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Ecosystem Implications of Invasive Aquatic Plants and Aquatic Plant Control in Florida Springs

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Summary

Nonnative and nuisance plants such as water hyacinth, water lettuce, and hydrilla are a primary management concern in many Florida springs. In fiscal year 2005 – 2006, the Department of Environmental Protection's Bureau of Invasive Plant Management spent approximately $173,000 to control these plants in springs, primarily through the use of chemical herbicides. This chapter reviews a broad range of literature to outline what is known and unknown about 1) the history of these plants and their control in Florida; 2) the growth potential of the nonnative plants in springs as a function of elevated nitrate-nitrogen concentrations; 3) the social and ecological consequences of aquatic plant overgrowth; 4) the ecological risks associated with current aquatic plant control methods; and 5) the potential benefits of alternative aquatic plant management approaches in some springs systems.

The Literature: What is Known

- Major problems with nonnative plants in Florida began with the introduction of water hyacinth, a floating aquatic plant, into the St. Johns River in the late 19th century. Water hyacinth was documented in several springs ecosystem along the St. Johns River by the mid 1890s. Chemical control programs have maintained water hyacinth populations at low levels throughout Florida since the mid-1970s.

- Historical sightings by William Bartram indicate that water lettuce, a floating aquatic plant, has been present in a number of Florida springs since at least 1765. Scientists disagree as to whether water lettuce was present in Florida before European colonization, or was introduced by early Spanish settlers. Chemical control programs have maintained water lettuce at low levels throughout Florida since the mid-1970s.

- Hydrilla, a submersed aquatic plant, became established in several areas of Florida, including the Kings Bay/Crystal River springs complex, by 1960. Sustained control of hydrilla has proven more difficult than the floating plants in Florida. Most aquatic plant management costs in Florida springs ecosystems over 2005 – 2006 were associated with chemical control of hydrilla.

- There are clear relationships between nitrogen enrichment and increased growth of water hyacinth, water lettuce, and hydrilla in non-flowing aquatic systems. Such overgrowth can have severe adverse effects on native plant communities, navigation, fisheries, and recreational desirability.

- Water hyacinth and water lettuce emit allelopathic compounds capable of suppressing a number of algal taxa. Water hyacinth, water lettuce, and hydrilla all can be effective competitors with nuisance algae due to nutrient uptake, shading, faunal habitat, direct filtration, and allelopathic mechanisms.

- Ecosystem surveys indicate that water hyacinth, water lettuce, and hydrilla provide attractive habitat for crayfish, apple snails, amphipods, fish, manatees, and other springs fauna at moderate levels of coverage.

- Copper and diquat herbicides may have significant toxicological effects on algal and faunal community dynamics at levels used for aquatic plant control.

- *Lyngbya wollei*, a filamentous cyanobacterium of great concern in many Florida springs, is notable for its relative resistance to herbicidal compounds as compared to other common algal and cyanobacteria taxa.

- Depression of dissolved oxygen due to decaying biomass is a primary concern to animals following aquatic plant control.

- Biotypes of hydrilla that are resistant to fluridone, a systemic herbicide commonly used for hydrilla control in Florida lakes, have been documented in recent years. There is also increased concern about the potential evolution of hydrilla strains that are resistant to Aquathol, the contact herbicide most commonly used to control hydrilla in springs.

- Established biological control organisms are known to adversely affect water hyacinth, water lettuce, and hydrilla in some springs systems, although biocontrol organisms generally do not maintain aquatic plant populations at low levels achieved by chemical control. A promising biological control for hydrilla, *Cricotopus lebetis*, has been documented in Kings Bay/Crystal River.

The Literature: What is Not Known, and Recommendations for Future Research

- The few studies available for springs and other flowing waters have not definitively determined a concentration of nitrate-nitrogen in springs that would be limiting to any of the nonnative plants. Nutrient assays in flowing water mesocosms and/or *in situ* field studies are needed to develop nitrate-nitrogen limitation values for nonnative plants in springs conditions.

- Observations from several springs suggest a “boom-bust” successional sequence in which nonnative plants first out-compete native plant communities, and then suffer catastrophic population crashes associated with aquatic plant control or natural disturbances. It is hypothesized, but not known, that succession of springs into algal-dominated ecosystem states may be promoted by the nutrient pulses and ecological openings associated with the rapid loss of aquatic plant populations.

- The effects of allelopathic compounds emitted by nonnative plants on algal dynamics in springs ecosystem are not presently known.

- Ecosystem effects of long-term aquatic plant control have not been well-studied in the specific context of Florida springs. Variables such as dissolved nutrients, dissolved oxygen, biomass deposition, and floral and faunal community structure should be monitored before and after major aquatic plant control operations in Florida springs.

- Water hyacinth and water lettuce are currently being managed for algal-suppression, nutrient recovery, and biomass utilization in a number of tropical countries, including places in which they are considered nonnative. While it is not known if such methods would be helpful in springs ecosystems, careful experimentation with floating plant treatment methods may be worthwhile in highly degraded springs ecosystems where these plants are established.

- Long-term effects of biocontrol organisms, including the possibility of improved efficacy over time, are not well-studied in nonnative plant populations in springs ecosystems. Increased research into biocontrol organisms and experimental release in springs ecosystems, particularly those affected by hydrilla, should be a priority for adaptive ecosystem management.

INTRODUCTION

One of the primary management concerns in many of Florida's freshwater spring systems is the growth of nonnative invasive plants. Although there are more than a dozen nonnative aquatic plants established in Florida's springs ecosystems, the vast majority of historic and ongoing management expense is associated with three species: water hyacinth (*Eichhornia crassipes*), hydrilla (*Hydrilla verticillata*), and water lettuce (*Pistia stratiotes*) (Bureau of Invasive Plant Management 2007). Many researchers and managers fear that rising nitrate-nitrogen levels in Florida springs may further promote growth of these, and perhaps other, nonnative plants to the overall detriment of native plants and animals (e.g., Florida Springs Task Force 2000; Loper *et al.* 2005).

Aquatic plant control programs that primarily target hydrilla, water hyacinth, and/or water lettuce are actively employed in several major springs systems, including Rainbow River, Silver River, Wekiva River, Weeki Wachee River, Wakulla River, and Kings Bay/Crystal River (Bureau of Invasive Plant Management 2007). Selective application of chemical herbicides is the primary operational method for aquatic plant control, although manual and mechanical harvest methods are also used in some springs systems. Approximately $173,000 was spent by the Florida Department of Environmental Protection (DEP) for aquatic plant control in springs ecosystems in 2005 – 2006. Over 80% of this amount was allocated for herbicidal suppression of hydrilla in Rainbow River, Weeki Wachee River, Wakulla River, and Silver River (Bureau of Invasive Plant Management 2007).

This review chapter begins by generally describing the introduction, ecological effects, and historical control of the major invas ive aquatic plant species in Florida. Available scientific literature is then used to explore four sets of questions raised by the presence of invasive plants and their ongoing management in Florida springs:

1. To what extent is increased nitrate-nitrogen a factor in the spread of invasive plants, and at what level is invasive plant growth limited by nitrate-nitrogen in springs?

2. What are the potential implications of invasive plant proliferation on ecosystem structure and function in springs?

3. What are the potential implications of aquatic plant control on ecosystem structure and function, particularly in terms of shifting springs toward more algal-dominated ecosystem?

4. For springs in which increased algal dominance is the primary conservation concern, are there opportunities for experimenting with alternative aquatic plant management strategies that attempt to utilize the known functions of extant invasive plants in support of long-term ecosystem recovery goals?

Major Invasive Aquatic Plants: HIstory and Control in Florida

Water Hyacinth

Water hyacinth is a floating aquatic plant native to South America's Amazon River drainage. Introduced into many countries throughout the subtropics and tropics in the late 19th and early 20th centuries, water hyacinth is now commonly regarded as one of the world's most problematic invasive plant species (Holm *et al.* 1977). A number of researchers have found that, under ideal conditions, water hyacinth is more productive than any other known vascular plant (Gopal 1987). This extremely high productive potential permits water hyacinth to quickly overgrow and out-compete other plant species (Schmitz *et al.* 1993), particularly in ecosystems affected by elevated nutrient levels and other forms of anthropogenic disturbance (Gopal 1987).

The ecological and economic effects of water hyacinth overgrowth are often quite dramatic and severe. Along with the competitive displacement of native plant communities, one of the most common ecological consequences of water hyacinth overgrowth is severe depression of dissolved oxygen in underlying waters due to the synergistic effects of rapid deposition of organic matter from senescing leaves, restriction of phytoplankton production due to shading, and interference with atmospheric oxygen exchange (Penfound and Earle 1948; Joyce 1985). Development of anoxic conditions under water hyacinth can directly lead to exclusion of fish and other oxygen-dependent species, thereby radically changing the structural composition of faunal communities (Schmitz *et al.* 1993). In addition, human economies are often adversely affected by restricted navigation, loss of fisheries access, and siltation of drainage systems that can be associated with the formation of substantial water hyacinth cover in a water body (Gopal 1987).

It is generally accepted that water hyacinth was first introduced into Florida in 1885 by a Palatka-area farmer who obtained a specimen from an exhibit at the 1884-1885 World's Industrial and Cotton Centennial Exposition held in New Orleans (Buker 1982). The plant was apparently propagated in a small garden pond, with excess plants periodically thrown into the nearby St. Johns River (Buker 1982). The subsequent effects of this introduction are legendary. By the early 1890s, the discarded plants had multiplied to such an extent that extremely large floating mats of water hyacinth became established at many locations along the St. Johns River and its tributaries (see Figure 1). Boat navigation and logging operations along the river flood plain were both severely curtailed, and massive accumulations of the plant were even reported to structurally undermine the columns of several railroad bridges (Webber 1897).

Aided in large part by farmers who valued the prolific plant for cattle forage (Buker 1982) and an organic mulch source for citrus trees planted in sandy soils (Maltby 1963), water hyacinth continued to spread rapidly into many of the state's other drainage basins throughout the first half of the 20th century. Water hyacinth was reported in several springs of the St. Johns River basin, including Volusia Blue Spring, Green Cove Springs, Silver River, and the Wekiva River, as early as the 1890s (Webber 1897), and introductions into new springs systems continued throughout the 20th century. Reports from the Panhandle's spring-fed St. Marks River suggest that water hyacinth was first introduced into that system as late as the 1970s (Bartodziej and Leslie 1998).

