and had significantly higher concentrations on average during 2012 ($F=10.3$, $p<0.01$). *Hydrilla* bed sites in all inflows had the lowest average NO_3-N concentrations during the growing season 2012 (Table 3.4). Similarly, NO_3-N concentrations in the outflow were lowest during the growing season of 2012 and were greater during 2013 and 2014 (Figure 3.3).

Flint River DOC concentrations were significantly higher during 2013 and early 2014 ($F=15.7$, $p<0.01$)(Table 3.4). DOC concentrations in the Chattahoochee River arm exhibited very little change throughout 2012 and 2013 but were significantly lower in 2014 ($F=4.8$, $p<0.05$). Spring Creek DOC concentrations were lower during the later annual time periods among all three years. DOC concentrations in the *Hydrilla* sites followed similar patterns in the corresponding rivers (Table 3.5). DOC concentrations in the outflow were higher in 2013 on average compared to 2012 or 2014. PO_4-P remained at or near the detection limit of 5 μg/L during the majority of the study period in all areas of the lake.

Chlorophyll a concentrations were higher on average within the *Hydrilla* sites when SAV was present in all inflows and were significantly higher in the Flint River ($t=4.7$, $p<0.001$)(Figure 3.3). Average chlorophyll a concentrations in the mixing area of the dam were lower in the 2012 growing and post growing season compared to either 2013 or 2014 (Figure 3.4). Higher maximum concentrations were also observed during 2013 (36 μg/L).

Discussion

Hydrological Effects on Nutrient Inflow

Hydrology within the ACF Basin is influenced by a variety of factors because of the size of the basin and the diverse land uses of the region (LaFontaine et al. 2015). The rivers flowing into Lake Seminole differ chemically and physically because of the variation in geology and land (Peterson et al. 2013). Thus, hydrologic variation will affect concentrations of chemical constituents differently in each river and overall. Greater discharge during 2013 and 2014 contributed to a small increase in NO_3-N concentrations in the Chattahoochee River, decreases in Spring Creek, and no differences in the Flint River. Overall, NO_3-N concentration in the outflow was not closely related to discharge (Figure 3.5). These results are consistent with the abundant contributions of NO_3-N rich groundwater into the system as well as external inputs from agricultural practices (Allums et al. 2012). Increases in discharge may move more particulate and dissolved N from the wetlands and agricultural fields, particularly in the Flint River, into the system while reducing the relative contribution of groundwater. Thus, while forms of N vary, overall N concentrations remain elevated in the system regardless of discharge. Conversely, increases in discharge led to higher DOC concentrations in the Flint River and Spring Creek, while having no effect on concentrations in the Chattahoochee. DOC concentration in the outflow was related to discharge (Figure 3.6). Regional flushing from wetlands during high flow events likely contributed to increases in DOC in the Flint River and Spring Creek (Golladay and Battle 2002). The presence of storage reservoirs along the Chattahoochee River and less groundwater inputs helps to mitigate any changes in DOC concentration caused by increased discharge (Peterson et al. 2013).

Nutrient Processing Within SAV Beds

Significant increases in both DO and pH in the surface water within SAV beds of all arms indicate that high levels of photosynthetic activity are occurring when SAV is present. The production of O_2 and utilization of CO_2 during photosynthesis cause both DO and pH to increase. Significant decreases in both DO and pH in the water column near the sediment were also observed when SAV was present. The dense canopy of *Hydrilla* reduces light penetration, thus limiting O_2 production near the sediment surface (Langeland 1996). As plant material and other organic matter accumulate on the sediment, decomposition further reduces dissolved O_2 through microbial consumption. These processes can create hypoxic conditions near the sediment. Labile C is released through the decomposition of plant material as well as from live plants via exudates into the water. The presence of a labile C source stimulates microbial metabolism and the corresponding processes undertaken by the microbial community (Shivers et al. 2016).

NO_3-N concentrations were the least within the *Hydrilla* sites during 2012, which was also a time period of reduced flow velocity and increased SAV coverage. The high level of photosynthesis by *Hydrilla* requires an ample supply of nutrients, and *Hydrilla* can import nutrients through the roots in the sediment or directly from the water column (Barko et al. 1988). Thus, *Hydrilla* can directly reduce NO_3-N concentrations by direct uptake. The presence of rooted macrophytes can reduce water velocity causing increased deposition of suspended particles as well as allowing a higher residence time locally for water and decomposing organic matter (Sand-Jensen and Mebus 1996). The reduced O_2 conditions at the sediment as well as an ample supply of labile C and sufficient N create conditions conducive for denitrification (Caffrey and Kemp 1992; Holmroos et al. 2015). Combining a reduction in flow velocity with appropriate conditions for denitrification results in NO_3-N being converted to N_2 and leaving the system. NO_3-N concentrations increased in the Spring Creek *Hydrilla* site in 2014 when *Hydrilla* was slow to return and decreased in the Chattahoochee River *Hydrilla* site, when *Hydrilla* began to return. Therefore SAV, particularly *Hydrilla*, can affect NO_3-N concentrations both directly and indirectly.

SAV Controls on Nutrient Retention

Concentrations of NO_3-N in the reservoir outflow were the least during the growing season of 2012. This period also had the lowest flow and the highest spatial coverage of SAV. Interestingly, NO_3-N concentrations in the three inflows were at typical levels. Combining the patterns of inflow and outflow NO_3-N concentrations along with the high spatial coverage of SAV indicates that SAV was contributing to the processing of NO_3-N within the reservoir. This relationship was supported during the growing season of 2014. During this time, discharge from the inflows was similar to 2012, but the spatial coverage of SAV, particularly of *Hydrilla*, was low and NO_3-N concentrations in the outflow remained elevated. Similar decreases of DIN below SAV beds occurred after reemergence of SAV in the Chesapeake Bay (Gurbisz and Kemp 2014). Overall, these patterns provide support that invasive SAV can control nutrient processing on a reservoir-wide scale within a shallow lake, such as Lake Seminole.

In addition to affecting NO_3-N, the presence of SAV also can affect PO_4-P. Water column concentrations of PO_4-P are consistently low within Lake Seminole. However, concentrations of TP in the sediments of the lake are high, reaching levels consistent with eutrophic lakes (Waters et al. 2015). SAV stabilizes the sediment and prevents sediment resuspension thus reducing the internal cycling P (Scheffer 2004). Thus, the presence of SAV might contribute to the low concentrations observed in the water column.

Hydrilla, an aggressive invader, dominates the SAV coverage in Lake Seminole and has for some time (Grodowitz et al. 2003; Shivers 2010). It is used for phytoremediation of aquatic pollution in its native range. Previous studies have demonstrated that *Hydrilla* can obtain nutrients from both the water column and the sediment (Barko et al. 1988). In areas where *Hydrilla* is non-native, aggressive management procedures are employed to limit its spread, however management of *Hydrilla* becomes difficult once the plant has become established. It is not clear if native vegetation, such as *Potamogeton illinoensis*, would maintain the same level of nutrient retention as *Hydrilla*. Future management efforts need to consider the overall ecosystem function resulting from a switch from invasive to native SAV, and the costs associated, both economic and environmental, of invasive SAV eradication efforts. In areas where *Hydrilla* is established, the ecosystem services provided by *Hydrilla* may exceed the costs of removal efforts.

Rivers to Lakes – Discharge and SAV alter ecosystem function

One of the primary reasons that SAV is able to exert control over nutrient retention is that Lake Seminole is a shallow lake. Shallow lakes can have alternate stable states when abiotic and biotic drivers cause a change between two different states. During this change, a lake shifts from a clear water state dominated by macrophytes to a turbid state dominated by phytoplankton (Scheffer et al. 1993, Loverde-Oliveira et al. 2009, Hilt et al. 2011). These states are generally self-reinforcing thus both exist as stable, but alternate states. Cycling between these states can vary in regularity and frequency, and the drivers of the shift can change depending on local conditions. Lakes that shift frequently due to abiotic factors, such as low winter temperatures or seasonal ice cover, may lack the necessary mechanisms to reinforce a stable state (Bayley et al. 2007). SAV provides a mechanism that serves to reinforce a stable state by promoting clear water (Loverde-Oliveira et al. 2009). However, over longer time scales SAV coverage may reduce conditions for growth as a result of nutrient retention by SAV and subsequent eutrophication caused by internal nutrient cycling from sediments (Hutchinson 1975; van Nes et al. 2007). Increased suspended sediment resulting from increased river flow can cause sudden shifts in SAV coverage (Findlay et al. 2014; Gurbisz and Kemp 2014). These studies demonstrate similar dynamic shifts in SAV coverage that were observed in Lake Seminole but were located in river to estuary settings (Hudson River and Chesapeake Bay).

Because Lake Seminole is a run-of-the-river reservoir, it functions differently than many other types of lakes, including deeper reservoirs whose main function is water storage. Therefore, it is useful to provide a description different from the alternate stable state theory for the way in which run of the river reservoirs function as opposed to other types of lakes. The transitional nature of a run of the river reservoir occurs when the reservoir switches from functioning as a river to functioning as a lake. During periods of high river flow, Lake Seminole exists in a riverine state with very little nutrient retention. In contrast, during average or low river flow Lake Seminole functions more as a lake and has greater potential to retain nutrients. The nutrient storage capacity is partially dependent on the spatial coverage of SAV, which is also controlled by river flow and the associated effects of light penetration in the water column. Therefore, managing the coverage of SAV through environmental flows, a late winter or early spring flood pulse in Lake Seminole, could delay the annual onset of *Hydrilla*. This delay would reduce nuisance coverage of *Hydrilla* while sustaining sufficient coverage for beneficial ecosystem services, such as maintaining water quality and food web dynamics. Chlorophyll a concentrations were not higher when SAV was not present thus the turbid algal state was not reached. The lack of an algal-driven turbid state allows SAV to return quickly when the suspended sediment loads decrease. One indication of this switch to phytoplankton production occurred when algal blooms were observed, along with a spike in chlorophyll a, in the mixing area of the lake near the dam during 2013. Although the main channel near the dam is too deep to have extensive SAV, the bloom was most likely the result of the decrease in overall SAV resulting in more available nutrients near the dam. Therefore, hydrology drives the shift between river and lake function by mediating the coverage of SAV.

