RESTORING PATTERN WITHOUT PROCESS IN LAKE RESTORATION: A LARGE-SCALE LITTORAL HABITAT ENHANCEMENT PROJECT ON LAKE TOHOPEKALIGA, FLORIDA

By

ZACHARIAH C. WELCH

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2009

ACKNOWLEDGMENTS

My experiences at the Florida Cooperative Research Unit, where I worked and studied from 1999 to 2009, far exceeded my most optimistic expectations. My advisor, Wiley Kitchens, kept me involved in a multitude of projects and tasks, inundating me with anything and everything to do with research and academia. The environment he and Franklin Percival provide for students and staff is unparalleled and directly responsible for any accomplishments I have had over the last 10 years. Their unique combination of humor, guidance, support, freedom, and pressure to perform beyond your own expectations is truly a recipe for success. This is clearly evident by the caliber of my peers, all of whom were instrumental at different stages of my graduate experience. I would also like to thank Peter Frederick, whose undergraduate Wetlands Ecology course I took so many years ago inspired me to pursue all areas wet and muddy, introducing me to the greatest ecosystems on the planet.

I would be remiss not to thank the people who gave me the strength to tackle all of life's challenges with unwavering love, support and guidance: my parents, Curt and Sandy, and my wife, Christa Zweig. My parents are ultimately responsible for all my past and future successes, having instilled in me every good quality I possess. My wife, whom I met during my graduate career, was an ear when I had to vent, a colleague when I needed sound advice, a shoulder if I had to lean, and a refuge when I wanted to get away. Thanks to all those who supported me through this wonderful experience.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

RESTORING PATTERN WITHOUT PROCESS IN LAKE RESTORATION: A LARGE-SCALE LITTORAL HABITAT MODIFICATION PROJECT ON LAKE TOHOPEKALIGA, FLORIDA

By

Zachariah C. Welch

December 2009

Chair: Wiley M. Kitchens
Major: Interdisciplinary Ecology

Muck removal is an extreme habitat restoration technique, where heavy machinery is used to remove dense vegetation and accumulated organic material from lake shorelines. This approach is used to combat accelerated plant growth and subsequent litter deposition, following decades of altered hydrologic schedules, elevated nutrient levels, and exotic species introductions. This study explored the efficacy of the technique, using results from the largest muck-removal application to date.

Vegetation communities were monitored from 2002 to 2008, including two years prior to restoration and four years after. Before muck removal, *Pontederia cordata* represented the dominant community in the zone of annual water level fluctuation, as compared to *Panicum repens*, which was dominant in the 1950's. Four years after muck removal, *P. repens* had expanded slightly from its pre-restoration levels, but the dominant species in treated areas was *Vallisneria americana*. This submersed species had no record of ever being prevalent in the system, and represented a novel community.

Muck removal effects were short-lived in the shallowest areas of the littoral zone, with sites < 0.75 meters in depth recovering to pre-treatment levels within 3–4 years of reflooding. Deeper sites (> 1.0 meter) generally had the largest impacts, with entirely new communities established within three years of treatment. These results suggest that future projects focus on deeper-water emergent communities, as dense vegetation may quickly recolonize shallow shorelines.

There was concern among managers that hurricanes passing over the lake immediately following muck removal dramatically altered the outcome of the project, but this study found otherwise. While corresponding high water events undoubtedly delayed recovery in treated areas, the compositions of early colonizers were not changed. The same compositions found just prior to hurricane passage were found the following growing season, and the eventually-dominant communities did not appear until nearly two years after the storm events. These results suggest that initial water levels were less important in determining restored community types than the longer-term hydroperiods within treated areas.

CHAPTER 1
INTRODUCTION

Ecosystem Restoration

Ecosystem restoration has become increasingly important over the last decade (Suding et al. 2004) and its application increasingly complex. In the simplest case restoration and degradation can be depicted as linear processes traveling in opposite directions along parallel pathways (Dobson et al. 1997), with recovery occurring when the appropriate stressor is removed from the system. Restoration efforts usually begin by re-establishing historical structure or species mix (pattern), and/or the environmental conditions (processes) that permit a site to become self sustaining (Parker 1997). For example, prairie restoration may begin with re-introducing fire to eliminate woody species encroachment (Doren and Whiteaker 1990). This "applied succession" approach (Niering 1987), where re-establishing key structuring processes produces a desired pattern through self-organization (Mitsch and Wilson 1996) works well when a single constraint exists (Suding et al. 2004).

The degree to which restoration is possible, however, is generally limited by the severity of degradation and the effort that can be applied (National Research Council 1992). In reality, degradation is not a linear process and involves multiple paths of change in species abundances and ecosystem function (Zedler 2000). As ecosystems move through multiple states of degradation (Hobbs and Norton 1996), there are disturbance thresholds that may be crossed, making reversal much more difficult, if not impossible (Whisenant 1999, Lindig-Cisneros et al. 2003). Recent studies have shown that feedbacks can develop between novel communities and degraded environmental conditions that result in resilience to restorative change, even after key structuring

processes (fire, nutrients, hydrology) have been restored (Bakker and Berendse 1999, Zedler 2000, Suding et al. 2004). For example, fires may be ineffective at restoring prairie grass communities if invading woody species impact burn efficacy, resulting in a novel composition (Anderson et al. 2000). Similarly, overgrazing in semi-arid systems and subsequent shrub encroachment can lead to changes in soil characteristics and water availability that cannot be reversed by simply easing grazing pressure (van de Koppel et al. 1997).