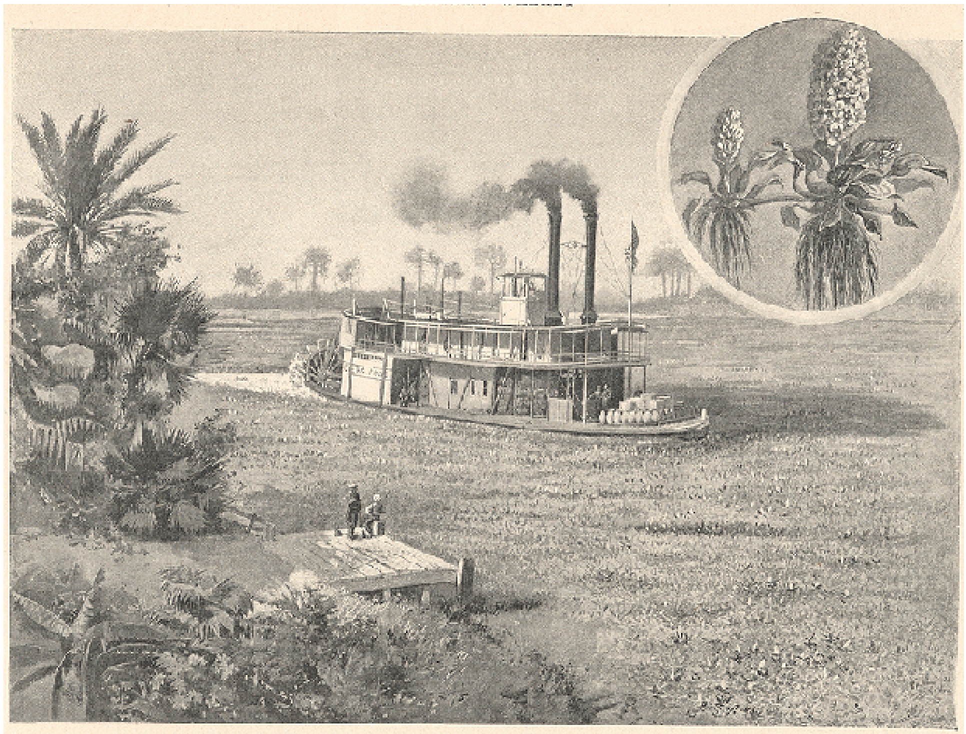

Figure 1 – *Water hyacinth overgrowth in St. Johns River. Illustration from March 19, 1898 edition of Harper's Weekly, as adapted by University of Florida Center for Aquatic and Invasive Plants.* *http://aquat1.ifas.ufl.edu/guide/stboatbg2.gif*

The history and evolution of efforts to bring water hyacinth under control in Florida are almost as legendary as the plant's rapid spread. The United States Rivers and Harbors Act of 1899 contained specific provisions authorizing the United States Army Corps of Engineers to destroy water hyacinth in navigable waters, and the Florida Legislature at nearly the same time enacted a law that prohibited the intentional transfer of water hyacinth into new waterways (Buker 1982). Sodium arsenite and other inorganic herbicide sprays were briefly used by the Corps of Engineers for hyacinth control around the turn of the century, but reports of severe cattle mortality associated with these sprays led both the Florida Legislature and U.S. Congress to prohibit use of these compounds in Florida by 1905 (Buckman and Company 1930).

As a result of this prohibition, most hyacinth control efforts from the turn of the century through the 1940s involved three techniques: 1) construction of physical barriers to prevent movement of plants into new areas; 2) manual labor to dislodge plants and facilitate downstream discharge into the Atlantic Ocean; and 3) mechanical shredding and/or harvest of plants using large machines (Buckman and Company 1930; Buker 1982 see Figure 2). While such methods were successful in terms of removing major plant blockages, they apparently were insufficient for abating the proliferation of water hyacinth. Thus, the spread and areal extent of water hyacinth coverage continued to increase in Florida throughout the first half of the 20th century, peaking at approximately 51,000 acres in the early 1960s (Schardt 1997; see Figure 3).

Figure 2 *– Water hyacinth shredder in the Withlacoochee River, circa 1940. Photo by United States Army Corps of Engineers, as adapted by the University of Florida Center for Aquatic and Invasive Plants.* *http://plants.ifas.ufl.edu/guide/mechconold7js.jpg*

By all accounts, the invention of the organic phenoxy herbicide 2,4-D in 1942 marked an important turning point in water hyacinth control. Unlike the inorganic herbicidal sprays used previously, 2,4-D effectively controlled water hyacinth at dosages that posed little direct toxic risk to cows, fish, and other animals (Joyce 1982), likely because its mode of herbicidal action specifically targets plant hormonal production. A number of 2,4-D-based spraying programs that targeted heavily concentrated populations of water hyacinth in Florida commenced in the late 1940s and continued to expand throughout the 1950s and 1960s (Schardt 1997).

While these early 2,4-D programs were successful in rapidly suppressing water hyacinths, many observers expressed concerns about mass nutrient releases, heavy organic detritus loads, and severe algal blooms that tended to follow large-scale aquatic plant control operations (e.g., Clugston 1963; Tilghman 1963). Over the late 1960s and early 1970s, aquatic plant control researchers and practitioners addressed these concerns by developing a management philosophy that came to be known as maintenance control (Schardt 1997). Adopted into state law in 1974 as the official guiding principle for aquatic plant management, maintenance control is defined by the operational goal of maintaining water hyacinths (and other invasive nonnative aquatic plants) at the “lowest feasible level” (Florida Statute 369.22). Inherent in this objective is a pragmatic acknowledgment that eradication of the invasive aquatic plants is impractical, but that control at population numbers that do not interfere with beneficial uses of water bodies can be maintained. Aside from the obvious objective of effectively suppressing nonnative plants, some research suggests that maintenance of plants at small populations may reduce overall detrital loading and herbicide use as compared to less frequent treatment of large plant populations (Joyce 1985; Schardt 1997). Since the 1970s the maintenance control program has greatly reduced the overall population of water hyacinth throughout the state (see Figure 3), generally through sustained use of 2,4-D, diquat dibromide (a contact herbicide), and glyphosate (a systemic herbicide) (Bureau of Invasive Plant Management 2007). Potential implications of herbicidal control methods used for water hyacinths and other invasive plants in springs ecosystems are discussed in more detail in later sections of this chapter.

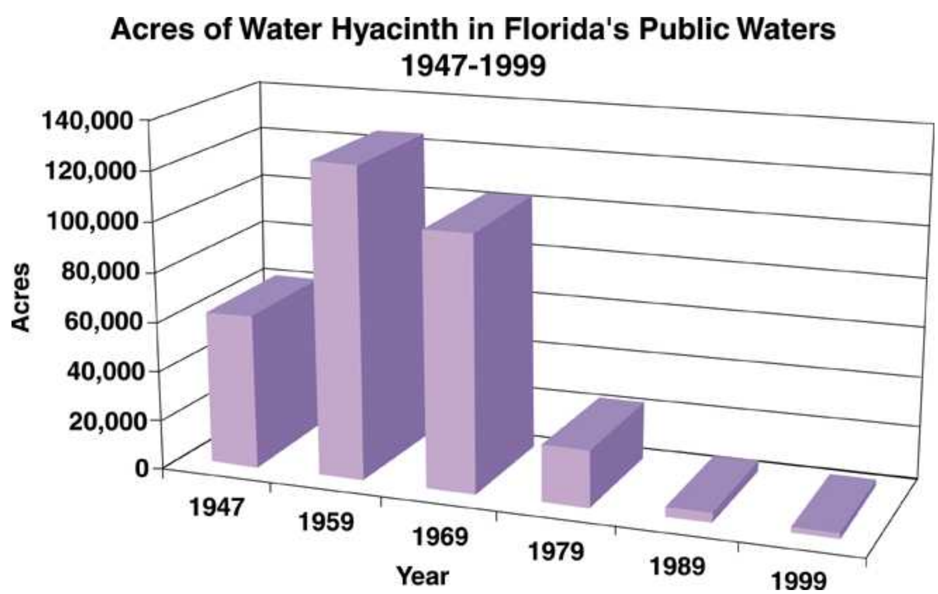

Figure 3 *– Effects of maintenance control operations on water hyacinth populations in Florida.Graph adapted from Florida Department of Environmental Protection, Bureau of Invasive Plant Management.* http://www.dep.state.fl.us/lands/invaspec/images/Graph%20wh%20acres.jpg

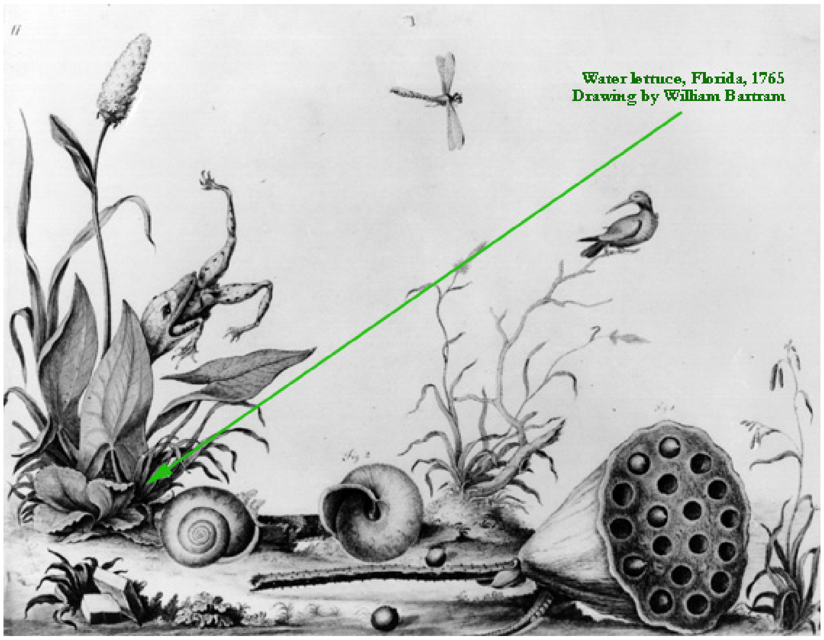

Figure 4 – *Water lettuce in Florida, 1765. Drawing by William Bartram, as adapted by Swarthmore College.* http://www.swarthmore.edu/Humanities/kjohnso1/pictures/stratiotes.jpg

Water Lettuce

Like water hyacinth, water lettuce is a floating aquatic plant that can commonly reach nuisance levels in Florida and other areas of the tropics and subtropics (Holm *et al.* 1977). The basic economic and ecological concerns about water lettuce are quite similar to those of water hyacinth, namely that its prolific floating growth habit can serve as an impediment to navigation, block drainage canals, out-compete native plants, and radically change aquatic communities through increased siltation and depression of dissolved oxygen concentrations (Schmitz *et al.* 1993).