In a changing climate, local and regional conditions are expected to be different in the future with greater oscillations between wet and dry seasons. These changes will create further complexities and uncertainties, particularly in watersheds that are already stressed by anthropogenic influences. Management of water resources at the watershed scale must take into account nutrient processing and storage at the reservoir level and the drivers, both abiotic and biotic, that affect biogeochemical cycling in order to maintain water quality.

Table 3.1: The spatial coverage (km^2) of total SAV and *Hydrilla* between 2012 and 2014.

	2012	**2013**	**2014**
Total SAV (km^2)	35.5	22.9	18.3
***Hydrilla* (km^2)**	35.0	20.9	13.9

Table 3.2: Dissolved Oxygen (DO) and pH measurements at *Hydrilla* sites annually and three year averages at different depths. Mean ± s.d.

	Surface		**Middle**		**Deep**		**Annual**		
	SAV Present	SAV Absent	SAV Present	SAV Absent	SAV Present	SAV Absent	2012	2013	2014
pH	8.6±0.8	7.8±0.3	8±0.7	7.8±0.4	7.6±0.4	7.8±0.2	8.2±0.8	7.7±0.4	7.9±0.3
DO (%)	129±45	91±15	89±44	85±14	43±32	85±14	95±46	80±36	90±23

Table 3.3: NO_3-N concentrations (µg/L) within the three inflows between 2012 and 2014. Mean ± s.d.

	Flint River	**Chattahoochee River**	**Spring Creek**
Pre2012	887±21	534±30	2706±1098
Early2012	902±111	404±215	1537±743
Grow2012	905±156	272±105	2527±319
Post2012	1153±68	231±20	2771±784
Pre2013	413±16	634±100	468±54
Early2013	837±245	487±78	1478±596
Grow2013	765±285	386±61	653±343
Post2013	1352±41	444±21	2127±507
Pre2014	655±236	721±136	887±247
Early2014	850±362	568±111	1029±926
Grow2014	1211±163	208±125	2483±285

Table 3.4: NO_3-N concentrations (μg/L) within *Hydrilla* sites located in the three rivers. Mean ± s.d.

	Flint River	**Chattahoochee River**	**Spring Creek**
Pre2012	874±6	596±3	1482±17
Early2012	299±172	400±184	685±240
Grow2012	263±94	67±64	30±58
Post2012	579±235	164±49	1384±682
Pre2013	416±17	643±128	534±315
Early2013	647±75	420±87	963±360
Grow2013	651±233	347±33	44±113
Post2013	1216±70	433±6	719±803
Pre2014	643±199	660±123	845±93
Early2014	833±293	463±96	1161±658
Grow2014	603±277	195±76	902±465

Table 3.5: DOC concentrations (mg/L) within *Hydrilla* sites located in each of the three rivers. Mean ± s.d.

	Flint River	**Chattahoochee River**	**Spring Creek**
Pre2012	4.36±0.08	5.62±0.45	0.99±0.36
Early2012	1.99±1.58	4.10±0.52	4.08±2.92
Grow2012	1.18±0.38	4.12±0.48	0.58±0.28
Post2012	1.61±0.26	3.98±0.64	0.54±0.25
Pre2013	8.78±1.00	4.88±0.79	10.22±0.79
Early2013	4.45±1.86	4.41±0.59	3.51±2.12
Grow2013	6.31±0.63	4.66±0.59	9.42±1.69
Post2013	3.22±0.29	4.26±0.62	0.69±0.82
Pre2014	5.31±1.23	3.54±0.05	5.39±0.69
Early2014	5.73±1.38	4.14±0.78	7.00±2.86
Grow2014	1.35±1.05	3.66±0.76	0.34±0.45

Table 3.6: DOC concentrations (mg/L) in the three inflows of Lake Seminole. Mean ± s.d.

	Flint River	**Chattahoochee River**	**Spring Creek**
Pre2012	4.31±0.03	5.60±0.06	1.44±0.03
Early2012	3.19±0.76	4.33±0.14	3.25±1.09
Grow2012	1.55±0.37	4.20±0.21	2.22±0.55
Post2012	2.41±0.65	4.43±0.72	1.30±0.29
Pre2013	8.54±1.00	4.73±0.86	10.02±2.41
Early2013	4.72±1.30	4.16±0.19	3.07±1.15
Grow2013	6.28±0.42	4.38±0.68	5.64±3.44
Post2013	3.21±0.31	4.01±0.46	0.87±0.95
Pre2014	5.22±1.14	3.95±0.23	5.38±0.60
Early2014	5.38±1.16	4.20±0.68	5.76±2.08
Grow2014	1.86±1.00	3.28±0.16	1.61±0.19

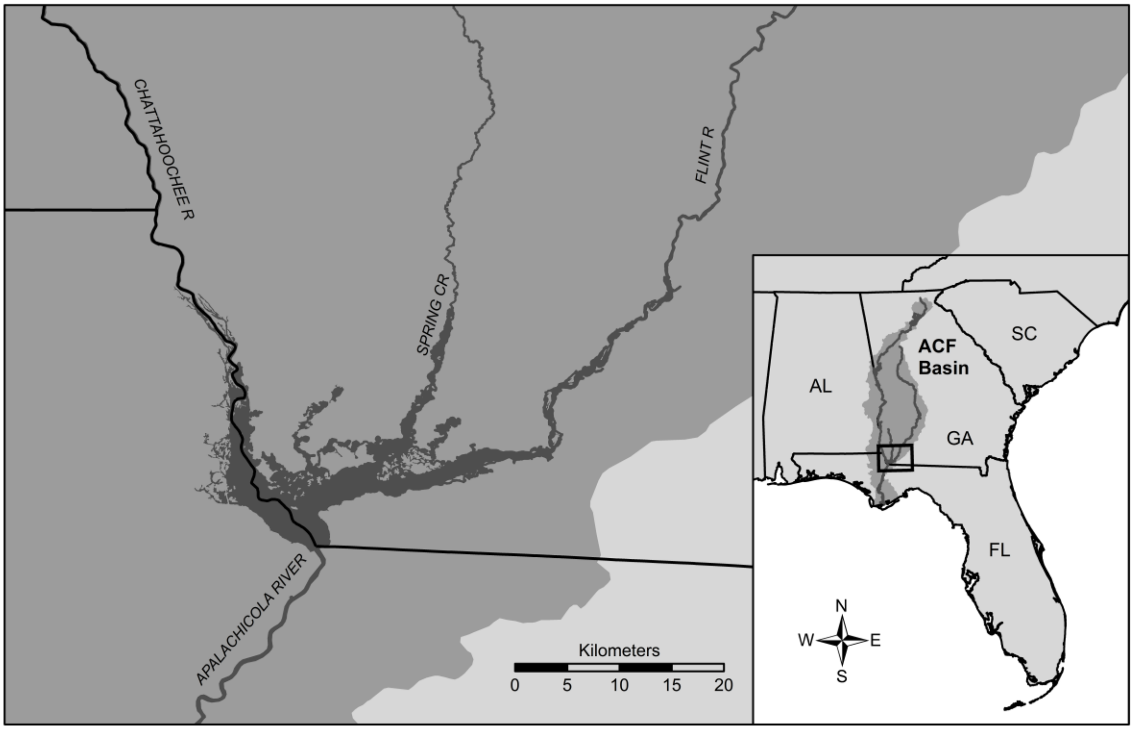

Figure 3.1: Lake Seminole is located in southwestern Georgia and is formed from the confluence of the Flint River, the Chattahoochee River, and Spring Creek. The Apalachicola River is the outflow and flows south into the Gulf of Mexico.

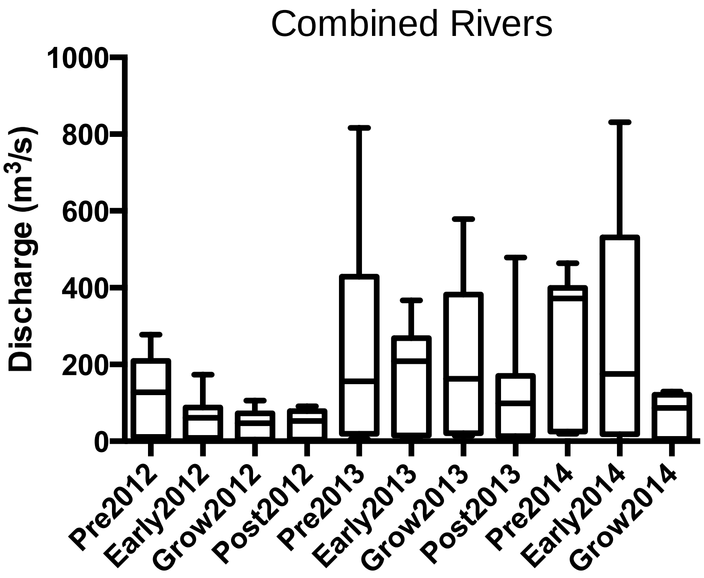

Figure 3.2: The combined average annual discharge of the three inflows (Flint River, Chattahoochee River, and Spring Creek) of Lake Seminole. The boxes represent median, 25th and 75th percentiles and the whiskers represent min and max values.

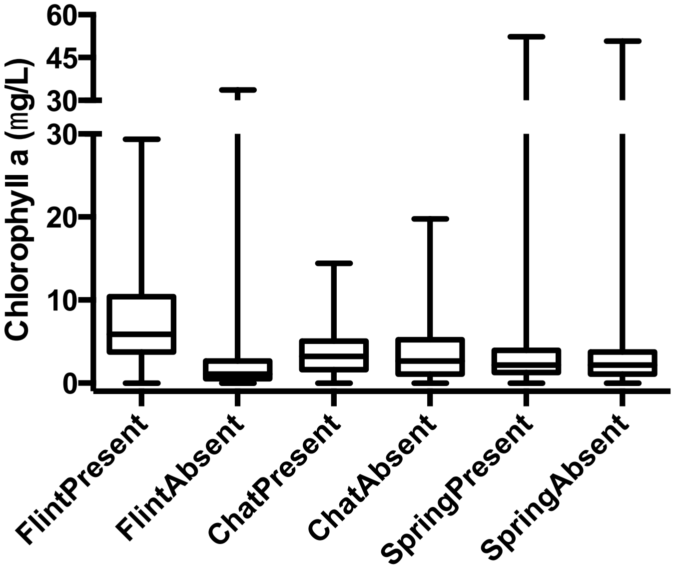

Figure 3.3: Chlorophyll a concentrations (μg/L) with SAV present and absent within the *Hydrilla* sites in each river. The boxes represent median, 25th and 75th percentiles and the whiskers represent min and max values.