To further complicate matters, there are many cases where historical structuring processes may no longer be restorable; natural disturbances like fires and floods are often suppressed or eliminated entirely from the system. Prescribed burns are increasingly difficult to conduct near urban areas, and historical flood levels in urbanized watersheds cannot be achieved without property losses. Essentially, the historical range of environmental variability in many ecosystems no longer exists, and restoring these key structuring processes may no longer be an option (Seastedt et al. 2008).

Lakes and wetlands near urban areas are prime examples of such ecosystems, where a permanent loss of historical water level fluctuations and their crucial role in maintaining function and pattern is often accompanied by invasive or exotic species introductions and nutrient pollution (Havens et al. 1996). How can restoration succeed under such novel conditions? One approach is to find surrogates for lost processes; Infrequent, catastrophic fires in forests have been replaced by clear-cut logging (Hunter 1993) and spring-grazing by cattle has replaced frequent fires in prairie grasslands (Seastedt et al. 2008). In lakes and wetlands, managers have long used drawdowns in place of natural droughts, but, like prescribed burning, this becomes

increasingly difficult in large systems or where recreational activities are interrupted. Additionally, new communities established under higher nutrient loads and stabilized water levels can reduce the efficacy of infrequent drawdowns (Moyer et al. 1989), maintaining dominance over more desirable communities even after drawdowns. In some cases, heavy machinery has been used to speed up organic sediment and biomass removal during drawdowns in an attempt to restore desired plant communities and substrate qualities to degraded systems (Moyer et al. 1995, Hoyer et al. 2008).

In warm-water, shallow lake systems, decades of excessive vegetation growth under eutrophic and stabilized water conditions can lead to thick, organic substrates and the establishment of highly competitive plant monocultures. Dense vegetative growth can impede navigation, alter fish communities (Killgore et al. 1989) and foraging efficiency (Diehl 1992), and combined with exotic species introductions can have dramatic impacts on shallow, warm-water lakes (Hoyer and Canfield 1997). As with many aquatic ecosystems, the disturbance regime (flood/drought cycle), species pool, and geochemical conditions of these systems are or will soon be outside of their historical ranges. To combat these effects, an aggressive restoration approach has been implemented in several such systems across Florida.

This technique, hereafter referred to as muck removal, involves exposing parts of the littoral zone with drawdowns, removing accumulated organic material, and regulating initial plant establishment with selective herbicide treatments. The goal of these projects is ultimately to improve fish spawning habitat, recreational access, and overall water quality by removing dense littoral vegetation and associated organic substrates, and reducing the abundance of rapid litter-producing species like cattail

(*Typha* spp.) and pickerelweed (*Pontederia cordata*) in the near-shore littoral zones (Hoyer et al. 2008).

While several studies of this technique have focused on sport fish response (Moyer et al. 1995, Allen et al. 2003), little information exists about actual habitat changes following these restoration activities (but see Moyer et al. 1987, Tugend and Allen 2004). These types of extreme management approaches represent the challenges facing restoration ecology in the future, specifically where historical structuring processes cannot be restored. Many inland waterbodies are or will soon be facing issues like those of many Florida lakes, and it serves as an excellent example of intensifying management efforts to replace natural processes in aquatic system restoration. This paper will focus on the largest application of this muck removal application to date, which took place on a central Florida lake, Lake Tohopekaliga.

Lake Tohopekaliga

Lake Tohopekaliga (hereafter referred to as Lake Toho) is one of several large lakes located in the upper Kissimmee River basin, collectively draining thousands of square kilometers into the Kissimmee River and ultimately Lake Okeechobee (Figure 1-1). Lake Toho and an adjacent sister lake, East Lake Toho, are the northernmost lakes in the basin, lying between the Orlando and Mount Dora Ridges in the Osceola Plain. This plain consists mainly of poorly drained, clayey sediments with poor groundwater recharge, having over 73 lakes at least 3.2 ha in size (HDR Engineering 1989). Most of the lakes in this region were formed from solution activities and are precipitation driven.

Lake Toho is the largest lake in the Osceola Plain, covering an area of 8,176 ha with an average depth of 2.1 m at maximum pool (16.75 m NGVD) (HDR Engineering 1989, Remetrix LLC 2000). The immediate watershed is 340 km^2, though an additional

686 km^2 of East Lake Toho watershed ultimately drains into Lake Toho through canal C-31 (HDR Engineering 1989). Nearly half of these 1334 km^2 are drained primarily by two main stream systems: Shingle Creek, located north of Lake Toho and flowing directly into the northwest side of the lake; and Boggy Creek, northeast of Lake Toho and flowing into East Lake Toho. Depending on precipitation and the operation of control structures on C-31 (drainage canal from East Lake Toho to Lake Toho) either Shingle Creek or the discharge from East Lake Toho can account for as much as 50% of the inflow to Lake Toho (Fan and Lin 1984, HDR Engineering 1989).