Unlike water hyacinth, there is significant uncertainty as to the origins of water lettuce and its introduction to Florida. Most of this uncertainty derives from William Bartram's frequent reports of water lettuce along the Suwannee River and St. Johns River during his Florida travels in the 18th century (Stuckey and Les 1984). Some researchers speculate that water lettuce observed by Bartram possibly stemmed from an introduction of the plant during the Spanish colonial period (e.g., Stuckey and Les 1984), while others argue that water lettuce's Florida population may have preceded European contact by millennia (e.g., Stoddard 1989). Bartram's writings make specific note of large water lettuce populations in or near the Suwannee River's Manatee Springs and several springs along the St. Johns River, indicating that these springs have had water lettuce populations for well over two centuries. Other historical accounts in springs include Webber's (1897) sighting of large water lettuce populations in the Wekiva River during the late 19th century, and Carr's (1994) reports of water lettuce as a common component of springs ecosystems throughout north Florida during the 1940s. Field observations by Odum (1957) suggest that water lettuce growth in Silver Springs during the mid 20th century followed distinct seasonal patterns and that large population accumulations were often suppressed by insect herbivory.

It is commonly suggested that water hyacinth's similar habitat requirements and superior competitive abilities led to a large-scale displacement of water lettuce in Florida during the late 19th and early 20th centuries (Schmitz *et al.* 1993; Carr 1994). However, large populations of water lettuce quickly emerged in Florida and other states after the commencement of water hyacinth control in the 1950s, likely due to water lettuce's relative resistance to 2,4-D (Eggler 1953; United States Army Corps of Engineers 1973). Researchers during the mid 1960s discovered that water lettuce was controlled effectively by diquat dibromide (Weldon and Blackburn 1967), and since that time water lettuce and mixed stands of water lettuce and water hyacinth in Florida have been almost exclusively treated with this herbicide as part of maintenance control programs (Mossler and Langeland 2006). One exception is the spring-fed Ichetucknee River, where a control program based solely on hand removal of plants has drastically reduced water lettuce populations in much of the river over the past several years.

Hydrilla

Hydrilla is a submersed aquatic plant native to Southeast Asia and Africa. Commonly imported into Florida by the aquarium trade during the mid 20th century, naturalized populations of hydrilla were identified in several Florida waterways by the early 1960s (Schmitz *et al.* 1993). Over subsequent decades the plant has rapidly spread into many aquatic systems throughout Florida and the southeast United States. Of the $29 million requested by Florida's Bureau of Invasive Plant Management (2007) for aquatic plant control in public waters for 2007 – 2008, well over half ($16 million) is marked for ongoing hydrilla suppression. The Bureau of Invasive Plant Management (2007) also reported that approximately $142,000 was spent for hydrilla control in spring systems such as Wakulla River, Weeki Wachee River, Silver River, and Rainbow River in fiscal year 2005 – 2006.

Several features make hydrilla an extremely effective and problematic invasive species. Perhaps most critical to its spread is the viability of even very small plant fragments, which are often inadvertently brought into new water bodies by boat trailers and propellers (Schmitz *et al.* 1993). Once established in a water body, hydrilla has the ability to grow from sediments up to the water surface (often referred to as "topping out") and form a canopy that can effectively shade out native submersed species, severely restrict navigation, and interfere with flood control structures (Schmitz *et al.* 1997; Jones and Beardall 2005). In addition, hydrilla's root system is characterized by many large tubers that often resprout after leafy growth is suppressed through herbicides or other disturbance (Schardt 1997). Some research suggests that hydrilla may also have lower light requirements for photosynthesis relative to native submersed plants, thereby allowing it to colonize deeper areas of water bodies that previously would have been free of vascular plant growth (Van *et al.* 1976). Like the floating species discussed above, large-scale hydrilla coverage can result in the depression of dissolved oxygen levels due to reduced atmospheric diffusion and suppression of phytoplankton production in underlying waters (Schmitz *et al.* 1993). Dense hydrilla also has been known to adversely affect sports fisheries by providing increased habitat cover that restricts prey availability for species such as large mouth bass (Bureau of Invasive Plant Management 2007).

Figure 5 *– Hydrilla in Wakulla Springs, 1998. Photo by Vic Ramey, University of Florida Center for Aquatic and Invasive Plants* *http://aquat1.ifas.ufl.edu/wakhyd.jpg*

Although the deleterious effects of hydrilla overgrowth are quite dramatic, some research indicates that hydrilla can benefit certain fish and wildlife populations. For example, it is commonly reported that moderate hydrilla coverage provides superior game fish habitat (Schmitz *et al.* 1993), which leads many fishermen to advocate for management strategies that maintain significant hydrilla coverage in popular fishing lakes (Jones and Beardall 2005). Hydrilla is also known to provide highly attractive habitat for manatees (Campbell and Irvine 1977), certain macroinvertebrates (Schramm and Jirka 1989), and diverse assemblages of native water fowl (e.g., Johnson and Montalbano 1984; Esler 1990). Thus, one of the most complex challenges currently facing Florida's aquatic plant managers is development of techniques that better maintain the positive habitat values of hydrilla in areas where it is permanently established, while still preventing severe overgrowth and spread of the plant into new areas (Jones and Beardall 2005).

Modern hydrilla control methods in Florida rely heavily upon fluridone, a slow-acting systemic herbicide, and endothall, a fast-acting contact herbicide (Jones and Beardall 2005). Because effective treatment by fluridone requires long contact times that are prohibitively difficult and expensive to obtain in flowing systems, a dipotassium salt formulation of endothall (trade name Aquathol) is typically used for hydrilla control in springs (DEP 2005). However, serious concerns about the long-term sustainability of current chemical control methods are raised by recent findings of independently evolved fluridone-resistant hydrilla biotypes in Florida lakes frequently treated with fluridone (Michel *et al.* 2004). Although no endothall-resistant strains have been identified, many researchers argue that future development of resistance among hydrilla populations repeatedly treated with endothall, such as those in springs, is possible or perhaps even inevitable (Jones and Beardall 2005).

Diquat and copper (including chelated copper and copper sulfate formulations) are the major herbicides aside from fluridone and endothall that are currently listed for hydrilla control (Langeland 1996; Bureau of Invasive Plant Management 2007). Copper and diquat were commonly used for hydrilla control in the spring-fed Kings Bay/Crystal River complex during the 1970s and early 1980s (Haller *et al.* 1983), but apparently with uneven operational success (Dick 1989). Recent research indicates that copper and diquat may be most effective against hydrilla when applied together and/or in combination with endothall (e.g., Pennington *et al.* 2001), and such a strategy may be increasingly employed in Florida due to resistance concerns (Jones and Beardall 2005). However, increased use of copper for hydrilla control in some Florida springs is problematized by regulatory language that places restrictions on copper herbicide usage in areas frequented by manatees (State of Florida Division of Administrative Hearings 1993). These restrictions on copper herbicides were adopted by the Florida DEP in response to the documentation of elevated copper levels in the tissues of Kings Bay/Crystal River manatees (O'Shea 1984) and in the sediments of water bodies, including Kings Bay/Crystal River, in which copper was commonly used as an herbicide/algaecide throughout the 1970 and 1980s (Leslie 1992). Toxicological concerns associated with chemical control of hydrilla are discussed at greater length in subsequent sections of this chapter.

NITRATE-NITROGEN AND NONNATIVE PLANTS IN SPRINGS

The increased nitrate-nitrogen contamination observed in springs throughout Florida is of great concern to ecosystem managers and the general public. Most direct research into the ecosystem effects of nitrate-nitrogen in springs has focused on filamentous algae such as *Lyngbya wollei* and *Vaucheria* sp. (Cowell and Dawes 2004; Stevenson *et al.* 2004). However, significant concerns have also been expressed about the potential for nitrate-nitrogen to favor the proliferation of water hyacinth, water lettuce, hydrilla, and other invasive nonnative plants (Florida Springs Task Force 2000; Loper *et al.* 2005).

Although there is a fairly large body of literature that describes nutrient uptake of these aquatic plants for the purposes of wastewater treatment and other forms of environmental remediation (see Ho and Tsang 1998; Gu 2006), much less direct productivity research has been conducted at nutrient concentrations or conditions relevant to those in Florida springs. As discussed in more detail below, the available literature strongly suggests that nitrogen limitation of these plants in most Florida springs would only occur, if at all, at the upper bounds of background aquifer nitrate-nitrogen concentrations.

Water Hyacinth and Nitrogen Limitation

A topic explored throughout the vast literature about water hyacinth ecology and control is the growth and uptake responses of water hyacinth to increased loading of nutrients. A common observation is that water hyacinth problems tend to be most serious in waters that suffer from nutrient enrichment, and, thus, nutrient mitigation is often recommended as a strategy for reducing plant growth (Gopal 1987). Limitation by either phosphorus or nitrogen is most common, although low levels of calcium, potassium, and iron have also been found to limit water hyacinth growth (Gopal 1987). While nitrogen limitation to water hyacinths is frequently indicated when N/P ratios are less than 7 (Wilson *et al.* 2005), experimental trials indicate that, at very high nutrient levels, dissolved nitrogen typically will be depleted by water hyacinth stands at higher rates than phosphorus due to both luxury uptake by plants and denitrification (Reddy and Tucker 1983).

The natural concentrations of phosphorus, calcium, phosphorus and iron in typical Floridan aquifer water (Scott *et al.* 2004) are of sufficient quantity to make it unlikely that water hyacinth historically would have been limited by these nutrients in most Florida spring ecosystems. While long-term enrichment trends observed in springs provide a compelling rationale for considering nitrate-nitrogen the parameter of most concern for water hyacinth growth in Florida springs, the few direct studies of water hyacinths in springs have not definitively determined a concentration of nitrate-nitrogen that might limit biomass production. For example, Bartodziej and Leslie (1998), in a long-term study on the spring fed St. Marks River, report a water hyacinth biomass doubling time of 10 days at nutrient levels of 0.28 mg/l TN[1] and 0.06 mg/l TP. Because this biomass doubling time is essentially the same as those recorded in Japanese experiments (Sato and Kondo 1981, cited in Bartodziej and Leslie 1998) where water hyacinth was grown under conditions of extremely high nutrient enrichment (28 mg/l TN and 7.7 mg/l TP), Bartodziej and Leslie (1998) conclude that the observed nutrient levels in the St. Marks River were not a limiting factor for water hyacinth growth. Similarly, Odum's (1957) measures of water hyacinth productivity in Silver River, which at the time of study in the mid 1950s had a nitrate-nitrogen level of 0.4 mg/l, indicate that nutrients were not a major limiting factor.