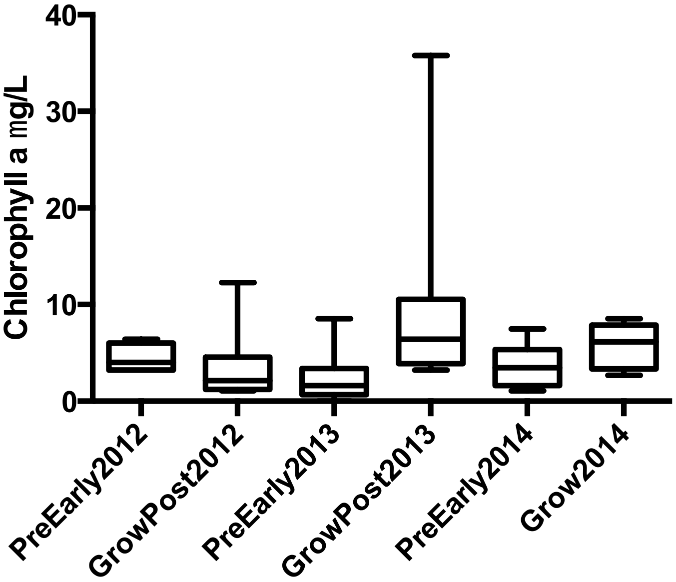

Figure 3.4: Chlorophyll a concentrations (μg/L) in the mixing zone of the three inflows in front of the dam. The boxes represent median, 25th and 75th percentiles and the whiskers represent min and max values.

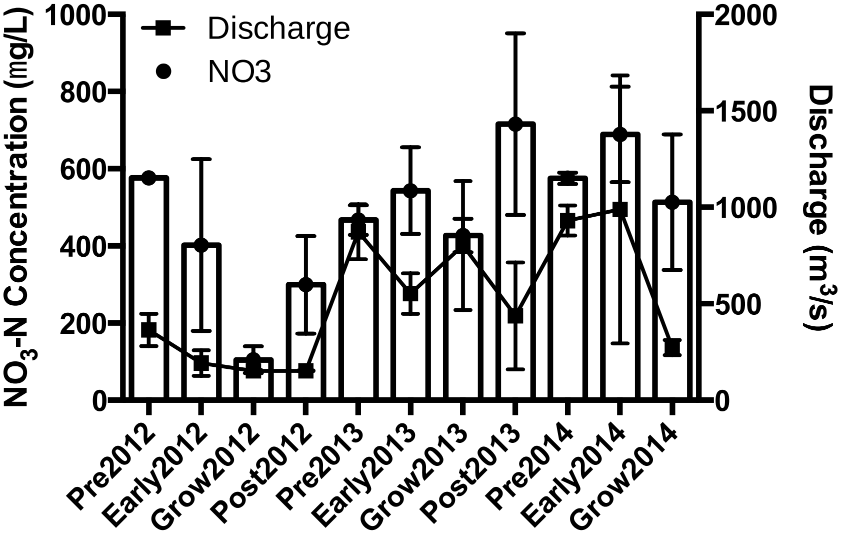

Figure 3.5: NO_3-N concentration (μg/L) and discharge (m^3/s) of the Apalachicola River below the dam. Error bars are s.d.

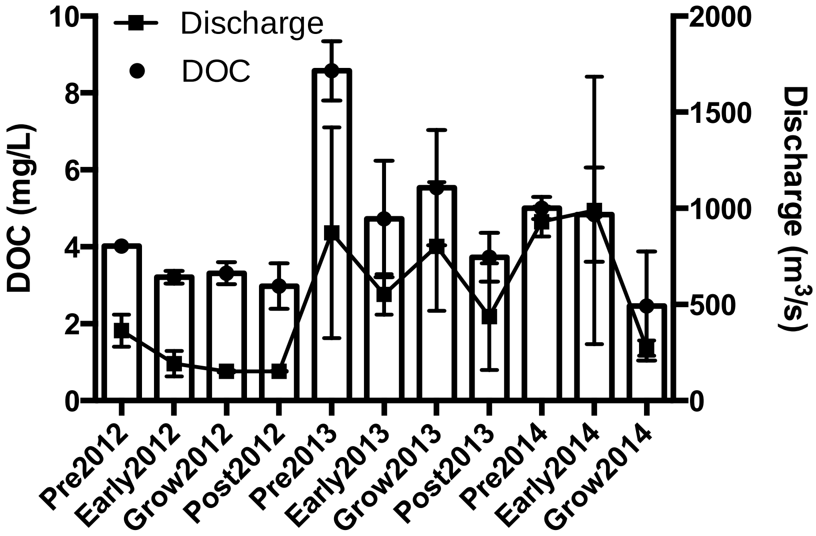

Figure 3.6: DOC (mg/L) and discharge (m^3/s) of the Apalachicola River below the dam. Error bars are s.d.

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CHAPTER 4

INVASIVE SPECIES INTERACTIONS AFFECT NUTRIENT CYCLING: A MESOCOSM EXPERIMENT

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Abstract

Lakes and reservoirs are important sites for biogeochemical cycling. Reservoirs can also facilitate the spread of invasive species, which can create new combinations of species with unknown effects on ecosystem function. This experiment investigated the effects of combinations of three invasive species (*Hydrilla*, *Corbicula*, and *Pomacea*) on nutrient cycling. The three invasive species used were modeled after invasive distributions in the shallow reservoir, Lake Seminole, GA, USA. To assess these effects, a mesocosm experiment was designed using different combinations of the invasives. Physical and chemical parameters of water quality were measured in all of the mesocosms weekly for the duration of the 5-week experiment. Nitrogenous compounds were strongly affected by *Hydrilla* and *Pomacea*, with NO_3-N concentrations decreasing in *Hydrilla* mesocosms and NH_4-N and TN increasing in *Pomacea* mesocosms. Overall, *Hydrilla* reduced inorganic N and stored N as biomass and *Pomacea* converted stored N to available organic and particulate N. These conversions have the potential to cause a decrease in ecosystem function as N concentrations increase within the water column. *Corbicula*, when present, helped to mitigate these increases in N concentrations. As climate change and human influence continue to create new combinations of species, it is important to understand the effects on ecosystem function produced by these novel combinations of species.

Introduction

Freshwater ecosystems are important for the biogeochemical cycling of nitrogen, phosphorus, and carbon as water moves from the terrestrial landscape to the oceans (Cole et al. 2007; Harrison et al. 2009; Tranvik et al. 2009). Because of their position in the watershed, reservoirs serve as integrators of land use and sentinels for change (Schindler 2009; Williamson et al. 2009). To assess how reservoirs affect nutrients transmitted downstream, an understanding of nutrient transformation within reservoirs is required. The assessment becomes complicated because reservoirs are also important habitats used by many species. Moreover, the recreational use of reservoirs facilitates the spread of invasive species when boating and fishing result in accidental dispersal (Havel et al. 2005; Strayer 2010). Consequently, novel ecosystems are created when invasive species form new biotic communities with unknown direct and indirect interactions (Hobbs et al. 2006; Williams and Jackson 2007). These interactions can cause diminished water quality, toxic cyanobacterial blooms, and diseases among fish-eating birds (Byers et al. 2013; Wilde et al. 2005).

The current research uses an experimental approach to examine for the first time the combined effects of three non-native species that are widely distributed in lakes and reservoirs and are currently impacting the shallow reservoir, Lake Seminole, GA, USA. These non-native species are: a submerged macrophyte (*Hydrilla verticillata*), a sediment-dwelling bivalve (*Corbicula fluminea*) and a grazing gastropod (*Pomacea maculata). Hydrilla verticillata* is a rooted macrophyte, native to Asia, that is a highly successful invader capable of growing in a wide array of water conditions, ranging from oligotrophic to eutrophic habitats (Langeland

1996). *Hydrilla* utilizes nutrients from both the water column and the sediment and can affect overall nutrient cycling in aquatic ecosystems (Barko et al. 1988; Sousa 2011). *Corbicula fluminea*, also native to Asia, are freshwater clams and are widely dispersed in new habitats (Darrigran 2002). These clams can adjust their filtration rate for optimum efficiency resulting in a higher clearance rate of organic and inorganic material compared to native mussels (Atkinson et al. 2011; Vaughn and Hakenkamp 2001). Because of the high abundance of organisms and their capability of linking the water column and sediments through pedal feeding, *Corbicula* can impact biogeochemical cycling (Sousa et al. 2008). Snails of the genus *Pomacea maculata*, native to South and Central America, are voracious herbivores that feed on aquatic vegetation, such as *Hydrilla* (Baker et al. 2010). *Pomacea* are successful invaders because of their high feeding and growth rates as well as high fecundity (Barnes et al. 2008; Morrison and Hay 2011). These snails have the potential to alter ecosystem function through removal of the submerged littoral vegetation (Carlsson et al. 2004).

As climate change continues to warm inland waters and humans continue to aid dispersal, invasive species will establish different combinations of non-native species. It is important to understand how these interactions will affect water quality and to be able to predict the effects when multiple invasive species establish new assemblages. To date, there have been no studies that have investigated the combined effects of *Hydrilla*, *Corbicula*, and *Pomacea*. The goal of this experiment was to determine the effects on water quality of different combinations of these three invasive species. It was expected that *Hydrilla* would take up and store nutrients, thereby reducing dissolved nutrient concentrations. *Corbicula* was also expected to reduce total nutrient concentrations by incorporating nutrients in their biomass. In contrast, *Pomacea* was expected to increase total nutrient concentrations through its grazing on *Hydrilla* and excreting nutrients into the water column.

Methods

Site Description

Lake Seminole is a 152 km^2 impoundment located in southwestern Georgia and is the last of a series of reservoirs within the Apalachicola-Chattahoochee-Flint (ACF) Basin (Figure 4.1). Lake Seminole is a shallow lake with a mean depth of 3 m and a maximum depth is 10.7 m. The Chattahoochee River, the Flint River, and Spring Creek are the major surface inflows into the lake and drain a combined land area of 46,141 km^2. The outflow from Lake Seminole is the Apalachicola River, which flows into the Apalachicola Bay in the Gulf of Mexico. Groundwater contributes a smaller component of inflow and outflow of the lake. Submerged aquatic vegetation (SAV) can cover large areas of the lake during the growing season and the SAV community is dominated by *Hydrilla verticillata*. *Hydrilla*, native to Asia, was introduced into the lake in the 1960s and can cover up to 70% of the lake under optimal conditions (Brown and Maceina 2002).