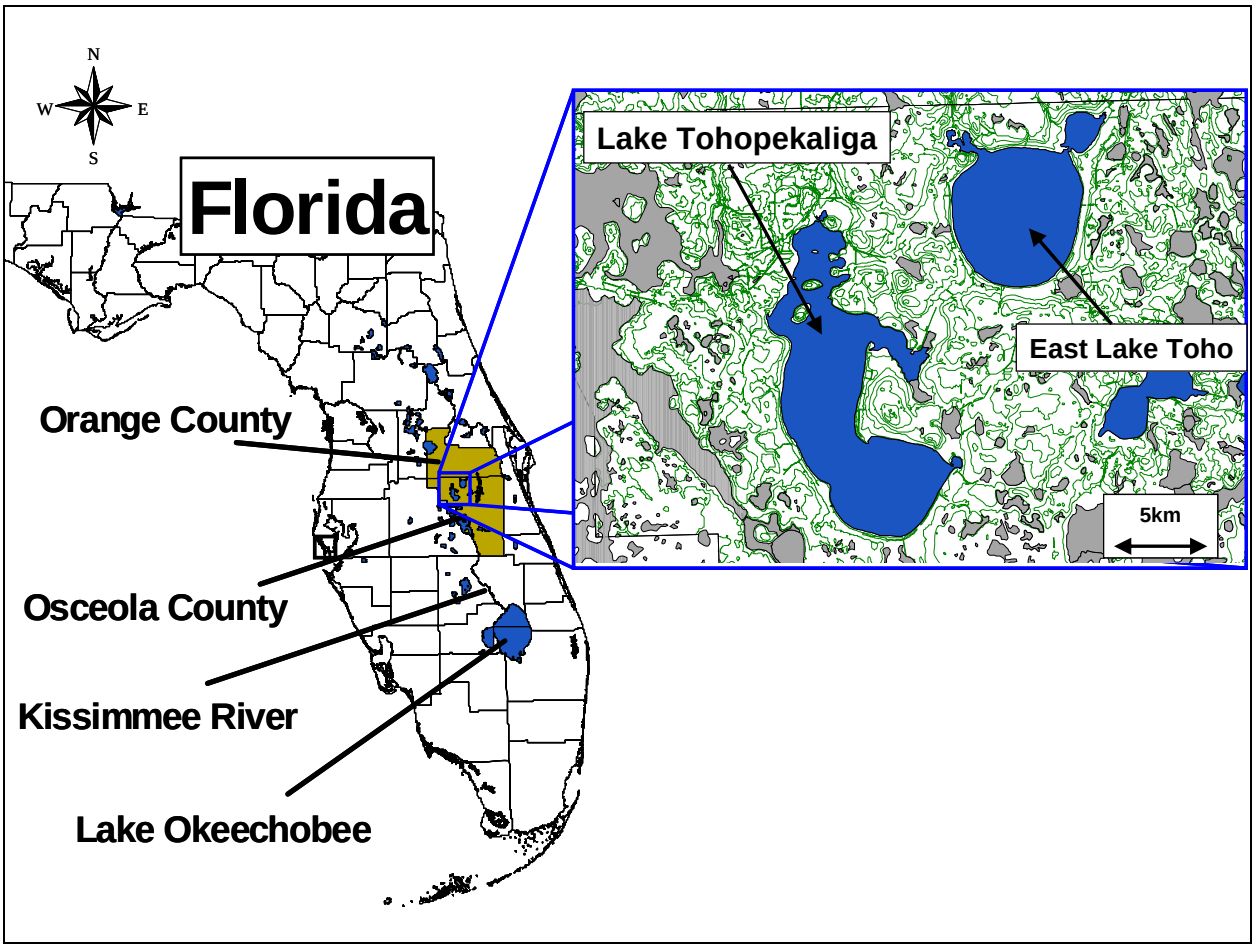

Figure 1-1. Location of Lake Tohopekaliga and East Lake Toho in relation to Lake Okeechobee and the Kissimmee River.

Brief History

Historically, much of the watershed in the upper Kissimmee River basin was dominated by wetlands, with lakes bordered and interconnected by large wet prairie sloughs, including the connection of Lake Toho and East Lake Toho by Fennel and Cross Prairies (HDR Engineering 1989). This network of waterbodies flowed south primarily through the Kissimmee River, virtually connecting waters of interior central Florida to Lake Okeechobee.

As early as the 1850s, pioneers began to modify the hydrology of the system and by 1884 a navigable waterway was opened from Kissimmee all the way to Fort Myers (HDR Engineering 1989). After the Florida Legislature passed the General Drainage Act in 1913 (Chap. 298, FS), a reported 108 km (67 mi) of canals were dug throughout the Shingle and Boggy Creek Basins (Blackman 1973). Catastrophic hurricanes in the 1940s sparked several flood control projects with major changes occurring in the upper Kissimmee River basin by 1957. These projects were designed to construct levees and control structures on the south ends of the larger lakes, to improve channels to downstream lakes, and for regulation of upper lake levels within a 0.6–1.2 m range (HDR Engineering 1989, U.S. Army Corps of Engineers 1956). Water control structures and canals regulating flows to and from Lake Toho were completed in 1964 (Blake 1980), marking the end of natural water level fluctuations. This resulted in a stage reduction from at least 3.2 m to a maximum of 1.1 m (Wegener et al. 1973). Figure 1-2 shows the sharp contrast between the dynamic, astatic condition prior to impoundment in 1964 and the stabilization that has occurred since.