Two recently developed water hyacinth models present nitrogen concentration values that could be expected to limit water hyacinth growth in some aquatic systems. Wilson *et al.* (2005) develop a synthetic model indicating that water hyacinth growth responds to nitrogen concentrations according to a logarithmic function, with the most dramatic increases in specific growth rate occurring between 0.1 and 1 mg/L of TN. While these nitrogen concentrations clearly fall within a range of direct relevance to Florida springs, direct inference of these results into springs conditions is confounded by the model's stated omission of flow velocity effects on nutrient availability and growth response. A water hyacinth growth model developed by Mahujchariyawong and Ikeda (2001) for Thailand's Tha-Chin River suggests that maximum growth rate of the water hyacinth requires 0.16 mg/l TN and 0.02 mg/l TP. Although this model does have the notable advantage of accounting for nutrient availability and replacement as affected by flow velocity, inferential caution is warranted due to important morphological, chemical, and climatic differences between the Tha-Chin River and typical Florida springs systems.

Perhaps the most intriguing clue about potential nitrate-nitrogen thresholds for water hyacinth in Florida springs comes from Webber's (1897) observation of water hyacinth plants showing a stunted growth form in the Silver River during the late 19th century. A data record reported by the USGS from 1907 indicates a nitrate-nitrogen concentration of 0.03 mg/l in Silver Springs (Munch *et al.* 2006). Taken together with the scientific literature discussed above, it is reasonable to hypothesize that Webber's (1897) observations may be indicative of nitrate-nitrogen serving as a physiological constraint to water hyacinth growth in the Silver River at the

[1] All nitrogen concentrations reported by Bartodziej and Leslie (1998) are in terms of TN. Relative contribution of nitrate-nitrogen to the TN measurement is not given.

background water quality levels of the late 19th and early 20th century. Confirmation of this suggested relationship, however, would require detailed assays of water hyacinth growth response to variable nitrate-nitrogen concentrations in flowing mesocosms, and/or comparative field studies of water hyacinth growth characteristics in springs systems, including those with background levels of nitrate-nitrogen.

Water Lettuce and Nitrogen Limitation

The similarity of growth and uptake responses observed for water hyacinth and water lettuce under experimental nutrient treatments (e.g., Aoi and Hayashi 1996) may make it reasonable to assume that the potential nutrient limitation thresholds for water lettuce growth in Florida springs are similar to those of water hyacinth. For example, it is well-established that water lettuce, like water hyacinth, will remove much higher levels of dissolved nitrogen than are necessary to sustain its maximum growth (Aoi and Hayashi 1996). Schmitz *et al.* (1993) hypothesize, while also noting the lack of specific studies testing this hypothesis, that increased levels of nitrogen may favor water lettuce to out-compete native submersed plants in freshwater systems throughout Florida.

Unfortunately, there is still very little research suggestive of the nitrate-nitrogen concentrations that might limit water lettuce production in Florida springs. Productivity measurements given by Odum (1957) indicate that growth of water lettuce in Silver Springs, much like water hyacinth, was not limited by nitrate-nitrogen levels of 0.4 mg/l. Instead, Odum's (1957) work suggests that extreme accumulation of water lettuce in Silver Springs was largely prevented by downstream export, seasonal senescence, and insect attack. More anecdotally, Webber's (1897, 13) reports of "large quantities of the water lettuce" in the Wekiva River during the late 19th century could suggest that background nutrient levels in that particular spring fed river were not a serious limiting factor for water lettuce growth. As suggested above for water hyacinth, detailed growth assays and/or comparative field studies would be needed to make more definitive determinations about the effects of nitrate-nitrogen enrichment on water lettuce population dynamics in Florida springs.

Hydrilla and Nitrogen Limitation

As a rooted submersed plant, determination of dissolved nutrient limitation for hydrilla is inherently more difficult than for the floating plants due to the confounding influences of sediment nutrient availability and uptake. With that said, a variety of evidence is suggestive of important relationships between hydrilla growth and increased nitrogen enrichment in Florida's aquatic systems. For example, tank experiments clearly indicate that hydrilla's growth and ability to out-compete native tape grass (*Vallisneria americana*) under high light conditions increases as a function of increased sediment nitrogen (Smart *et al.* 1994; Van *et al.* 1999). Similarly, Barko and Smart (1986) identified positive correlations between hydrilla shoot density and sediment nitrogen levels in field studies of North American lakes. More recent field surveys presented by Gu (2006) indicate a marginally significant relationship between dissolved total nitrogen and the extent of hydrilla occurrence in Florida lakes, although stronger correlative relationships were identified with other water quality parameters such as alkalinity, pH, and total dissolved phosphorus.

It must be cautioned, however, that straightforward inference from these studies into Florida springs conditions is confounded by at least two factors: 1) whether or not there is a significant positive relationship between dissolved nitrate-nitrogen and sediment nitrogen in springs ecosystems; and 2) what effects stream flow may have on dissolved nutrient availability for hydrilla and other submersed plants (Canfield and Hoyer 1988). Following this second point, Terrell and Canfield (1996) found that dissolved nitrogen availability for aquatic plants in Kings Bay/Crystal River, which had a mean TN concentration of approximately 0.26 mg/l at the time of study (neither nitrate-nitrogen contribution to TN nor sediment nitrogen were reported), greatly exceeded the biological demands necessary for maximum growth and accumulation of hydrilla. Based on this finding, Terrell and Canfield (1996) concluded that nutrient reduction likely was not an effective strategy for reducing growth of hydrilla in Kings Bay/Crystal River. Detailed studies that take into account dissolved nutrient availability, sediment nutrient stores, flow rates, native plant competition, and hydrilla productivity would be needed to determine if nitrate-nitrogen reduction is a feasible strategy for hydrilla suppression in the context of other Florida springs.

NONNATIVE PLANTS AND ALGAL COMMUNITY DYNAMICS

While overgrowth of nonnative invasive plants is a serious management issue, most conservation and management concern in Florida springs over recent years has been associated with increased cover of filamentous algae and cyanobacteria such as *Vaucheria* sp. and *Lyngbya wollei* (Stevenson *et al.* 2004). Given the strong trophic and structural associations between native aquatic plants, epiphytic algae, and animal communities historically found in springs ecosystems (Odum 1957), it stands to reason that the obvious structural changes in plant community caused by invasive plant growth potentially could trigger structural changes in the algal and animal communities.

This section utilizes scientific literature about major invasive plants to explore two mechanisms by which these plants might contribute to a successional trajectory in which undesirable algae become dominant in springs ecosystems. The first proposed mechanism, referred to as “boom bust,” focuses on the implications of the increased productivity, biomass accumulation, and vulnerability to catastrophic losses and rapid community reorganization that are associated with invasive plant communities. The second proposed mechanism focuses on the allelopathic properties of the invasive plants, with particular attention to the potential implications of algicidal allelopathy.

Boom-Bust Hypothesis

Perhaps the most basic functional trait shared by water hyacinth, water lettuce, hydrilla and other invasive aquatic plant species is higher productivity relative to competing native plants (Schardt 1997). Thus, the introduction of a successful invasive aquatic plant is almost axiomatically associated with a boom cycle in which more biomass is produced and accumulated in the ecosystem. Another feature of water hyacinth, water lettuce, and hydrilla in Florida is that these initial booms are often followed by rapid population crashes, or busts. These busts can be caused by aquatic plant control or a variety of stochastic natural events such as saltwater storm surges

(Terrell and Canfield 1996), high water/floods (Bartodziej and Leslie 1998; Bureau of Invasive Plant Management 2007), and killing frosts (Joyce 1985; Schardt 1997).

Figure 6 gives a simplified diagram of mechanisms by which a boom bust cycle associated with invasive plants potentially could lead to increased nuisance algae in springs systems. The diagram shows that one major ecosystem effect often associated with invasive plants is competitive displacement of native plant species (e.g., Schmitz *et al.* 1993; Bartodziej and Leslie 1998), some of which may have previously suppressed the growth of problematic algae such as *Lyngbya wollei* (see Doyle and Smart 1998). While there is significant evidence to suggest that hydrilla, water hyacinth, and water lettuce are likely to suppress algal production through shade, nutrient uptake, and other feedbacks (e.g., Cohen 1993; Cowell and Botts 1994; Kim *et al.* 2001), it is plausible that the sequence of competitive displacement of native plants followed by a bust cycle characterized by destruction of dominant invasive plant populations may favor succession by opportunistic filamentous algae. Filamentous algae have been observed to fill in such ecological voids after aquatic plant control of hydrilla in Kings Bay/Crystal River (Cowell and Botts 1994) and Wakulla River (Loper *et al.* 2005). Similarly, Evans (2007) observed an apparent increase of filamentous algal biomass in the Ichetucknee River following manual removal of water lettuce. Large algal blooms following control of water hyacinths, while not specifically documented in Florida springs systems, have been documented in other ecosystem contexts (see Clugston 1963; Bicudo *et al.* 2007).