Mesocosm Design

Mesocosms were constructed using 55-gallon plastic containers to create a series of “limnocorrals” with open bottoms. A pilot study in 2014 revealed that transferring sediment into the mesocosms produced a long period of highly turbid conditions followed by large algal blooms. The mesocosms were anchored to the sediment with metal fence posts to prevent movement due to wave action. The tops of the mesocosms were covered with plastic mesh (2.25 cm diameter) to prevent snails from crawling out while allowing high intensity of light. Eight treatments were included: *Hydrilla* only; *Corbicula* only; *Pomacea* only; *Hydrilla*/*Corbicula*; *Hydrilla*/*Pomacea*; *Corbicula*/*Pomacea*; *Hydrilla*/*Corbicula*/*Pomacea*, and control were applied to two rows of mesocosms in a randomized block design for a total of 16 mesocosms with two replicates of each treatment.

Mesocosm Biota

Hydrilla plants were collected near the mesocosm installation site, placed in pots, and allowed to acclimate *in situ* to being potted for a minimum of two weeks before being placed in the mesocosms. The number of stems and length of stems were measured and recorded so that approximately the same amount of *Hydrilla* was placed into each mesocosm. *Hydrilla* was replaced weekly in treatments where *Pomacea* were present.

Corbicula were collected from sandy sediment directly adjacent to the mesocosm site. The number (13) and size (20-25 mm) of *Corbicula* that were added to each mesocosm receiving the *Corbicula* treatment represent the overall lake density based on surveys of *Corbicula* (Patrick 2015).

Adult *Pomacea maculata* individuals of approximately the same size (47-64 mm) were collected from the Flint River arm of Lake Seminole. Three individuals were placed into each mesocosm receiving the *Pomacea* treatment. The number of *Pomacea* used was based on density estimates from Conner et al. (2008) (Conner et al. 2008).

All species were collected from the mesocosms at the end of the experiment and the appropriate species-specific measurements were taken.

Physical/Chemical Measurements

Water quality measurements were made and water samples were collected from the mesocosms weekly for five weeks. Temperature, dissolved oxygen (DO), pH, and conductivity were measured *in situ* using a Hydrolab Quanta from Hach Laboratories. Measurements were taken from the middle of the mesocosm. Turbidity was measured using a handheld turbidity meter (Oakton T-100). Water samples were collected in 1L Nalgene polycarbonate bottles and placed on ice until returning to the lab. Water samples were filtered through pre-ashed 0.7 μm glass fiber filters within 24 hours of collection and either stored below 0°C (chl a, NO_3-N, PO_4-P, TN, and TP) or between 0-5°C (NH_4-N and DOC). DOC was measured using a Shimadzu TOC-L Total Carbon Analyzer. NO_3-N, NH_4-N, and PO_4-P concentrations were measured using a Lachat QuikChem 8500 and using methods adapted from Lachat standard methods 10-107-04-1-B, 10-107-06-1-G, and 10-115-001-B, respectively. TN and TP samples were digested using an autoclave persulfate digestion and concentrations were determined using a Lachat QuikChem 8500 and the standard Lachat methods 10-115-01-4-C (TP) and 10-107-04-4-C (TN). Chlorophyll a was extracted from filters using a 90% acetone extraction method and analyzed using a spectrophotometer according to the spectrophotometric determination of chlorophyll from the 20th edition of Standard Methods for the Examination of Water and Wastewater.

Statistical Analysis

Statistical tests and graphics were created using GraphPad Prism 6. Repeated measures two-way ANOVAs (alpha = 0.05) were used for data analysis. A post-hoc Dunnett's test was utilized to compare the various treatments to the control mesocosms.

Results

Biota

Total stem length of *Hydrilla* increased in all treatments without *Pomacea*. The average increase was 443.6 ± 292.6 mm, which was a 184% increase. The number of *Corbicula* increased in all but one mesocosm in which 8 of 13 original individuals were recovered. The average increase in *Corbicula* was 41 ± 19 individuals per mesocosm. All *Pomacea* individuals were recovered in 6 out of 8 mesocosms. In the remaining two mesocosms, one individual was deceased at the end of the experiment and one was deceased and replaced during the experiment.

Physical Measurements

Mesocosm temperature varied less than 2°C over the duration of the experiment and there were no significant differences between the mesocosms (Table 4.1). Trends in DO differed depending on the mesocosm treatment. *Hydrilla* treatments, except if *Pomacea* were present, had higher DO than the other treatments (Table 4.1). DO was significantly lower than the control for the *Corbicula*/*Pomacea* treatment ($F=11.2$, $p<0.05$). There were no significant pH differences between treatments and control, but pH was higher in *Hydrilla* and *Hydrilla*/*Corbicula* treatments (Table 4.1). Conductivity decreased slightly in all mesocosms except for the *Hydrilla*/*Pomacea* treatments, although none of the treatments were significantly different (Table 4.1). There were also no significant differences in turbidity among any of the treatments and the control. The effect of time was significant for all physical and chemical variables as conditions in the mesocosms changed from the beginning to the end of the experiment.

Chemical Measurements

Principal components analysis using ln-transformed data revealed that *Hydrilla* and *Pomacea* presence affected NO_3-N, NH_4-N, and organic N concentrations (Figure 4.2). The first two axes explain 64% of the variance with axis 1 associated with organic N and NH_4-N, and axis 2 associated with NO_3-N. All initial mesocosms were clustered together demonstrating that initial physical conditions were consistent among the mesocosms. Clusters of *Hydrilla* points indicate a strong initial decrease in NO_3-N concentrations after initial experimental setup.

NO_3-N concentrations decreased in all mesocosms during the experiment (Table 4.2). Mesocosms containing *Hydrilla*, *Corbicula*, and the *Hydrilla*/*Corbicula* combination decreased significantly compared to the control mesocosm ($F=16.8$, $p<0.05$)(Figure 4.3). Total nitrogen (TN) concentrations in the control mesocosm decreased during the experiment (Table 4.2). Decreases in TN were also observed in *Hydrilla*, *Corbicula*, and *Hydrilla*/*Corbicula* treatments, although these concentrations were not significantly different from the control. TN concentrations were significantly higher in all *Pomacea* treatments (*Pomacea*, *Hydrilla*/*Pomacea*, *Corbicula*/*Pomacea*, *and Hyd/Corb/Pom*) compared to the control ($F=28.1$, $p<0.05$) (Figure 4.4). PO_4-P concentrations remained low in all treatments and none were significantly different from the control (Table 4.2). Total phosphorus (TP) concentrations increased in all mesocosms during the experiment and the *Hydrilla*/*Pomacea* treatment was significantly higher than the control (F=4.4, $p<0.05$) (Figure 4.5). NH_4-N concentration trends were variable among the treatments with non-significant decreases observed in *Hydrilla* and *Corbicula* treatments and significant increases in *Hydrilla*/*Pomacea, Corbicula*/*Pomacea, and Hyd/Corb/Pom* (F=23.5, $p<0.05$) (Figure 4.6). DOC and chlorophyll a concentration trends were also variable among the treatments and no significant differences were observed.

Discussion

Biota and Physical Differences Among Mesocosms

A major concern with mesocosm experiments is ensuring that starting conditions and temperature during the experiment remain consistent among the mesocosms. Based on the initial physical and chemical measurements, the starting conditions were similar for all mesocosms. Additionally, there were no significant differences in temperature among the mesocosms during the experiment. Neither temperature, nor initial conditions were drivers of observed differences among mesocosms. Substantial growth of *Hydrilla* indicated that plants were healthy and the mesocosms had good growth conditions. Decreases in DO and pH were observed for all mesocosms except for the *Hydrilla* and *Hydrilla*/*Corbicula* treatments. The stable DO and pH in the *Hydrilla* treatments result from O_2 release and CO_2 uptake during photosynthesis (Carpenter and Lodge 1986; Langeland 1996).

Chemical Differences Among Mesocosms

Nitrogenous compounds, both organic and inorganic, were significantly altered in *Hydrilla* and *Pomacea* treatments. NO_3-N decreased sharply and quickly in the *Hydrilla*, *Corbicula*, and *Hydrilla*/*Corbicula* treatments. *Hydrilla* plants can utilize N directly from the water column and these decreases in NO_3-N resulted from direct uptake by the plants (Ambasht 1991). The ability of *Hydrilla* to take in and internally store large quantities of nutrients is well established (Gu 2006). This effect occurred after the freshwater inflow during between weeks 1 and 2. Conversely, total nitrogen increased significantly in all treatments where *Pomacea* where present, with the largest increases in combination with *Hydrilla*. *Pomacea* are voracious grazers and can consume 0.2 grams of *Hydrilla* per gram of snail mass per day (Baker et al. 2010). Feeding by snails caused release of dissolved nutrients and particulate material into the water and the resulting increase in TN. Filter feeding by *Corbicula* helped to lower the increase in TN caused by *Pomacea* as concentration in the combined *Hydrilla*/*Corbicula*/*Pomacea* mesocosm were lower than the increase observed in the *Hydrilla*/*Pomacea* mesocosm. A similar study by He et al. (2014) also found that bivalves reduce TN without a corresponding increase in dissolved N (He et al. 2014). In the current study NH_4-N concentrations were significantly higher in treatments combining *Pomacea* with other biota. These increases can be attributed to the feeding and metabolic activity of *Pomacea*. NH_4-N can be released through the decomposition of plant material that results from *Pomacea* feeding (Li et al. 2009; Pinowska 2002). The large increases in the *Hydrilla*/*Pomacea* treatment are potentially problematic as the concentrations are near the EPA guidelines for acute ammonia toxicity for aquatic organisms (Huff et al. 2013). Overall, the presence of *Hydrilla* reduces the inorganic pool of N. *Hydrilla* increases organic N as stored plant biomass and does not by itself affect the organic pools of N available in the water column. The addition of *Pomacea* causes a conversion of N stored as biomass in plant material to organic N in the water column.