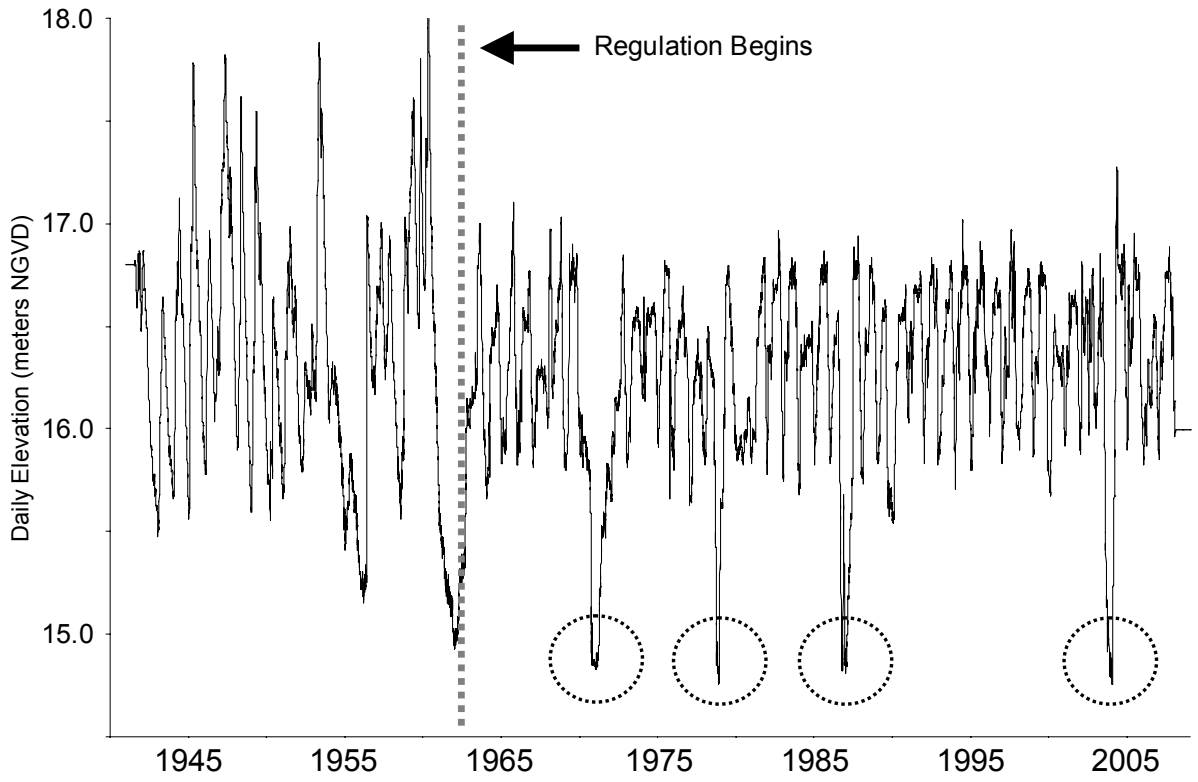

Figure 1-2. Daily mean water elevations in meters (NGVD) from January 1942 until Jun 2008. The dashed gray vertical line represents the approximate time of impoundment in 1964 while the dashed circles indicate managed drawdowns. The natural drought in 1962 and flood in 1960 were the lowest and highest on record at that point.

Sewage treatment plants began pumping effluent into the Shingle and Boggy Creek basins as early as the 1940s, and by 1986 an estimated 113 million liters per day (30 million gallons) were being discharged into these systems (Wegener et al. 1973). Though water quality problems were recognized and attributed to these plants in 1969 (Wegener 1969), discharges were not completely eliminated until 1988. By that point nutrient loading and water level stabilization had noticeably affected littoral habitats, water qualities, and fish populations (Moyer et al. 1989). Mean lake phosphorous (total)

levels dropped 85% from 1980 to the mid 1990's (0.82–0.11 mg/L), while total nitrogen dropped 50% (2.69–1.30 mg/L) (Williams 2001).

Previous Studies

In 1969, the Florida Fish and Wildlife Conservation Commission (FFWCC) recommended that all effluent discharges into Lake Toho be stopped and that a managed drawdown be performed in hopes of sparking seed germination and recolonization of desired species (Wegener 1969). The first managed drawdown of the lake took place in 1971, lowering the water from a high pool stage of 16.75 m to 14.65 m (55–48 ft) NGVD (National Geodetic Vertical Datum). The lake was held there for nearly six months and drought conditions further extended the refilling to high pool stage until March of 1973. During this period the FFWCC conducted studies on fish, invertebrates, vegetation, soils, algae, and water chemistry (Wegener et al. 1973). Vegetation studies consisted of fixed sampling along line transects established perpendicular to the shore, ranging from above high pool stage to the lakeward extent of emergent vegetation. Frequencies of occurrence of species were recorded based on a form of line intercept method using a five-pointed rake (Sincock et al. 1957). At that time the only vegetation considered a nuisance was water hyacinth (*Eichhornia crassipes*) and the overall expansion of littoral communities into the lake by 16% was hailed as a success (Wegener and Williams 1974).