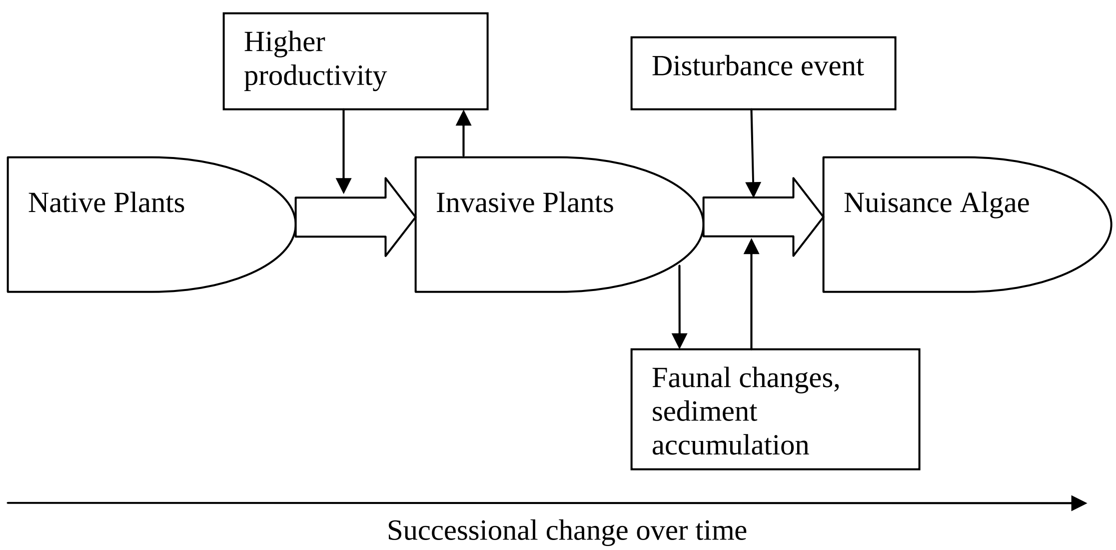

Figure 6 *– Conceptual diagram of boom-bust hypothesis in Florida springs*

A mechanistic feedback that may further favor proliferation of nuisance algae after a boom bust invasive plant cycle is implied by the work of Stevenson *et al.* (2007), who found that nutrient enrichment of sediments was significantly associated with presence of nuisance algae in springs. While there has to date been no detailed study of nutrient accumulation in springs sediments as a function of aquatic plant control or nonnative plants, aquatic plant control activities were suggested as a possible source of enriched sediments documented by Wetland Solutions, Inc. (2006) in the Wekiva River and Rock Springs Run system. More detailed study of such relationships appears warranted in springs, particularly because invasive plant growth and control has been linked with nutrient enrichment of sediments in other ecosystem contexts. For example, Brenner *et al.* (1999) suggested that the introduction and subsequent chemical treatment of water hyacinth and hydrilla likely was a major contributor to nutrient enrichment and bulk density increases documented in the sediments of Lake Hell 'n' Blazes from approximately 1900 to 1995. Similarly, Grimshaw (2002) identified chemical treatment of water hyacinth and water lettuce as a significant source of nutrient-rich organic sediments in the Kissimmee River and Lake Okeechobee. In a highly detailed study of water hyacinth control (based on a "trituration" technique of shredding the aquatic plants and loading the biomass into the water column) in Mexico's Valsequillo reservoir, Mangas-Ramirez and Elias-Gutierrez (2004) recorded increases of ammonia from 3 mg/l to 60 mg/l in sediment interfaces, a 320% increase in dissolved nitrate-nitrogen, declines in dissolved oxygen to below 0.4 mg/l, increased rates of organic sedimentation, disappearance of most fish, and large blooms of cyanophytes in the reservoir following weed trituration.

Although these studies are suggestive of the impacts that invasive aquatic plants and subsequent control efforts may have in terms of sediment enrichment in springs, it is important to note that a variety of factors such as flow velocity, external inputs of organic matter, upwelling of nutrient rich groundwater through karst streambeds, and the densities and accumulation of plant biomass in specific springs would all be expected to exert significant influence over sediment nutrient levels. Detailed measurements of sediment nutrients, dissolved nutrients, and plant/algae community characteristics in discrete samples taken directly before, directly after, and in sequential intervals following aquatic plant control would provide invaluable information about the overall ecosystem effects of current management techniques on springs ecosystems.

Allelopathy Hypothesis

Algal community composition in springs and other streams are clearly shaped by ecological factors such as nutrient availability, flow velocity, light intensity, grazer abundance, and substrate quality (e.g., Stevenson *et al.* 2007). In addition to these more general ecosystem variables, algal communities are also shaped by complex competitive and/or synergistic interactions between algae and vascular plants at the species level. Emission of allelopathic compounds, or compounds that directly suppress the growth of other primary producers, is increasingly regarded as one of the most important, if not well understood, competitive factors in aquatic systems (Gross 2003).

Several scientific studies indicate that water hyacinth, water lettuce, and hydrilla all emit allelopathic compounds that restrict growth of algal and/or plant competitors. In the case of water hyacinth, Jin *et al.* (2003) conducted lab experiments indicating that various compounds extracted from water hyacinth roots had algicidal properties on *Chlorella* sp., *Scendesmus obliquus*, and undifferentiated phytoplankton that were comparable in activity to copper sulfate – a commonly used commercial algicide. Similarly, Aliotta *et al.* (1991) isolated several allelopathic chemicals from water lettuce that showed inhibitory effects on seventeen of nineteen algal cultures, with *Lyngbya kuetzingii* and *Chlorella saccharophila* showing no inhibition. While specific algicidal compounds have not been identified in hydrilla to date, Kulshresthna and Gopal (1983) did find that hydrilla negatively affected the growth of vascular aquatic plant

Ceratophyllm sp. through allelopathic mechanisms. However, Glomski *et al.* (2002) later argued that allelopathy is only a very minor factor in hydrilla's overall competitive success against other aquatic plants.

The potential implications of algicidal allelopathy in the floating plants are interesting to consider in the context of Florida springs systems. On the one hand, allelopathic emissions from floating plants may be a mechanism by which fringe mats of floating plants in spring runs serve as a constraint for algal growth and accumulation in habitat areas beyond those covered by the plants, including beds of native submersed plants located in the main stream flow. If this is the case, then the algicidal properties of floating plants may potentially serve as a buffer against algal overgrowth in nutrient-enriched springs. On the other hand, it is plausible that persistent presence of allelopathic compounds with algicidal properties might select for relatively resistant algal taxa, potentially including *Lyngbya* sp. (e.g., Aliotta *et al.* 1991).

Better understanding of the algicidal activity of floating plant allelopathic emissions on springs-specific algae species would require isolation of algicidal compounds and detailed bioassays similar to those conducted by Aliotta *et al.* (1991) and Jin *et al.* (2003). In addition, measurements of the concentration ranges for such compounds in the water of springs would be required to understand the extent to which allelopathic mechanisms may be an important driver of algal community selection in springs communities.

AQUATIC PLANT CONTROL AND ALGAL SUCCESSION

Control of nonnative invasive plants is one of the most common management actions performed in Florida's aquatic ecosystems, including many of the state's springs. As discussed above, chemical control using herbicides registered by the EPA for use in aquatic systems is the primary tool used by aquatic plant managers. The most obvious ecological concern associated with use of aquatic herbicides is non-target damage to native plants, algae, and animal communities, either through direct toxicology of herbicides or the ecological consequences of rapid plant senescence. Although aquatic plant managers and herbicide applicators take great precautions to avoid major non-target impacts, the complexities of ecosystems make some non-target damage unavoidable.

This section reviews literature associated with two of the most plausible and commonly suggested mechanisms by which chemical control of nonnative invasive plants can disrupt aquatic ecosystems: 1) preferential selection of herbicide resistant algae species; and 2) suppression of key algal-grazing fauna through direct toxicology and/or habitat destruction. Potential implications of these mechanisms for Florida springs, particularly in terms of succession towards filamentous algae/cyanobacteria communities, are also discussed.

Herbicide Selection Hypothesis

Development of herbicide resistance among algae has been repeatedly demonstrated at both the cellular level of individual species (i.e., a specific algal species evolves resistance to an herbicide) and the ecological level of community assemblages (i.e., more herbicide-resistant species become dominant) (e.g., Solberg and Higgins 1993; Boswell *et al.* 2002; Garcia-Villada *et al.* 2004; Cooke *et al.* 2005; Lopez-Rodas 2007). Thus, a major concern associated with repeated use of herbicides in aquatic systems is the potential selection for herbicide-resistant algal biotypes. In particular, recent research suggests that some herbicide-resistant algal species often may be less palatable and/or nutritious to algal-grazing fauna, thus causing a cascade effect on faunal community structure and overall ecosystem organization (e.g., Weiner *et al.* 2007). This section discusses potential algal-selection concerns associated with the major herbicides used in Florida springs: copper, diquat, endothall, glyphosate, and 2,4-D. When relevant information is available, attention is particularly given to potential selection concerns associated with *Lyngbya wollei*.

Copper

Copper compounds are most often used in aquatic systems as algaecides, but are listed an approved method for control of hydrilla and other submersed plants species in Florida (Bureua of Invasive Plant Management 2007). Largely due to concerns about sediment contamination and bioaccumulation risks in manatees (O'Shea 1984; Facemire 1991; Leslie 1992), copper herbicides have not been widely used in Florida since the early 1990s. However, copper herbicides were used extensively for hydrilla control in the Kings Bay/Crystal River ecosystem during the 1970s and 1980s (Haller *et al.* 1983), and currently are being researched as a potential option for filamentous algae control in Kings Bay/Crystal River.

Development of copper resistant algal communities is a well-documented risk associated with long-term usage of copper herbicides. Recent research, for example, indicates that repeat exposure to copper sulphate can facilitate evolution of copper-resistant strains in both the cyanobacterium *Microcystis aeuruginosa* (Garcia-Villada *et al.* 2004) and the green algae *Chlamydomonas reinhardtii* (Boswell *et al.* 2002). Cooke *et al.* (2005) report that repeated treatment with copper sulfate resulted in increasingly copper resistant algal communities in a number of lakes and reservoirs throughout the northeastern United States. With such selection dynamics in mind, it is notable that *Lyngbya* sp. and *Oscillatoria* sp., which are problematic taxa in some Florida springs (Stevenson *et al.* 2004), are known for their ability to develop copper resistant biotypes (Spencer and Lembi 2005). Evans *et al.* (2007) argue that such selection dynamics may provide a key clue for better understanding of algal community dynamics in Florida spring systems, such as Kings Bay/Crystal River, where copper herbicides have been used historically.

Diquat

Scientific literature indicates that concerns associated with selection of herbicide-resistant algae communities may also be associated with large-scale use of diquat dibromide in Florida springs. Diquat is most commonly used for treatment of mixed stands of water lettuce and water hyacinth, but has also been used for control of hydrilla and other submersed species in some springs systems (Haller *et al.* 1983). Although residues of diquat do accumulate in aquatic sediments, most recent research suggests that diquat forms complex bonds with sediments that render it biologically unavailable (Emmett 2002).

Bioassay research indicates that there is a wide range of tolerances among algal taxa to diquat exposure. Peterson *et al.* (1997) found that 50% inhibition of biomass production occurred among two green algae taxa (*Scendesmus quadricauda* and *Selenastrum capricornutum*) at concentrations of approximately 0.6 mg/l of diquat, while 50% growth inhibition for diatoms (*Nitzschia* sp. and *Cyclotella meneghiana*) and cyanobacteria (*Oscillatoria* sp. and *Pseudoanabaena* sp.; *Microcystis* sp.) occurred at concentrations approximately one order of magnitude lower (0.074 mg/l and 0.079 mg/l of diquat, respectively). Phlips *et al.* (1992), however, found a wider range of diquat sensitivity among the taxonomic groups, with *Euglena gracilis*, *Chlorella vulgaris*, and *Skeletonema costatum* showing high levels of tolerance to diquat (50% inhibition predicted at over 2.94 mg/l). *Lyngbya wollei* showed a higher level of tolerance to diquat (50% inhibition predicted at a range of 0.081 mg/l to 0.205 mg/l of diquat) in the Phlips *et al.* (1992) bioassays as compared to the cyanobacteria tested by Peterson *et al.* (1997). Aquatic plant control observations indicate that diquat often proves ineffective for long-term control of *Lyngbya wollei* (Bayne 2005), which may be suggestive of an evolutionary resistance capability with regards to diquat in this cyanobacterium.