The lack of change in PO_4-P concentrations in all of the mesocosms is a result of the low ambient PO_4-P concentrations. Inorganic P concentrations are consistently at or below detection limit within Lake Seminole (Shivers et al. 2016). It is likely that PO_4-P is taken up by the biotic community as soon as it becomes available. The majority of P in the water column is stored as organic P in biota. The combination of *Pomacea* with *Hydrilla* significantly increased total P concentrations. Similar to the effect on total N, feeding by *Pomacea* releases P into the water column where it can be utilized by the biotic community (Li et al. 2009). *Hydrilla* can utilize either P from the water column or the sediment, therefore the translocation of P from the sediment to the shoots of *Hydrilla* effectively mobilizes P stored in the sediment (Barko and Smart 1980). The release of excess P by *Pomacea* feeding on *Hydrilla* is mitigated by the presence of *Corbicula* as the *Hyd/Corb/Pom* treatment was not significantly different from the control.

Possible Effects on Ecosystem Function

As anthropogenic influences continue to contribute to the translocation and expansion of invasive species, novel ecosystems and new combinations of invasive species will be created (Buckley and Catford 2016; Hobbs et al. 2006). Reservoirs are prime examples of novel ecosystems, being created by humans and facilitating the spread of invasive species (Havel et al. 2005, 2015; Johnson et al. 2008). *Hydrilla* was the first invasive species in Lake Seminole with its introduction in the 1960s. More recently, *Corbicula* and *Pomacea* have been introduced into the lake and have increased in densities over the last few years (Marzolf 2015; Patrick 2015).

Hydrilla is capable of covering large parts of the shallow water and, as a result of this coverage, it can affect nutrient cycling on a lake-wide scale (Sousa 2011). Results from this mesocosm experiment are consistent with other studies demonstrating that *Hydrilla* causes a reduction in NO_3-N within the water column (Mukherjee et al. 2008; Upadhyay et al. 2016). *Hydrilla* can also utilize P from both the water column and the sediment. Therefore, N and P are concentrated within the biomass of *Hydrilla* plants. The addition of *Pomacea* and subsequent feeding on *Hydrilla* releases the stored N and P, primarily in particulate form as evidenced by increases in total N and P, but not NO_3-N and PO_4-P. Lake Seminole has high concentrations of P, similar to eutrophic lakes in Florida, stored in the sediment (Waters et al. 2015). The combination of *Pomacea* and *Hydrilla* has the potential to release the P stored in the sediment into the water column. Excess P in the water column combined with sufficient N could severely degrade water quality as algal blooms, particularly by cyanobacteria, become increasingly common (Davis et al. 2015; Kosten et al. 2012).

The presence of *Corbicula* helps to mitigate the effects of *Pomacea* feeding on *Hydrilla*. *Corbicula*, through filter feeding, remove particulates from the water, thus reducing total N and P. Native mussels generally filter larger particles than *Corbicula* but would also reduce particulate N and P in the water column. As many native mussel populations are declining, continued conservation of these organisms would help to ensure ecosystem services provided by filter feeders are maintained. These services are particularly important if new species that increase particulates in the water column are introduced.

As climate change can result in range expansion and humans continue to spread invasive species, the potential for different combinations of invasive species to co-occur increases. It is important to be able to predict the ecosystem effects when new combinations are established. If *Pomacea* populations increase in areas where SAV is present, it is likely that nutrients stored in biota and sediments will be released into the water column. Excess nutrients cause a host of water quality issues, including the proliferation of algal blooms. Warmer water is known to increase growth rates of toxic cyanobacteria and can be considered in additional research where water temperature can be manipulated along with combinations of invasive species. Additional research is needed to investigate the effects of other new combinations of species, both invasive and native, that are likely to co-occur as potential geographic ranges change and ecosystem processes are affected.

Table 4.1: Physical measurements of the eight mesocosm treatments (variability is represented by s.d.)

		Control	**Hyd**	**Corb**	**Pom**	**Hyd/Corb**	**Hyd/Pom**	**Corb/Pom**	**Hyd/Corb/ Pom**
DO (mg/L)	Initial	8.6±0.4	8.1±0.3	8.0±0.4	8.4±0.2	8.4±0.6	8.5±0.9	8.6±0.3	8.0±0.1
	Week 5	5.7±0.5	8.1±0.5	7.9±0.0	6±0.9	7.7±1.0	5.0±0.2	3.6±0.4	4.7±1.2
pH	Initial	8.3±0.1	8.2±0.0	8.2±0.1	8.3±0.0	8.2±0.1	8.2±0.0	8.2±0.0	8.2±0.0
	Week 5	8.1±0.0	8.7±0.4	8.2±0.1	7.9±0.2	8.8±0.3	7.8±0.2	7.6±0.0	7.7±0.2
Temp (°C)	Initial	31.8±0.1	31.8±0.0	31.8±0.1	31.8±0.1	31.6±0.0	31.7±0.0	31.7±0.1	31.8±0.2
	Week 5	31.0±0.2	30.6±0.2	30.5±0.1	31.0±0.3	30.8±0.1	30.9±0.0	30.6±0.1	30.9±0.2

Table 4.2: Chemical measurements of the eight mesocosm treatments (variability is represented by s.d.)

		Control	**Hyd**	**Corb**	**Pom**	**Hyd/Corb**	**Hyd/Pom**	**Corb/Pom**	**Hyd/Corb/ Pom**
NO_3-N (µg/L)	Initial	398±10	400±11	398±13	406±14	411±3	412±9	402±7	406±2
	Week 5	89±5	1±1	3±3	156±53	1±1	68±4	80±49	130±26
TN (µg/L)	Initial	645±20	630±16	650±41	697±53	656±38	650±23	643±35	696±55
	Week 5	412±20	335±31	515±318	679±237	449±92	3602±678	981±222	1508±744
NH_4-N (µg/L)	Initial	21±2	22±4	21±2	18±1	20±2	23±5	19±2	24±2
	Week 5	29±5	6±5	10±8	128±71	12±1	2890±855	477±216	790±472
PO_4-P (µg/L)	Initial	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	Week 5	n.d.	n.d.	n.d.	n.d.	n.d.	6.7±1.03	n.d.	n.d.
TP (µg/L)	Initial	9±2	7±	8±4	12±4	11±2	8±2	10±4	12±5
	Week 5	16±1	13±2	21±16	19±3	16±2	40±7	18±2	22±3
DOC (mg/L)	Initial	3.4±0.1	3.5±0.1	3.3±0.2	3.5±0.1	3.6±0.1	3.4±0.1	3.4±0.1	3.3±0.1
	Week 5	2.6±0.2	2.0±0.9	2.8±0.7	2.0±0.9	3.7±0.9	3.8±0.7	2.5±0.6	2.9±1.2
chl a (µg/L)	Initial	2.0±0.3	1.9±0.3	1.2±0.5	1.5±0.9	1.9±0.3	1.6±0.0	1.7±0.3	2.0±0.5
	Week 5	3.7±0.8	3.9±1.0	18.7±15.1	2.9±0.5	7.9±6.2	11.3±7.2	3.7±1.6	3.2±2.4

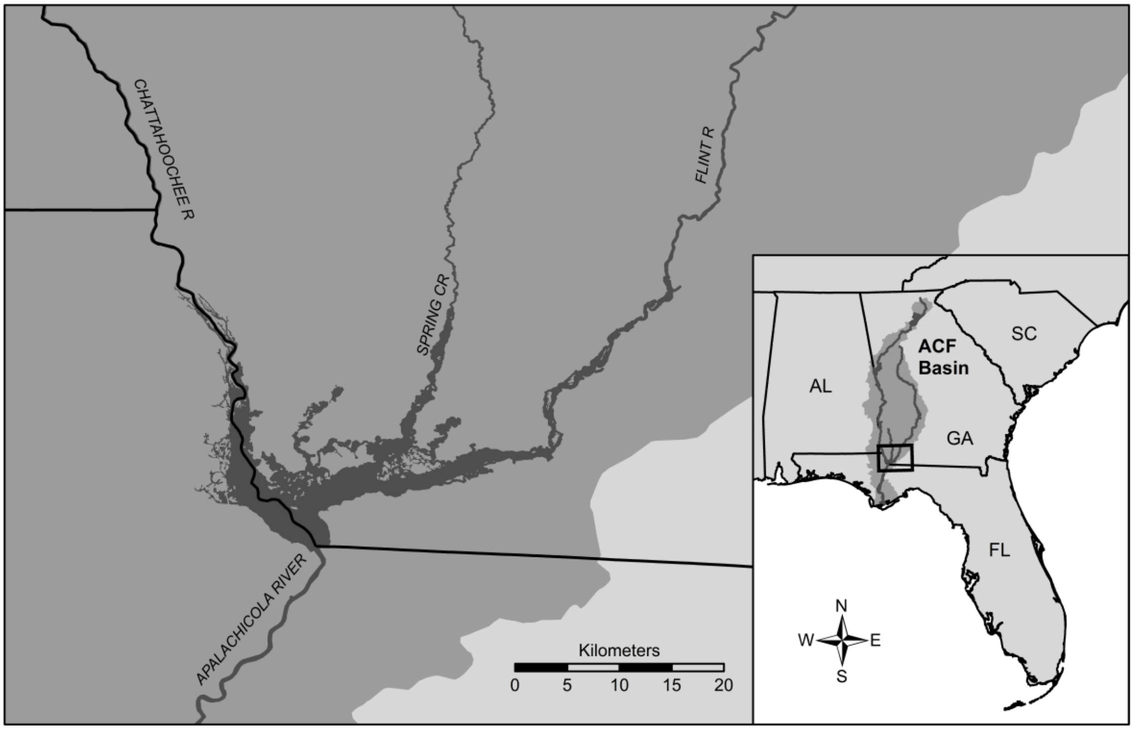

Figure 4.1: Lake Seminole is located in southwestern Georgia and is formed from the confluence of the Flint River, the Chattahoochee River, and Spring Creek. The Apalachicola River is the outflow and flows south into the Gulf of Mexico.