Another drawdown was performed in 1979 based on the successes of the previous effort. Sport-fish populations increased to a maximum by 1982 and then gradually declined to the lowest level since 1972 (Moyer et al. 1989). Based on these data it was assumed the habitat had degraded substantially and would no longer support maximum fish densities. No vegetation studies were conducted.

In 1987, the discharge of effluent to the lake was almost eliminated and another drawdown was performed. Contrary to the others, which were implemented to increase the density and area of the littoral zone in general, the purpose of this project was to eliminate dense, monocultural stands of vegetation (*Polygonum* spp. and *Pontederia cordata*) that had formed an organic barrier from accumulated organic matter; isolating many shallow areas of littoral zone to the point of blocking access of sport fish to important spawning grounds (Moyer et al. 1989).

The goal of the 1987 dry down was to reestablish native grasses in place of these dense, monocultural stands of unwanted vegetation. This marked the first mechanical muck-removal project, scraping approximately 172,000 m^3 of muck and vegetation from various sections of shorelines. After just two years, however, line transect studies established in 1986 showed an almost complete rebound of the vegetation targeted for removal (*Pontederia cordata*), though several grass species increased in frequency as well (Moyer et al. 1989).

A natural drought in 1991 gave lake managers another opportunity to remove some of the unwanted vegetation and two removal experiments were performed, one involving mowing the vegetation to a maximum height of 15 cm and the other, uprooting and removing it. It was found that *Pontederia* rebounded in both treatments, though at a slower rate after uprooting. Herbicide applications were also made in hopes of minimizing the regrowth of *Pontederia*, but were only effective at slowing regrowth.

Study Objectives and Methodology

Muck removal projects can provide important information to managers and restoration practitioners beyond the specific effects of individual projects. For one, they are prime examples of “aquatic gardening”, or using increased external inputs/efforts to

maintain or establish a desired pattern in a system, rather than restoring the key structuring processes that may have produced that pattern originally (Mitsch and Wilson 1996). Large-scale applications also provide an opportunity to implement adaptive management strategies, comparing pre- and post-restoration communities and testing the efficacy of new management activities before applying to other systems. Additionally, they provide an opportunity to study how aggressive management techniques perform at large scales; i.e. how well the results conform to predicted effects, and what might impact such outcomes. These are all important issues in restoration applications, and the following chapters of this paper will attempt to address them. These issues can be broken down into three primary questions, which are further discussed throughout the document:

- Can aggressive, intensive management efforts re-establish desirable littoral vegetation patterns without the structuring processes (hydrology, nutrients) that maintained those patterns historically?
- By comparing pre- and post-restoration littoral vegetation communities, what are the effects of this technique and how might these results be incorporated into future applications?
- How well did vegetation responses to a large-scale restoration project follow manager's predictions? Did environmental disturbances immediately following muck removal lead to unexpected results? What factors might need to be addressed before implementing expensive, intense restoration efforts?

Several study sites and sample designs were implemented to address these questions, and an outline of the differences is included below to aid interpretation.

Pattern without Process

The ability to re-establish vegetation patterns without historical structuring processes (Chapter 2) was studied on a variety of shorelines throughout the lake. Sampling occurred within the entire emergent littoral zone at these sites, both before

and after the project was initiated. The primary difference from the sites addressed in Chapter 3 is that sampling was conducted in both shallow and deeper sections of the emergent littoral zone, not all of which were mechanically scraped. Substrate quality and water levels limited the extent to which heavy machinery could drive onto the exposed lake bottom, which essentially restricted muck removal to an elevation of roughly 135 cm in water depth at maximum lake stage. Emergent vegetation extended tens or even hundreds of meters beyond those depths, to roughly 200 cm in depth at full pool. Thus, some of the samples were located in shallower, scraped sections of shoreline, and others were located in deeper, unscraped sections of shoreline. These scraped/unscraped designations may be confused with treatment and control plots that are addressed in Chapter 3. The important distinction is that the lake-wide study sites were all mechanically scraped, unless they occurred in areas too deep for muck removal. Thus, there are no “control” samples in these sites, only scraped (shallower) and unscraped (deeper).

Mechanical Muck Removal Effects

The pre- and post-restoration comparison of vegetation communities, or restoration effects, were derived from experimental study sites located along specific sections of shoreline that were on similar slopes and dominated by similar communities. Sampling within these sites was restricted to only those depths that mechanical removal could occur, and did not include the deeper-water, unscraped sections of emergent littoral zone that are included in Chapter 2.

Throughout Chapters 3 and 4, these study areas will be referred to as experimental sites, which contained both control and treatment plots. These study areas had sections of shoreline specifically delineated as control plots, which were not

mechanically scraped at any depth. The control and treatment plots in the experimental sites are not to be confused with the lake-wide sites that also contain scraped and unscraped samples, which refer to differences in water depth rather than experimentally applied treatments. It should also be noted that in the experimental sites, control plots were not necessarily devoid of all treatment, as they were still subjected to the managed drawdown that occurred throughout the lake.