A potential implication of the differential tolerances exhibited by algal-taxa is that repeat treatment with diquat may exert a chronic selective pressure that favors community-level dominance by diquat-resistant species and/or biotypes over time. Much like with the copper herbicides, diquat treatment history and sediment residues may be an important variable to consider in studies of algal community dynamics in Florida springs where this herbicide has been commonly used for aquatic plant control.

Endothall

The dipotassium salt formulation of endothall, which is generally referred to by the trade name Aquathol, is the primary herbicide used for control of hydrilla in flowing water systems. While Aquathol is not typically recommended for algae control purposes, an amine endothall salt (trade name Hydrothol) is registered for control of filamentous algae and submersed plants in Florida. However, Hydrothol is not commonly used in Florida's public waters due to its relatively high toxicity to fish and other aquatic fauna. Field observations suggest that Hydrothol applications often prove ineffective for *Lyngbya wollei* control (DuBose *et al.* 1997), and, as noted above for diquat, such observations may be indicative of an evolutionary resistance to endothall-based compounds among *Lyngbya* sp. Specific bioassays testing the algaecidal action of Aquathol would be needed to determine if repeated use of this compound has significant implications for algal community structure in Florida springs.

Glyphosate

An aquatic-registered form of glyphosate (trade name "Rodeo") is sometimes used for control of water hyacinths in Florida (Bureau of Invasive Plant Management 2007). While generally not used as an algaecide in aquatic environments, bioassays indicate that glyphosate does have algaecidal action. Wong (2000) reported significant growth inhibition of *Scendedesmus quadricauda* at 2 mg/l of glyphosate and complete inhibition at 20 mg/l. In very recent bioassay work with *Microcystis auroginosa*, Lopez-Rodas *et al.* (2007) reported considerable inhibition in the cyanobacterium from 10 mg/l to 60 mg/l of glyphosate solution, and observed the evolution of glyphosate resistant *M. auroginosa* biotypes at concentrations of 120 mg/l. While the glyphosate concentrations of concern to Lopez-Rodas *et al.* (2007) are at least an order of magnitude over realistic field concentrations associated with aquatic plant control (Langeland 2006), it is plausible that the lower end of concentrations showing growth inhibition in the Wong (2000) experiment may be reached during aquatic plant control operations. Bioassays testing glyphosate response curves of algal species in Florida springs would be needed to better determine algal-selection risks associated with this herbicide.

2,4-D

Algal toxicity bioassays with 2,4-D have found that this herbicide is generally non-toxic and even stimulatory to most algae and cyanobacteria at concentrations used for aquatic plant control (Okay and Gaines 1996; Wong 2000). The likely reason for the stimulatory effect is that 2,4-D's mode of herbicidal action is mimicry of the plant hormone auxin, rather than direct targeting of photosynthesis mechanisms. Toxic effects on algae are reported at over 200 mg/l of 2,4-D by both Okay and Gaines (1996) and Wong (2000), but such concentrations are well outside of those associated with aquatic plant control. Interestingly, Okay and Gaines (1996) report that the amine form of 2,4-D is preferentially consumed as a nitrogen source over nitrate-nitrogen by the phytoplankton *Phaedactylum tricornutum* and *Dunaliella tertiolecta* when 2,4-D is found at concentrations up to100 mg/l, meaning that changes in algal community could be promoted by 2,4-D through an enrichment mechanism, rather than a toxicity mechanism. Like with the other herbicides, specific bioassays testing growth response to 2,4-D among algal species found in Florida springs would be needed to better understand the community level effects of this herbicide.

Attractor – Catastrophe Hypothesis

A final mechanism by which invasive plants and their subsequent management may profoundly affect ecosystem structure in springs is through a sequential cycle that can be deemed "attractor-catastrophe," which is somewhat similar to the boom-bust cycle discussed above. The basic thrust of this hypothesis is that nonnative invasive plants can become preferred habitat, or serve as an "attractor," for key faunal species, but that this habitat ultimately becomes a persistent sink for faunal populations due to the bust cycle "catastrophes" that affect nonnative plant communities. Although any habitat disturbance that destroys non-native plant communities is potentially a catastrophic sink for associated faunal communities, primary focus is given here to the non-target toxic effects and/or general habitat disturbance that may be associated with aquatic plant control activities. The major rationale for this focus is that aquatic plant control activities are unique in the sense that they are directly controlled by management agencies, and thus may be adjusted for the purposes of adaptive learning.

Habitat Values of Water Hyacinth

Bartodziej and Leslie's (1998) long-term study of ecological communities associated with water hyacinth in the St. Marks River clearly demonstrates the high habitat values that can be provided by this nonnative plant in Florida springs. Contrary to other ecosystem contexts in which large mats of water hyacinth have been clearly shown to depress dissolved oxygen, coverage by water hyacinth in the flowing waters of the St. Marks River did not show significant oxygen profile differences as compared to strap-leaf sag (*Sagitraria kurziana*) or other native plant communities. While native strap-leaf sag in the St. Marks River was reduced by water hyacinth expansion, it was not displaced entirely as the water hyacinth community was rarely observed by Bartodziej and Leslie (1998) to reach more than 25% coverage along the river width (see Figure 7) due to consistent flushing of the floating plants by river current.

Figure 7 *– Water hyacinth fringe in River Rise Spring #3, St. Marks River. Photo by Northwest Florida Water Management District (2006).*
http://www.nwfwmd.state.fl.us/rmd/springs/Wakulla_StMarks/photos/rise3_1.jpg

Long-term faunal surveys indicated that the community associated with water hyacinths was generally more diverse in terms of invertebrate taxa and included significantly higher abundances of spring run crayfish (*Procambarus paludosus*), amphipods (*Hyalella azteca*), grass shrimp (*Palaemonetes paludosus*), and several fish species as compared to strap leaf sag communities (see Figure 8). Apple snails (*Pomacea paludosa*) were also found to have much higher population densities in water hyacinth compared to strap leaf sag. Conversely, rasp elimia snail (*Elimia floridensis*) populations in strap leaf sag were much higher than those found in water hyacinth communities (see Figure 8). Surveys of bird populations among water hyacinth in the St. Marks River indicated that water hyacinth was commonly used for forage habitat by little blue herons (*Egretta caerulea*) and tri-colored herons (*Egretta tricolor*), and was also observed to increase available nesting habitat for the common moorhen (*Gallinula chloropus*) (Bartodziej and Weymouth 1995).

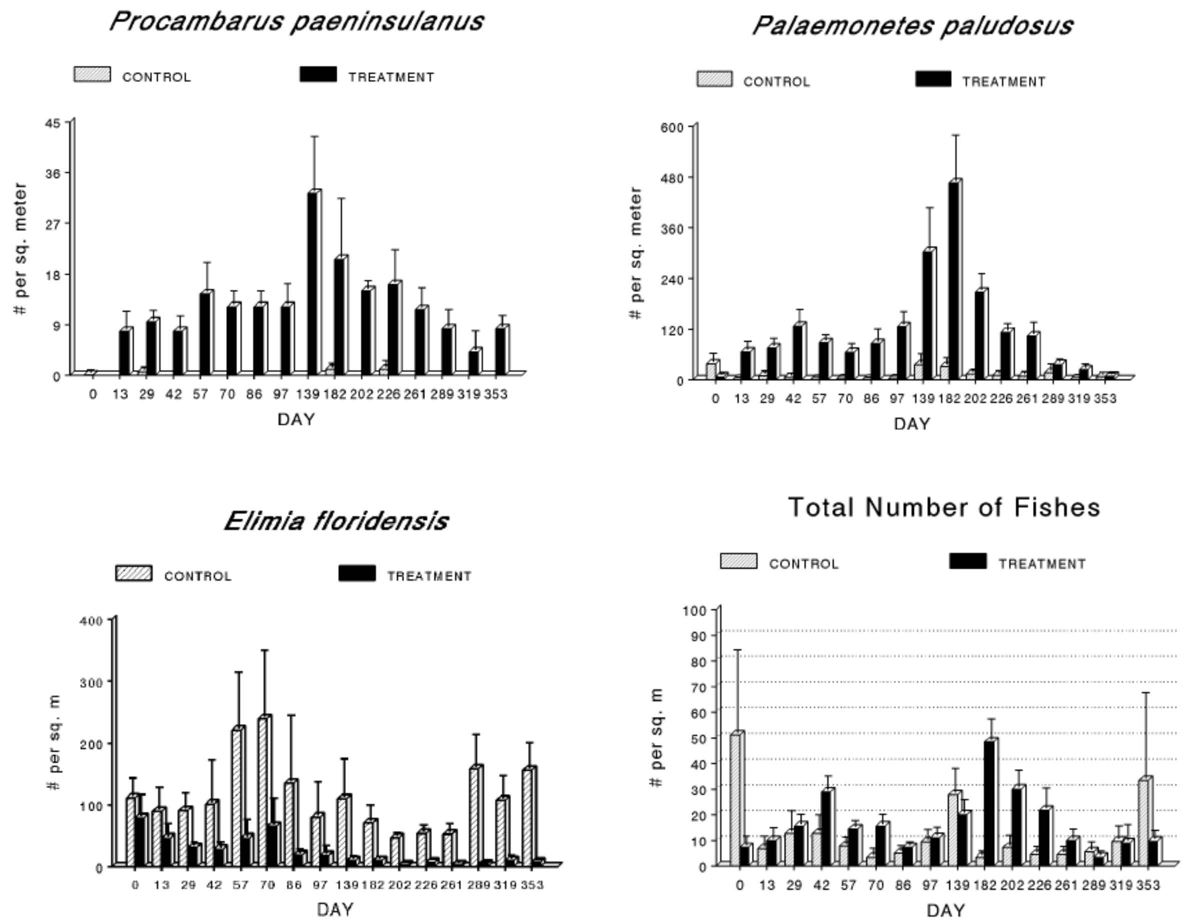

Figure 8 *– Ecosystem survey results from St. Marks River (Bartodziej and Leslie 1998) showing higher numbers of spring run crayfish* (Procambarus paludosus)*, grass shrimp* (Palaemonetes paludosus)*, and total fishes in water hyacinth (treatment) as compared to strap leaf sag communities. Rasp elimia snail* (Elimia floridensis) *populations are considerably higher in strap leaf sag.*

Habitat Values of Water Lettuce and Hydrilla

Detailed habitat assessments in a springs ecosystem are not available for either water lettuce or hydrilla. However, as suggested by Carr (1994), it may be reasonable to assume that the similar structure of water lettuce and water hyacinth is likely to provide habitat for a similar faunal species assemblage. Schmitz *et al.* (1993) note that water lettuce supports high concentrations of *Hyalella azteca*, and Evans (2007) anecdotally reports large numbers of spring run crayfish and apple snails in water lettuce harvested from the Ichetucknee River in 2000 – 2001. Similarly, Corrao *et al.* (2006) report high concentrations of apple snails on hydrilla and apple snail eggs on water lettuce at Wacissa Springs. In other ecosystem contexts, hydrilla is known to support large macroinvertebrate populations (Schramm and Jirka 1989) and attract diverse assemblages of water fowl (Johnson and Montalbano 1984; Esler 1990). Dramatically increased manatee utilization of Kings Bay/Crystal River beginning in the 1960s (Kochman *et al.* 1985) coincides with the introduction and rapid spread of hydrilla, a preferred manatee forage (Campbell and Irvine 1977), in that system.