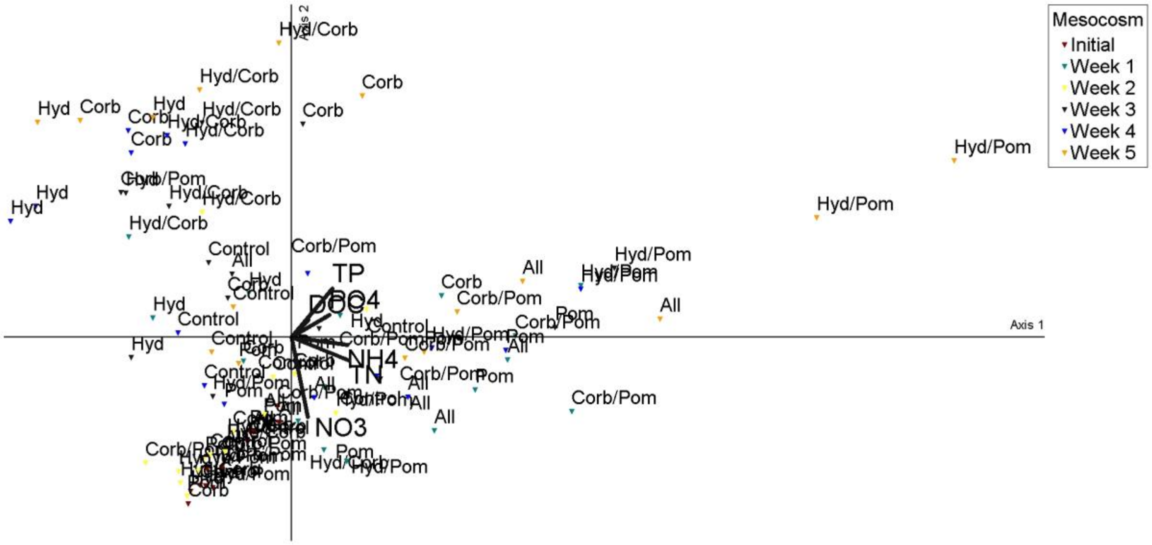

Figure 4.2: Results of PCA of ln-transformed data from initial measurements through week 5 for a suite of chemical variables (TP, PO_4-P, DOC, NH_4-N, TN, and NO_3-N).

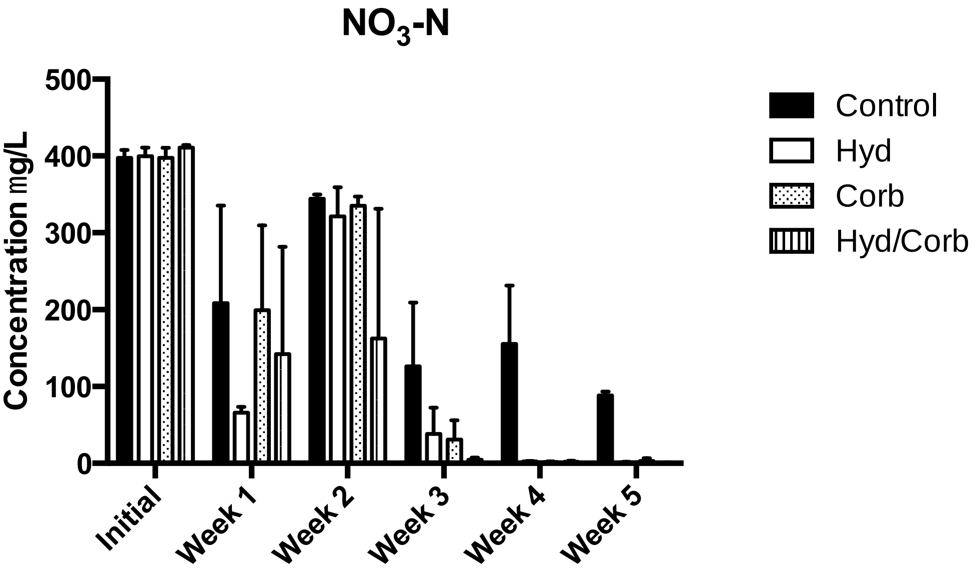

Figure 4.3: NO_3-N concentrations in four mesocosms (error bars are s.d.)

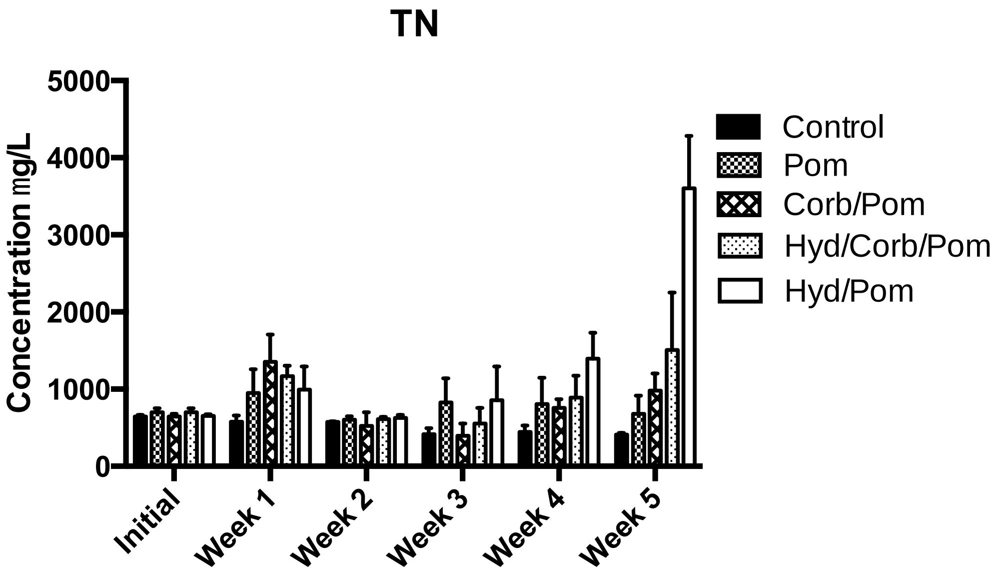

Figure 4.4: Concentrations of total nitrogen (TN) in five mesocosms (error bars are s.d.)

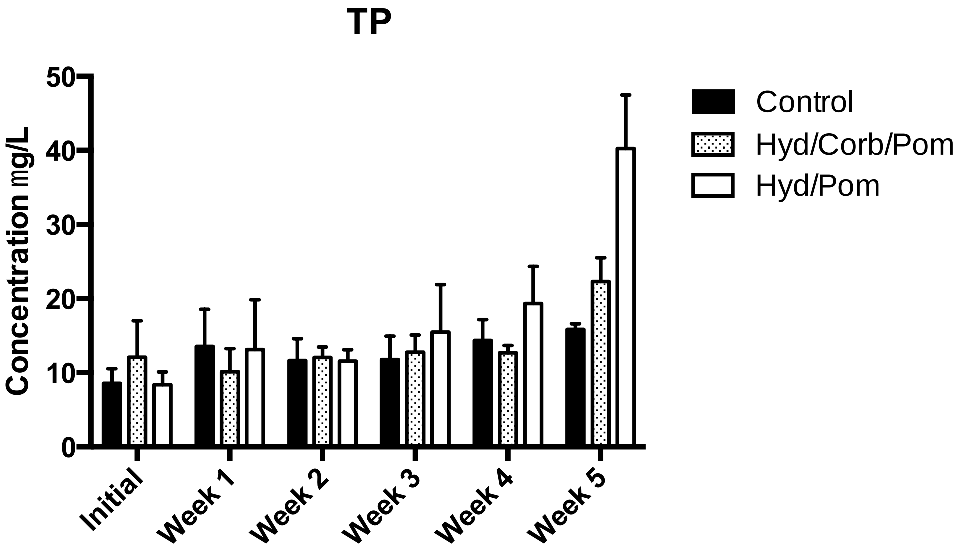

Figure 4.5: Total phosphorus (TP) concentrations in three mesocosms (error bars are s.d.)

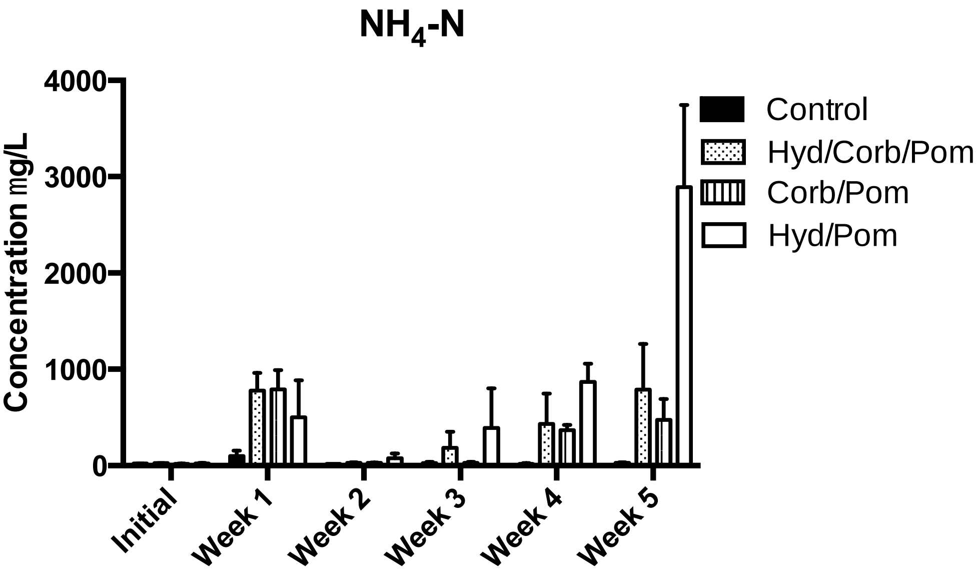

Figure 4.6: NH_4-N concentrations in four mesocosms (error bars are s.d.)

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CHAPTER 5

CO-OCCURRENCE OF A RECENT AND AN ESTABLISHED INVADER IN A SHALLOW, SUBTROPICAL RESERVOIR: WILL POMACEA GRAZING AFFECT HYDRILLA DISTRIBUTIONS AND WATER QUALITY?[1]

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[1] Shivers, S.D., N.S. Marzolf, A.P. Covich, and S.W. Golladay. Submitted to *Biological Invasions*.

Abstract

The recent introductions of invasive apple snails (*Pomacea maculata and Pomacea paludosa*) to a shallow reservoir have the potential to change the distribution of an established, invasive submerged macrophyte (*Hydrilla verticillata*). This study documents the presence and range expansion of these herbivores over a two-year period within Lake Seminole, a shallow sub-tropical reservoir located in southwestern Georgia, USA. Using egg masses laid above the water line as an indicator of snail presence, we counted the frequency of egg masses at 1 km intervals along the lake shoreline. We found that *P. maculata* and *P. paludosa* did not co-occur during the first year but were found extensively along the shoreline. During the second year, the species did co-occur and there was a net increase in locations present for both species indicating range expansion. Because apple snails are voracious herbivores, an expanding snail population has the potential to alter and reduce SAV assemblages, possibly changing lake nutrient cycling and sequestration.