Effects of Environmental Disturbances on Muck Removal Project

Chapter 4 draws on results from both the lake-wide and experimental study sites discussed above. There are also references to pre- and post-water-level regulation periods, as well as pre-and post-restoration. Water-level regulation occurred in 1964 and the restoration project took place in 2004. Both pre-and post-restoration vegetation communities are compared to pre-regulation (historical) communities, and care should be taken as to which event the pre- and post- designations are referring to.

Throughout this paper, vegetation compositions will typically be classified as communities, which in this case are simply a collection of species found at a specific place and time. Some studies have used the term in an abstract sense, referring to communities as a working mechanism or organism (e.g. Watt 1947), but throughout this paper it will be used in a concrete sense, strictly for classification purposes (e.g. McCune and Grace 2002). These groupings will represent specific abundances of one or more dominant species relative to one another along measured environmental gradients.

CHAPTER 2
RESTORING LITTORAL VEGETATION PATTERNS WITHOUT KEY STRUCTURING PROCESSES

Introduction

Restoration ecology has evolved from simple, succession-based approaches (van der Valk 1998) to addressing multiple constraints and degradation thresholds (Suding et al. 2004) as more complex systems and projects are undertaken. Regardless of the system or subject of restoration, the primary task is usually to re-establish historical structuring processes or key variables that have been lost and resulted in degradation (Mitsch 1998, Hunt et al. 1999). This approach of restoring the structuring processes necessary to re-establish a desired structure or species mix (pattern), relies on self-organization and self-sustenance of communities, minimizing external influence or energy inputs (Parker 1997). The frequency and intensity of fires, floods, and droughts (disturbance regimes), for example, are often the focus of restoration in forest (Cissel et al. 1999), prairie (Johnson and Matchett 2001), and wetland ecosystems (de Angelis 1998) because of their importance as key structuring processes.

The natural or historical range of variability of these processes have long been used as guides to maintain diversity, restore ecosystems, and influence future management actions (Landres et al. 1999). However, there are increasing numbers of systems where key structuring processes, or the historical range of environmental variability no longer exists, and restoring those conditions may not be economically or socially feasible (Seastedt et al. 2008). For example, large-scale, intense burn regimes that may have occurred historically cannot be safely implemented by managers, and even small-scale, low-intensity burns may be unacceptable near urban areas (Stephens and Ruth 2005). Many aquatic systems have altered flood/drought cycles that are

largely determined by water use or flood control needs (Hill et al. 1998, Havens and Gawlik 2005), and restoring historical conditions would jeopardize surrounding urban developments.

When key structuring processes are lost, external inputs (management efforts) must increase to maintain or restore desired patterns, which can ultimately resemble “intense gardening” or “landscape architecture” more than ecosystem restoration (Mitsch and Wilson 1996). This can be a gradual occurrence; as species pools or disturbance regimes slowly depart from historical conditions, management efforts increasingly focus on removing unwanted species or the effects of those species (higher fuel loads, increased peat deposition). Eventually these methods can constitute the majority of management effort.

This removal-based approach has been criticized as not necessarily capable of restoring any historical state, or even establishing a new, desirable state (Seastedt et al. 2008). Additionally, there are a growing number of examples where under prolonged degraded conditions, biotic and abiotic interactions create new feedbacks that result in resilience to restorative change, even if lost structuring processes could be restored (Baker and Berdense 1999, Zedler 2000, Suding et al. 2004). Changing environmental conditions (climate, disturbance regimes, etc.) and new combinations of native/introduced species have led to the development of novel ecosystems (Suding et al. 2004, Hobbs et al. 2006) and management strategies will have to be re-examined in many cases (Seastedt et al. 2008).

While most examples of novel ecosystems in the literature are terrestrial, lakes and wetlands could easily be at the forefront of this issue. Watershed development and

land use has long affected the hydrologic schedules, nutrient loads, and species pools of virtually every aquatic system (e.g. Davis and Ogden 1997), and managers have relied on removal-based approaches for decades to maintain desired patterns under altered conditions (e.g. exotic or invasive species removal). Current environmental problems resulting from past issues (regional expansion of exotics, unchecked nutrient loading) can consume the time and budgets of managers (Seastedt et. al 2008), so that new approaches and methods are slow to develop.

Most of our major water bodies are or will soon be permanently outside of their natural range of environmental variability. Hydrologic schedules will likely be increasingly determined by growing water supply and flood control demands, while global climate change may affect the frequency, intensity, and duration of flooding/drying events (Abrahams 2008). These new challenges could render traditional management approaches un- or even counter-productive, and focus may have to shift towards finding desirable or acceptable communities that provide biotic structure and ecosystem services under new conditions (Seastedt et al. 2008).

This paper focuses on a lake restoration project in central Florida, USA, as an example of the challenges facing many aquatic restoration projects in novel systems, and of the need to develop new management approaches. Classic 'removal-based' management efforts have not been able to prevent degradation from various water, nutrient, and species pool changes in this large, shallow, sub-tropical lake and increasingly expensive and intensive methods of habitat manipulation have been developed as a result (Moyer et al. 1995).

This paper focuses on a newer, intensive approach to lake restoration, where bulldozers, herbicides, and drawdowns are used to maintain desirable, native vegetation communities in a system now outside the range of natural variability. This technique, dubbed "muck removal", was developed as a method of removing accumulated organic material from the littoral zone, deposited after decades of excessive vegetation growth under eutrophic and stabilized water conditions.