Non-Target Concerns

As noted by Bartodziej (1992) for water hyacinth-associated amphipod populations and Corrao *et al.* (2006) for apple snails, the effects of habitat loss associated with aquatic plant control on faunal communities in springs is largely unknown. Corrao *et al.* (2006) suggested that direct removal of apple snails during harvest of hydrilla at Wakulla Springs and herbicide suppression of plants containing snail eggs at Wacissa Springs may have had significant negative effects on apple snail populations, but noted that more detailed studies would be necessary to test these observations. Similarly, Evans (2007) observed that harvest of water lettuce from Ichetucknee Springs resulted in direct mortality of several faunal species, including apple snails and spring run crayfish, but also noted that more detailed studies would be necessary to quantify the overall faunal impacts of plant harvest.

Use of copper herbicides has raised significant non-target concerns in Florida springs. Most notably, copper herbicide use in Kings Bay/Crystal River was discontinued in the late 1980s due to the finding of severe accumulation of copper in aquatic sediments (Facemire 1991; Leslie 1992) and the tissues of manatees (O'Shea 1984). More systematic concerns about long-term copper herbicide usage are suggested by Cooke *et al.* (2005), who note that dissolved copper can severely suppress zooplankton grazers and that sediment contamination can have long-term effects on the structure and function of benthic communities. Increased levels of *Lyngbya wollei* often were observed in Kings Bay/Crystal River subsequent to hydrilla herbicide treatments (see Cowell and Botts 1994), which led Evans *et al.* (2007) to hypothesize that toxicological suppression of grazer communities associated with copper herbicide usage may have contributed to subsequent algal overgrowth.

Risk assessments on four grazer species performed by Mastin and Rodgers (2000) indicate 50% lethal concentration dosages[2] (LC50) at 48 hours for copper herbicides between 0.011 mg/l – 0.029 mg/l for *Daphnia magna*; between 0.158mg/l to 0.433 mg/l for *Hyalella azteca*; between 0.374 and 0.114 mg/l for *Chironomus tetanus*; and between 0.019 and 0.48 mg/l for *Pimephales promelas*. Copper concentrations reported by Haller *et al.* (1983) in the water of Kings Bay following a copper herbicide treatment ranged from 0.002 mg/l to 0.011 mg/l, which is generally lower than the above LC50s (with the exception of *Daphnia magna*) reported by Mastin and Rodgers (2000). Dick (1989), however, reported that poor control of hydrilla using standard dosage rates sometimes led aquatic plant managers to apply significant higher rates of copper in Kings Bay/Crystal River than those monitored by Haller *et al.* (1983). Copper's toxicity to organisms in dissolved form generally decreases as a function of increased hardness due to carbonate-induced precipitation of copper compounds (Mastin and Rodgers 2000). Thus, it can be argued that non-target risks in Florida springs ecosystems from dissolved copper may be mitigated due to the relatively high hardness values in most springs as compared to the water hardness values (48 – 100 mg/l) reported in the Mastin and Rodgers (2000) experiment. Clearly,

[2] A 50% lethal concentration dose (LC) is the concentration of a chemical that results in 50% mortality of a test organism within 24 to 96 hours.

any future use of copper compounds in Florida springs ecosystems should be implemented cautiously and carefully monitored to minimize the secondary effects on fauna.

Risk assessments and toxicological data for diquat indicate that use of this herbicide may also raise serious non-target concerns for springs fauna. In a risk assessment for diquat conducted for the State of Washington Department of Ecology, Emmett (2002) reports that diquat is "very highly toxic" to *H. azteca*, with a LC50 of 0.048 mg/l, and "highly toxic" to the apple snail (*Pomacea paludosa*) with a LC50 of 0.34 mg/l. Nicholson and Clerman (1974) noted the high sensitivity of *H. azteca* to diquat toxicity in laboratory studies, and suggested that a combination of direct toxicity and the destruction of aquatic plants through herbicide usage were likely mechanisms for drastic *H. azteca* declines observed in New York's Chautauqua Lake during the 1960s and 1970s. Given that *H. azteca* is an important grazer of *Lyngbya wollei* (Camacho and Thacker 2006), it is reasonable to hypothesize that toxicological suppression of *H. azteca* potentially may be a factor in the increased dominance of *L. wollei* in Florida springs where diquat has been widely used.

Available literature suggests that very little non-target toxicological effects on fauna are associated with fluridone (e.g., Hamelink *et al.* 1986; Haag and Buckingham 1991), 2,4-D (Johnson and Finley 1980), or glyphosate (Langeland 2006) at concentrations used for aquatic plant control. However, Wang *et al.* (1994) does document bioaccumulation of 2,4-D after water hyacinth treatment in some fish species, and a breakdown product of 2,4-D (2,4-dicholorophenol) has been shown to have relatively high toxicity to earthworms (Roberts and Dorough 1984). Relyea (2005) has raised concerns about the effects of the Roundup formulation of glyphosate on amphibians, but Langeland (2006) notes that the toxicological effects reported by Relyea (2005) are associated with an adjuvant in Roundup that is not used in the aquatic-approved formulations of glyphosate (e.g., Rodeo).

Aside from habitat loss and toxicology, the other major concern associated with aquatic plant control is prolonged dissolved oxygen depression as plant biomass decays. Wetland Solutions, Inc. (2006) measured an increase in community respiration of 120% and a reduction of net primary production by 150% in a segment of Rock Springs Run following herbicide treatment of floating and emergent plants in December 2005. It was also noted that the trend of increased respiration continued for approximately two weeks following the herbicide treatment, thereby resulting in "a detectable but temporary impairment of the aquatic community in Rock Springs Run" (Wetland Solutions, Inc. 2006).

Some of the most detailed monitoring of aquatic plant control in a springs ecosystem has taken place over recent years in the Wakulla River. A report by DEP (2002) indicates that the stream condition index and habitat assessment scores at Wakulla River improved after an Aquathol treatment of hydrilla (Figure 9). However, significant non-target concerns were raised after state park biologists observed a significant die-off of spring run crayfish following at least one subsequent Aquathol treatment (DEP 2006). In response to these concerns, DEP (2006) conducted a management experiment in which crayfish were monitored following aquatic plant control. Twenty chambers containing crayfish were deployed immediately prior to herbicide application, and nineteen were retrieved after four days. The remaining chamber was initially missed, but retrieved with a live crayfish after nine days. Another twenty chambers were deployed nine days after the herbicide application and again retrieved four days later. Data sondes showed that dissolved oxygen dropped from as high as 4.3 mg/l to approximately 2.0 mg/l after the herbicide treatment, and Aquathol exposure was measured at concentrations that ranged from 0.41 mg/l to 2.06 mg/l – levels known to be well under toxicological thresholds for crayfish. Despite these low oxygen levels, only one crayfish death among the forty replicates was observed during the duration of the experiment. Although these results did not support the hypothesis that previously observed crayfish mortality was caused by aquatic plant control, the possibility of drastically reduced crayfish fitness as a result of prolonged dissolved oxygen depression that extended beyond the temporal scope of the experiments could not be ruled out (DEP 2006).

Wakulla Springs Herbicide Study					
Station			Wakulla Springs		
STORET			STMARKSSTORET01		
Station Nickname			WAKULLA SP		
Sampling Date			04/04/02 and 05/06/02		
Macroinvertebrate Parameters	4/4/2002	5/6/2002	Chemistry Data	4/4/2002	5/6/2002
SCI	19	21	Ammonia (mg/L)	0.01 U	0.019 I
SCI Evaluation	Poor	Good	Nitrate-Nitrite (mg/L)	0.73	0.79 J
Number of Taxa	17	16	TKN (mg/L)	0.06 U	0.06 U
EPT Index	2	0	Total Phosphorus (mg/L)	0.032 I	0.052
FL Index	6	8	Color (PCU)	5 U	5 U
% Dominant Taxon	35.42	51.33	Turbidity	0.6	0.35
% Diptera	58.33	81.42	Physical-Chemical Data	4/4/2002	5/6/2002
Total number of Chironomidae	9	11	Habitat Assessment	115	130
% Filter-Feeders	26.04	31.86	ecific Conductivity (umhos/c	320	316
Periphyton Parameters	4/4/2002	5/6/2002	Dissolved Oxygen (mg/L)	5	4.7
% Bacillariophyceae	90.7	89.63	pH (SU)	7.45	7.6
% Cyanophyceae	8.59	9.31	Temperature (deg C)	20.6	21.5
% Chlorophyceae	0.72	1.05			
Percent Dominant taxon	26.83	25.66			

***Figure 9** – Habitat and water quality assessments at Wakulla River before (4/4/2002) and after (5/6/2002) Aquathol treatment of hydrilla (DEP 2002).*

RECOMMENDATIONS FOR FURTHER RESEARCH

This chapter opened by asking four sets of questions related to nonnative plants in Florida springs. The first asked to what extent increased nitrate-nitrogen might be a factor in the spread of the invasive plants water hyacinth, water lettuce, and hydrilla, and at what level might invasive plant growth in springs be limited by nitrate-nitrogen. Available literature does not provide a clear answer for determining a concentration of nitrate-nitrogen that would be limiting to nonnative springs, but observations suggests that nitrogen limitation is most likely alleviated at the very low end, and perhaps even close to background, concentrations in Florida springs. Detailed nutrient assay experiments in flowing mesocosms and, in the case of hydrilla, with realistic sediment nutrient concentrations would be necessary to determine more accurate nutrient limitation parameters for nonnative plants in spring systems.

The second question asked about the potential implications of invasive plant proliferation on ecosystem structure and function in springs. Available literature indicates that biomass accumulation, suppression of native plants, and algicidal emissions associated with nonnative plants may produce feedback mechanisms that together make springs systems more prone to a successional trajectory of overgrowth by nuisance algal taxa. At the same time, scientific studies and observations indicate that the major invasive plants often provide highly attractive habitat for key springs ecosystem fauna and may support some feedbacks that could be expected to reduce algal overgrowth. Detailed habitat assessments, monitoring of sediment accumulation, and multi-year monitoring of vegetational succession patterns in nonnative plant communities would be needed to better understand the relationships between nonnative plants and algal overgrowth.