Introduction

Lakes and reservoirs are dynamic ecosystems that transport, transform, and store nutrients as water moves from the terrestrial landscape to the ocean (Harrison et al. 2009; Tranvik et al. 2009). Reservoirs, in particular, can facilitate the spread of invasive species because of their extensive drainage-basin connectivity and recreational fishing and boating (Johnson et al. 2009). Climate change, including warmer winter water temperatures, is also increasing the dispersal of tropical and subtropical species (Williamson et al. 2009). The introduction and proliferation of invasive species can alter nutrient cycling within reservoirs, thus changing ecosystem functions such as primary production (Carpenter et al. 2011).

Submerged aquatic vegetation (SAV) exerts strong effects on aquatic ecosystems. SAV can affect physical characteristics by reducing water velocity and increasing sedimentation rates, as well as promoting nutrient cycling in the water column and deposition in the sediment (Carpenter and Lodge 1986). Some invasive SAV, such as *Hydrilla verticillata*, can be highly productive and rapidly dominate large areas, especially in the littoral zone (Gu 2006).

Adult and juvenile apple snails of the genus *Pomacea* feed on SAV and can consume plant material at a high rate (Burks et al. 2011). Grazing by *Pomacea* can shift lakes from a macrophyte-dominated state to a turbid state dominated by phytoplankton (Carlsson et al. 2004). Once a shift occurs, returning to a clear-water state can be difficult (Scheffer 2009). This paper documents the intra-lake distribution of invasive apple snails and discusses the possible effects of interactions with *Hydrilla verticillata,* an invasive species of SAV.

Methods

Site Description

Lake Seminole is a 152 km^2 impoundment located in southwestern Georgia and is the most downstream reservoir within the Apalachicola-Chattahoochee-Flint (ACF) Basin (Figure 5.1). The mean depth of Lake Seminole is 3 m and the maximum depth is 10.7 m. The major surface inflows to the lake are the Chattahoochee River, the Flint River, and Spring Creek, which drain a combined land area of 46,141 km^2. The outflow is the Apalachicola River, which flows south and empties into Apalachicola Bay. SAV can extend over large areas of the lake with *Hydrilla verticillata* dominating up to 70% of the lake surface area, depending on water conditions and management actions by the US Army Corps of Engineers.

Snail Survey and Processing

We noted the apparent rapid spread of *Pomacea* in spring 2013 after initial sightings in 2008 and confirmation of establishment in 2011 (Robertson 2012). Therefore, a visual survey of apple snail (*Pomacea* spp.) egg masses was conducted during the summer months (June and July) of 2013 and 2014. Egg masses were counted by two observers during a 5-minute period at 97 pre-determined locations spaced every kilometer along the shoreline of the lake. This methodology established the presence or absence of snails and provided an estimate of abundance. Identification of egg masses produced by two species of *Pomacea* was based on their color and size (Hayes et al. 2012). The results of the egg mass counts were averaged to reduce variation by individual observers. Data were input to a Nomad GPS unit and post-processed using ArcMap 10.2.2.

Results

Two species of apple snails, *Pomacea paludosa* (Say, 1829) and *Pomacea maculata* (Perry, 1810), were found during the survey. In 2013, *P. maculata* were found at 19 locations on the Flint River arm of the lake and at two locations in Spring Creek (Figure 5.2) compared to being found at 21 locations on the Flint River and at 4 locations in Spring Creek in 2014 (Figure 5.3). *P. paludosa* were found at 51 and 55 locations on the Chattahoochee River, the Flint River, and Spring Creek in 2013 and 2014, respectively. No snails were found at 25 locations in 2013 and at 20 locations in 2014. The two species of snails did not co-occur during 2013 but did co-occur at three locations in 2014. *P. maculata* were found at 6 new sites during 2014, were not observed at 2 previous sites, and *P. paludosa* were found at 4 new sites. In 2013, greater mean numbers of *P. maculata* egg masses (mean = 73 ± 108) were counted at each location as compared to *P. paludosa* (mean = 51 ± 58). Greater maximum numbers of *P. maculata* egg masses (max count = 409) were observed compared to *P. paludosa* (max count = 200), however more *P. paludosa* egg masses were observed overall because of the greater number of locations where *P. paludosa* was found. In 2014, fewer egg masses were seen overall for both *P. maculata* (mean = 27 ± 32, max count = 130), and *P. paludosa* (mean = 32 ± 50, max count = 247), although large numbers of *P. paludosa* egg masses were observed at two locations (Table 5.1). The high degree of variability results from the clustered distribution of the snail egg masses. Egg masses from *P. maculata* were found primarily in one section of the Flint River while *P. paludosa* were more evenly distributed.

Discussion

Egg masses of *P. maculata* and *P. paludosa* were generally observed in discrete locations of the lake, which implies that adult snails are also currently segregated within the lake. At this early phase of colonization it is not clear if these two species compete with one another (Posch et al. 2013). The greatest abundance of *P. maculata* egg masses were found near Wingate's Lodge, which is also where the first snails were reported to the US Geological Survey in 2008. A subsequent survey in 2011 confirmed the presence of *P. maculata* along the southern bank of the Flint River and noted the potential for expansion, especially into the Chattahoochee and Spring Creek watersheds (Robertson 2012). Our surveys confirm that the range of *P. maculata* has expanded in the lake since 2011 and continued between 2013 and 2014. It is not known when *P. paludosa* was introduced into the lake as the only other documented observations are from isolated springs in Georgia (Thompson 2004). The current distribution of *P. maculata* might be due to an invasion epicenter located at Wingate's Lodge and subsequent range expansion. Snails were newly discovered in the Spring Creek drainage in 2013 and greater numbers of egg masses were seen in 2014, possibly indicating establishment near a boat dock. Egg masses were observed on boats in 2013 representing a possible dispersion vector. Ongoing research is investigating if local physicochemical conditions, such as water temperatures associated with submerged springs and pH values within the lake, are affecting snail distribution, and if the snails are dispersing beyond the lake into nearby ponds, lakes, and wetlands.

Overall, egg mass abundance declined in 2014 when compared to 2013. This decline is not necessarily an indicator of a reduced adult population. Using egg mass counts as a proxy for adult population size can be misleading (Darby et al. 1999). For this reason, egg masses are considered primarily as an indicator for the presence or absence of adults and as an indicator of potential abundance. Barnes et al. (2008) estimated conservatively that egg clutches could produce between 14-144 adult individuals, so the potential exists for a large increase in adult snail populations within a short time. Because apple snails feed heavily on both native and non-native submerged vegetation (Baker et al. 2010), increasing snail populations potentially increases grazing pressure on the SAV within the lake. *P. maculata* has higher growth and efficiency and lower mortality than *P. paludosa*. Additionally, *P. maculata* produces egg clutches containing over 1000 eggs whereas *P. paludosa* egg clutches contain 30 eggs on average (Morrison and Hay 2011). Therefore, *P. maculata* could be a superior competitor of *P. paludosa* as well as affecting the SAV within the lake.

SAV, dominated by *Hydrilla*, covers substantial portions of Lake Seminole during the growing season. Previous research has shown that the lake can function as a sink for NO_3-N during the summer months (McEntire 2010) and *Hydrilla* beds can be considered as “hot zones” of nutrient uptake and microbial nutrient transformations (Shivers 2010). Additionally, large sedimentary stores of phosphorus have been documented within the lake, particularly in the Flint River arm (Waters et al. 2015). A loss of SAV potentially destabilizes sediments and increases both internal loading and export of phosphorus. If *Pomacea* continues to spread and becomes more abundant, reductions in SAV coverage by grazing would result in less nutrient retention, mobilization of sediment nutrients, and potential degradation of ecosystem function. The outflow of the lake is the Apalachicola River, which discharges into Apalachicola Bay a regionally important source of shell- and finfish. Excess nutrients could degrade downstream water quality and threaten the near shore fishery.

The range of *Pomacea* is limited primarily by the minimum temperature during the coldest winter months as well as the pH of individual water bodies (Byers et al. 2013; Yoshida et al. 2014). The current range of *P. maculata* in the United States extends from Texas to South Carolina, and the potential range extends northward encompassing the majority of the southern Coastal Plain. If warmer winter temperatures become more frequent, *Pomacea* could move northward into previously uninhabitable lakes and wetlands (Horgan et al. 2014). It is possible that the persistence of *P. paludosa* on Lake Seminole is the result of increased winter temperatures. Introduction of *Pomacea* into novel habitats could result in community shifts and reduction in overall ecosystem function and disease transmission (Carlsson et al. 2004; Wilde et al. 2014). For this reason, it is critical to understand how *P. maculata* and *P. paludosa* interact with each other and with established invasive vegetation, such as *Hydrilla*, as well as native vegetation.

Table 5.1: The number of locations that egg masses were observed and the total number of egg masses counted for *P. maculata* and *P. paludosa* during 2013 and 2014.