There is a long history of managers combating dense growth of aquatic vegetation (Holm et al. 1969), as it can alter fish communities (Killgore et al. 1989), lower oxygen levels, and impede navigation and flood control (Little 1968). Faced with increased difficulty in implementing large-scale dry-downs, coupled with the rising costs, inefficacy, and unpopularity of broad-scale herbicide applications, managers developed a single, intensive disturbance effort to restore desirable communities. This approach involves drying parts of the littoral zone, removing accumulated organic material and unwanted, resilient species from the shorelines, and regulating initial vegetation succession with herbicides. The goal is to create a sandy bottom habitat with sparse emergent/submergent vegetation that supports important sportfish spawning and improves boater access (Moyer et al. 1995). These conditions are considered historical targets for muck removal restoration and are typical of systems with lower productivity or higher levels of disturbance than what is seen in this degraded system (see Grime 1979).

This study represents far more than one state's unique approach to combat decades of habitat degradation; it serves as an example of how systems continually change when important structuring processes are lost, and how management agencies

often rely on increasingly expensive, removal-based techniques despite criticisms of these approaches for nearly a decade (Holling 2001). This chapter addresses one important question facing restoration ecologists and poses another; can historical vegetation structure or pattern be restored under novel conditions? If so, at what cost should we maintain desired patterns when current processes no longer support them? To answer the former question I compared vegetation communities after muck-removal restoration (scraping) to early vegetation patterns before water levels were regulated in the 1960's. Specifically, I compared dominant species from the 1950's to those established in this study four years after restoration. It is my hope these results can be used to address the latter question, and perhaps reemphasize the need to shift our restoration targets and find new methods to manage ecosystems under increasingly novel conditions.

Methods and Analyses

Lake Tohopekaliga (hereafter referred to as Lake Toho) is one of several large lakes in the Upper Kissimmee River Basin in central Florida, USA. Each of these lakes is successively connected and jointly regulated to collectively drain thousands of square kilometers into the Kissimmee River and ultimately Lake Okeechobee (Ch. 1, Figure 1-1). Toho is located near the top of this chain of lakes, covering 8,176 ha with an average depth of 2.1 m (at maximum stage regulation of 16.75 m NGVD), with a watershed of roughly 334 km^2. Its volume has a large impact on water bodies downstream when drawdowns are implemented, especially since all lakes farther down the chain must be lowered to gravitationally drain Lake Toho (HDR Engineering 1989, Remetrix LLC 2000).

Water control structures were installed on the Kissimmee Chain and Lake Toho in 1964 (Blake 1980), reducing the variability of lake stages by approximately 1.5 m, to an annual range of 1.1 m (Ch. 1, Figure 1-2). Sewage effluent from up to three treatment facilities was discharged into the lake from roughly 1940 to 1988, reaching a maximum of 113 million liters per day in 1986 (Wegener et al. 1973). Decreases in water quality and fisheries production in the late 1960's were attributed to stage regulation and nutrient loading (Wegener 1969), beginning a series of drawdowns in 1971, 1979, 1987, and 2004 as a means of improving fish habitat.

Lake-stage data were collected from a South Florida Water Management District gauge located on the southern end of the lake, recording average daily water levels since January 1942. Indicators of Hydrologic Alterations (IHA) software was used to analyze pre (1942–1964) and post water-level regulation (1965–2008) periods, defined by the completion of water control structures in 1964. Both periods were analyzed for 30, 60, and 90 day maximum and minimum water levels, average monthly levels, and quartiles. Two 10 year periods before and after regulation, 1944–1954 and 1992–2002, were selected for further comparison between pre- and post-regulation periods. This was done to exclude some of the more extreme events in either period, including historical highs and lows experienced in the early 1960s, as well as managed drawdowns in the latter period. Water level structures were not completed on the Kissimmee Chain of lakes until 1964, but it seems reasonable that substantial changes were occurring in the watershed up to several years prior (beginning of construction), possibly contributing to the historical highs (1960) and lows (1962) recorded just prior to completion. Rather than use these events as representative of typical pre-regulation

fluctuations, the 10 year period characterized by more modest events and that occurred just prior to early vegetation studies (1956) was chosen. These two periods allowed comparison of relatively stable events, rather than just looking at differences in maximum and minimum stage levels, which would also be affected by rare climatic events. Water years were defined as June through May of the following year, corresponding with the beginning of the wet season and end of the dry season, respectively.

The largest muck removal project to date was implemented on Lake Toho in 2004, when water levels were dropped from 16.8 m to 14.9 m from November 2003 until June 2004. Approximately 6.5 x 10^6 m^3 of muck and vegetation were removed from over 80% of the shoreline and deposited at several upland sites, as well as 29 locations within the lake (FFWCC 2004). Water levels returned to normal by August 2004.

Sample Locations

Lake Toho has a variable littoral zone in terms of slopes, wave energy, and shoreline activities, which may result in differing plant communities. In order to capture this variability and provide lake-wide inference for treatment effects, five monitoring sites were selected from the less-developed, southern two-thirds of the lake that were uninterrupted by outflows, jetties, or other notable features (Figure 2-1). The goal of site selection was to represent the various habitat types and geomorphic conditions of the lake without complicating restoration responses with shoreline development or unusual features (creek outflows) within the plots.