The third question asked about the potential implications of aquatic plant control on ecosystem structure and function. What emerged from a review of literature was a wide range of concerns about possible algal selection, habitat loss, faunal toxicology, and dissolved oxygen suppression that may be associated with aquatic plant control. With the notable exceptions of circa 1980s work conducted by several agencies in Kings Bay/Crystal River due to concerns over copper herbicide contamination (Haller *et al.* 1983; O'Shea *et al.* 1984, Facemire 1991) and more recent work in Wakulla Springs associated with concerns over crayfish mortality after Aquathol applications (DEP 2005), there has been very little monitoring of the overall ecosystem consequences of aquatic plant control in springs ecosystems. To better understand the overall ecosystem effects of aquatic plant control in springs communities, detailed monitoring programs that measure key variables such as dissolved nutrients, dissolved oxygen, biomass deposition, and floral and faunal community structure should be monitored as a matter of course before and after major aquatic plant control operations.

As for the fourth question: are there opportunities for alternative management of invasive plants that may assist in the restoration of desired ecosystem functions in highly degraded springs and spring run ecosystems? Given the notorious history of these plants recounted above, the mere suggestion that there may be anything "good" or even redeemable about water hyacinth, water lettuce, or hydrilla in the context of springs ecosystems is undoubtedly controversial from the outset. However, discussions among ecological restoration practitioners indicate an increasing willingness to consider the proposition that, given the diverse realities of modern environmental change (e.g., climate change, nutrient enrichment, toxic contamination, and global species mixing), more adaptive approaches to nonnative species control should be considered (D'Antonio and Meyerson 2002; Ewel and Putz 2004; Gobster 2005). From an adaptive management perspective, the overriding questions might be: Are nonnative species management efforts directly leading to an even worse set of problems (e.g., succession into an even more undesirable ecosystem state), and, if so, how might future efforts be adjusted in the face of these emergent problems?

Assuming that the most prominent ecological concerns facing many springs ecosystems is the proliferation of nuisance algae such as *Lyngbya wollei*, an adaptive management question implied from several lines of evidence presented above is the extent to which aquatic plant control may be a contributing factor in this proliferation. A complementary question is how alternative methods of aquatic plant management could potentially help mitigate nuisance algae and/or restore habitat for desirable species.

But before exploring such alternatives in more detail, an initial boundary must be set that distinguishes between "prevention" and "control" when managing nonnative species. Clearly, none of the nonnative plants should be intentionally introduced into springs where they have not been present historically, and precautionary steps to prevent their introduction and/or spread into new systems should remain a high management priority. In addition, early detection and eradication efforts aimed at preventing newly discovered nonnative plant populations from becoming irreversibly established are also clearly justified. Instead, the opportunity for adaptive reflection is within those springs systems where nonnative plant species are extant and considered to be permanently established.

Alternative Management of Floating Plants

Establishment of selective biocontrol organisms often is regarded as the most sustainable long-term method for controlling water hyacinth, water lettuce, and other nonnative plants. A successful biocontrol organism should greatly reduce the potential for invasive overgrowth, which in theory should lessen, or even render unnecessary, the use of chemical herbicides and/or harvester machines over time (Center 1996; Dray *et al.* 2001). In practice, however, aquatic plant control methods in Florida have rarely been adjusted at a large scale in response to biocontrol introductions (Haller 1996). For springs in which current aquatic plant control methods may be a significant disturbance factor that selects for algal overgrowth, increased use of floating plant biocontrol organisms may be a promising alternative aquatic plant management strategy.

Interestingly, observations by Odum (1957) suggest that attack by an unknown insect (or insects) historically was an important control mechanism for water lettuce in Silver Springs. New research studies would be needed to determine whether or not such natural control mechanisms for water lettuce are currently at work in springs systems where water lettuce is established, or if the water lettuce moth (*Spodoptera pectinicornis*), an introduced biocontrol organism (Dray *et al.* 2001), is having significant control effects.

Center *et al.* (2005) found that herbivory by water hyacinth weevils (*Neochetina eichhorniae* and *N. bruchi*) greatly reduced the competitiveness of water hyacinth in relation to water lettuce. While water hyacinth's superior competitive abilities led to complete displacement of water lettuce, weevil herbivory allowed for competitive parity in which water lettuce could persist and, in some cases, become dominant. Bartodziej and Leslie (1998) evaluated the effects of water hyacinth weevil (*Neochetina eichhorniae*) on water hyacinth populations in the St. Marks River, and calculated that baseline weevil populations reduced the rate of water hyacinth expansion by approximately 10% over the course of a growing season. Bartodziej and Leslie (1998) also reported that augmentation of weevils successfully reduced population to an even greater extent, but estimated a prohibitively high augmentation cost of $40,000 per acre, or approximately 100 times the cost of chemical control. No field studies or augmentation estimates for water hyacinth moth (*Sameodes albiguttalis*), another effective biological control agent for water hyacinth in Florida (Center 1984), were given by Bartodziej and Leslie (1998). Revised studies of weevil and moth herbivory on water hyacinth population dynamics in Florida springs, particularly if paired with detailed study of regular aquatic plant treatment sites and provisional "no aquatic plant management" control sites, could potentially provide useful information for adjusting the intensity of aquatic plant treatment programs.

A more controversial alternative management strategy for floating plants is experimental utilization of these plants in support of ecosystem recovery in highly degraded springs ecosystems. Both of these plants are well known for their luxury uptake of nitrogen (Aoi and Hayashi 1996; Ho and Tsang 1998), and also are known for their ability to suppress algal production through direct shading, nutrient competition, allelopathy, and grazer habitat feedbacks (Joyce 1985; Aliotta *et al.* 1991; Cohen 1993; Ho and Tsang 1998; Kim *et al.* 2001; Jin *et al.* 2003). Mahujchariyawong and Ikeda (2001) detail an ambitious use of water hyacinth for nutrient remediation in Thailand's Tha-Chin River, and St. Johns River Water Management District recently has commissioned a project to better understand the nitrogen reduction implications of allowing for greater colonization of water hyacinth and water lettuce in Lake George (SJRWMD 2006). Detailed ecosystem surveys by Bartodziej and Leslie (1998) in the St. Marks River clearly indicate the high habitat value of water hyacinth to a diverse variety of native springs fauna, and observations suggest that similar habitat values are likely associated with water lettuce. In springs with large numbers of resident and wintering manatees, it is reasonable to suspect that an increased availability of water hyacinth, which is known as a nutritious and sometimes preferred manatee forage source (Lomolino 1977), might reduce herbivory pressure that can adversely affect desirable native submersed plant populations (Hauxwell *et al.* 2004). Studies could include small scale pilot projects that study the ecosystem effects of variable water hyacinth and water lettuce coverage levels in springs, particularly in those now affected by severe algal overgrowth. Comparisons among springs ecosystems with no aquatic control of floating plants (e.g., St. Marks River) and widespread control of floating macrophytes (e.g., Wekiva River) may also be valuable.

Alternative Management of Hydrilla

Alternative management of hydrilla poses more apparent concerns than water hyacinth and water lettuce, as the disruptions associated with hydrilla in some springs systems (e.g., Wakulla River) may actually be more severe than nuisance algae. In addition, the submersed growth habit makes hydrilla inherently harder to contain than the floating plants for the purposes of phytoremediation. However, hydrilla's apparent ability to evolve resistance to fluridone (Michel *et al.* 2004) and concerns that it may do the same for endothall (Jones and Beardall 2004) may force alternative management strategies.

The most serious problem associated with hydrilla in Florida springs is not that it provides poor wildlife habitat; rather, the major concern is its ability to form extensive topped out canopies that competitively exclude native plant species and radically diminish the recreational desirability of springs systems. Thus, the suggestion by Cuda *et al.* (2002) that herbivory by *Cricotopus lebetis*, an aquatic midge of unknown origin discovered in Kings Bay/Crystal River in 1992, may effectively prevent hydrilla from topping out is potentially of great importance for other springs ecosystems affected by hydrilla. Similar to the field observations of stunted hydrilla in Kings Bay given by Cuda *et al.* (2002), Van *et al.* (1998) found that hydrilla's competitiveness with *Vallisneria americana* was severely reduced in experimental treatments containing biocontrol organisms *Hydrillia pakistanae* and *Bagous hydrillae*. Increased experimentation with release of such biocontrol organisms clearly should be a priority for Florida springs ecosystems affected by well-established hydrilla populations.

Surprisingly, recent research in the Potomac River has identified significant positive correlations between hydrilla colonization and long-term recovery of native plants, including *Vallisneria americana* (Rybicki and Landwehr 2007). Cowell and Botts (1994) found that hydrilla coverage in Kings Bay had a significant negative relationship to coverage by *Lyngbya wollei*, perhaps indicating that hydrilla – particularly if overgrowth is controlled by constant herbivory by insects and, in some cases, manatees – could, similar to the Potomac River (Rybicki and Landwehr 2007), have valuable functional benefits in terms of guiding community succession away from filamentous algae and toward increased submersed plants in some springs systems. In springs ecosystems now affected by large hydrilla populations, management experiments might be set up to comparatively monitor the successional consequences of different control strategies (e.g., biocontrol, herbicides, manual removal, native plant restoration, and various combinations of these) over time.

CONCLUSION

There is little question that nonnative plant invasions have had profound effects on the aquatic environments of Florida, including many springs, over the past several decades. While it is reasonable to suspect that nitrate-nitrogen enrichment of springs may have contributed to overgrowth by nonnative aquatic plants, current studies provide insufficient information for making a definitive determination of nitrate-nitrogen concentrations that would effectively limit water hyacinth, water lettuce, or hydrilla growth in springs. Scientific literature suggests that both nonnative plant overgrowth and aquatic plant control techniques to suppress such overgrowth have the potential to serve as severe disturbances that could promote succession to algal dominated states in springs ecosystems. Because it is extremely unlikely that nonnative plant species can be entirely eliminated from systems in which they are established, the chapter argues that it may be beneficial to consider alternative and adaptive management strategies for nonnative plants, particularly in the context of springs and spring runs where algal overgrowth is now the primary management concern. Priorities for more adaptive aquatic plant management include: 1) intensive monitoring of ecosystem and successional impacts associated with current aquatic plant control methods; 2) increased research and experimentation with biocontrol organisms; and 3) careful experimentation with ecosystem recovery methods that utilize the nutrient uptake, algal suppression, and habitat values of floating plants.

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