	2013 locations	2013 egg masses	2014 locations	2014 egg masses
P. maculata	21	1530	25	700
P. paludosa	51	2613	55	1758

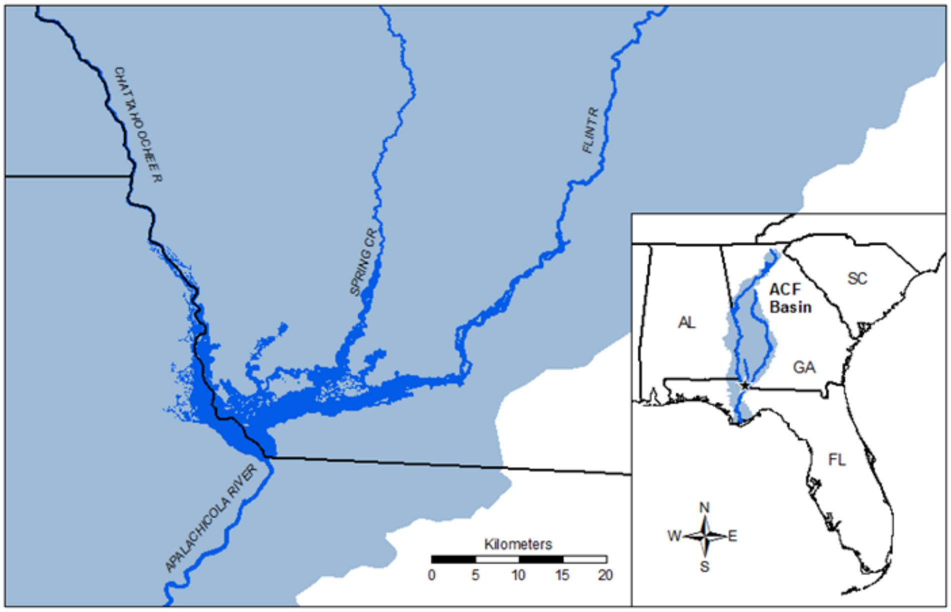

Figure 5.1. Lake Seminole is the last reservoir in the ACF Basin. The riverine inflows are the Chattahoochee River, Flint River, and Spring Creek. The outflow is the Apalachicola River, which is the largest flowing river in Florida and discharges into the Apalachicola Bay.

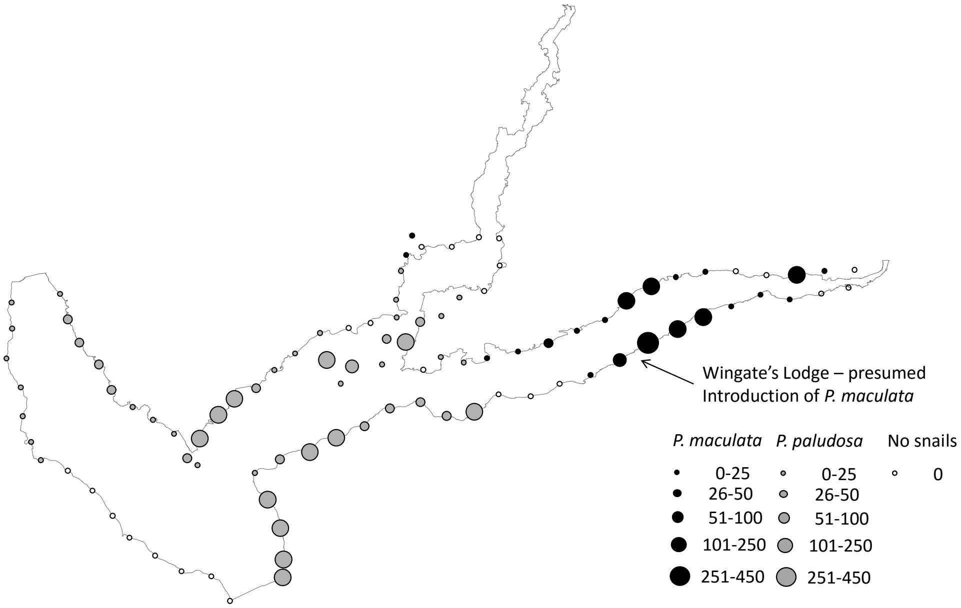

Figure 5.2: Egg mass counts from the summer of 2013. Each circle represents the mean number of egg masses counted by two observers in a five-minute period.

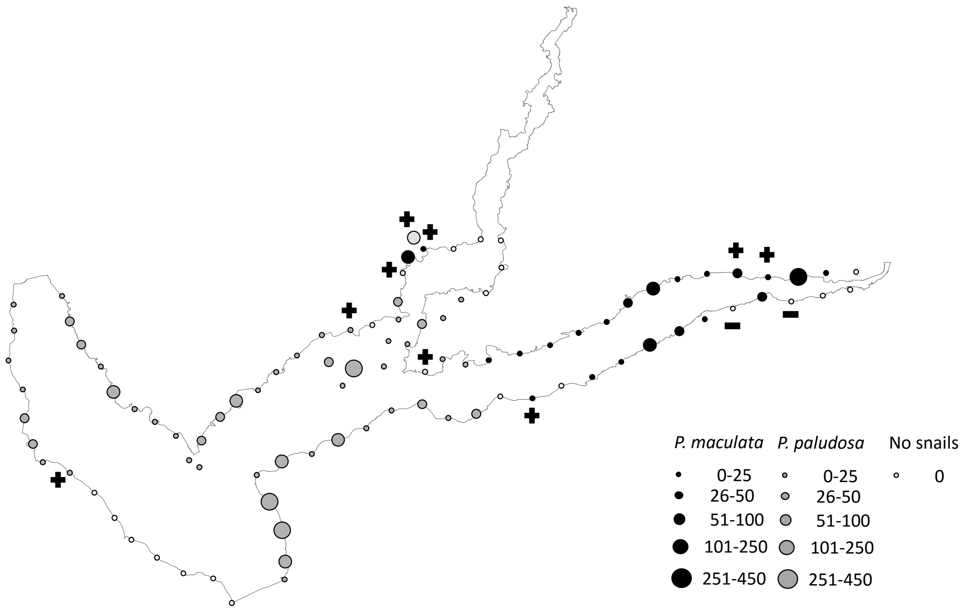

Figure 5.3: Egg mass counts from 2014. Snail presence at new locations is represented by a plus sign and absence at former locations by a negative sign.

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CHAPTER 6

CONCLUSIONS AND SUMMARY

Inland freshwater ecosystems are important sites for the biogeochemical cycling of nutrients and carbon even though their spatial coverage is small (Harrison et al. 2009; Finlay et al. 2013; Hanson et al. 2015). With an estimated global surface area of 1.5 million km^2, reservoirs play a crucial role in biogeochemical cycling that is expected to expand as the number of reservoirs increases (St Louis et al. 2000; Downing et al. 2006). Reservoirs also facilitate the spread of invasive species that can lead to the formation of novel ecosystems, and reservoirs themselves could be classified as novel as they are created by humans (Havel 2005; Hobbs et al. 2006). It is important to understand how these invasive species affect nutrient processing themselves and in concert with each other. This research project investigated how abiotic and biotic factors affected nutrient processing and retention.

Hydrilla verticillata is a submerged aquatic plant that covers extensive areas of Lake Seminole and affects water quality parameters. This study quantified the spatial coverage of *Hydrilla* by performing annual vegetation surveys between 2012 and 2014. During this time, *Hydrilla* coverage decreased severely. Hydrology also varied during the same time period. The first year of the study was the last year in a multi-year drought that created prime growing conditions for *Hydrilla*. Thus, coverage was at the highest point during the growing season of the first year. Precipitation increased in 2013 and 2014 causing increased inflow into the lake by three rivers (Chattahoochee River, Flint River, and Spring Creek). Overall, these changes in hydrology caused increased suspended sediment and water staining and reduced light availability in the water column. The reduction in light caused the spatial coverage of *Hydrilla* to decrease. Because *Hydrilla* is a productive plant that utilizes nutrients from the water column and the sediment, this reduction could cause alteration of biogeochemical cycling within the lake (Barko and Smart 1986).

To assess the effects of SAV reduction on nutrient processing, a comprehensive water quality monitoring program was established to quantify the concentrations of nutrients entering and exiting the lake. Concentrations of NO_3-N were lowest during the growing season that featured the highest SAV coverage. *Hydrilla* can directly reduce NO_3-N concentrations through direct uptake or indirectly by contributing to appropriate conditions for denitrification to remove NO_3-N from the system (Langland 1996; Holmroos et al. 2015). Therefore, these patterns provide support that SAV can control nutrient processing at a reservoir scale.

Hydrilla was introduced into the lake in the 1960s and two other invasive species, *Corbicula fluminea* and *Pomacea maculata*, have been introduced more recently. A mesocosm experiment was established to determine how different combinations of these species might affect water quality. *Hydrilla* and *Pomacea* strongly affected nitrogenous compounds as NO_3-N concentrations decreased in *Hydrilla* mesocosms and NH_4-N and TN increased in *Pomacea* mesocosms. Overall, *Hydrilla* reduced inorganic N and stored N as biomass and *Pomacea* converted stored N to available organic and particulate N. *Corbicula*, when present, helped to mitigate these increases in NH_4-N and TN concentrations. As climate change causes range expansion, it is important to understand how new combinations of invasive species will affect ecosystem function.

Because *Pomacea* was recently introduced, it was important to document the distribution of snails around the lake. To estimate the current range of *Pomacea*, egg mass surveys were completed over a two-year period. *Pomacea* were found extensively around the lake and appeared to undergo a range expansion in the second year. Apple snails are voracious herbivores and can feed on *Hydrilla*. If *Pomacea* populations reach high enough densities to affect overall SAV coverage, nutrient processing by SAV would be reduced followed by a reduction in water quality.

Overall, this research contributed to the understanding of nutrient processing and retention with a freshwater ecosystem. At high spatial coverage, *Hydrilla* does affect overall nutrient processing within the lake by reducing nutrient concentrations. These reductions are important because the outflowing river (Apalachicola River) discharges into the Apalachicola Bay, which is an important fishery and nursery for shellfish and finfish. *Hydrilla* is also an invasive species that is managed intensively. Future management strategies should consider the overall ecosystem services provided by *Hydrilla* when formulating management plans. In areas where *Hydrilla* is firmly established, the beneficial effects might outweigh the environmental and monetary costs of eradication efforts (Evans et al. 2007; Hershner and Havens 2008).

The alternate stable state theory describes how shallow lakes can switch between two different states. Shallow lakes can shift from a clear water state dominated by macrophytes to a turbid state dominated by phytoplankton (Scheffer et al. 1993, Loverde-Oliveira et al. 2009, Hilt et al. 2011). As a run-of the-river reservoir, Lake Seminole functions differently than other types of lakes, including deeper reservoirs that store water. Therefore, it is useful to provide a different description to describe how these lakes function. The transitional nature of a run of the river reservoir occurs when the reservoir switches from functioning as a river to functioning as a lake. During periods of high river flow, Lake Seminole exists in a riverine state with very little nutrient retention. In contrast, during average or low river flow Lake Seminole functions more as a lake and has greater potential to retain nutrients. The transition is driven by hydrological variation and the turbid state features suspended sediments and water staining, not algal blooms. Thus, the turbid state is not maintained or reinforced by biotic factors and the lake can return to a clear water state quickly. Therefore, hydrology drives the shift between river and lake function by mediating the coverage of SAV.

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