Sites 1, 3 and 4 were located on broad, gently sloping areas of shoreline, while Sites 2 and 5 were located on steeper, higher energy shorelines. Cattle ranching and grazing was the primary land use in all but sites 4 and 5, which were bordered by

infrequent residential housing. These locations represented the majority of shoreline community types and primary land use, giving the best inference as to lake-wide littoral response to treatment.

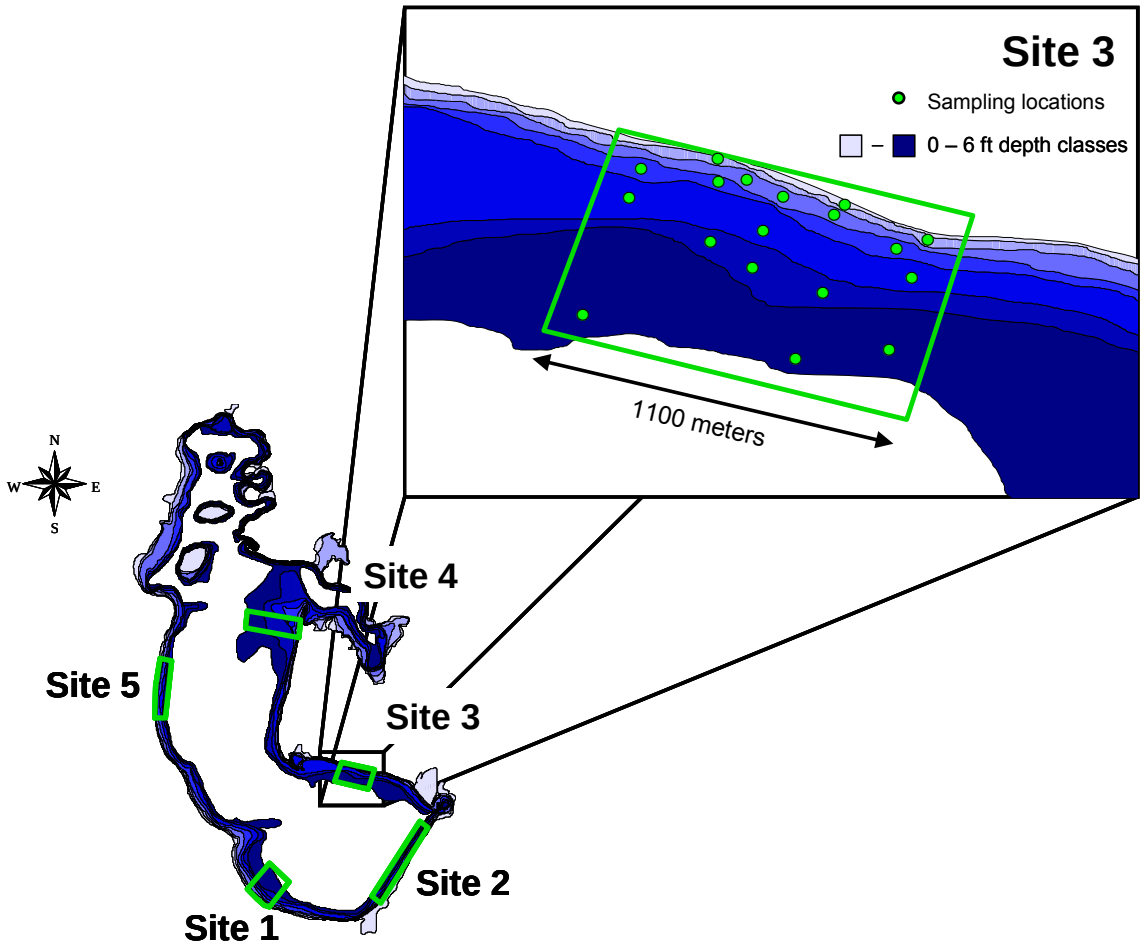

Figure 2-1. Location of study sites throughout the lake. Each site encompassed the entire width of the emergent littoral zone, to approximately 2 m in depth. Sample locations were randomly located within depth stratifications of approximately 35 cm each.

Samples were collected from all water depths occupied by the emergent littoral zone in order to monitor lake-wide vegetation changes, including those areas too deep for mechanical removal but still subjected to drawdown. The boundaries of each site were determined by placing a 60-ha rectangle on Digital Ortho Quarter Quads (DOQQ) with 1-m^2 resolution (1999) and bathymetric (Remetrix 2000) layers in ArcView GIS 3.2

software. The area of the rectangle remained constant but the shape was altered such that it encompassed the zone of 0–2 m in depth (0–6 ft) (i.e., the sites on steep slopes were stretched along the shore while those on gentle slopes extended much farther into the lake).

Sampling locations were stratified by five depth classes of approximately 35 cm (one foot) each (One = 30 – 65 cm, Two = 65-100 cm, Three = 100 – 135 cm, Four = 135 - 170 cm, and Five = 170 - 205 cm). The three shallowest classes (30 – 135 cm) were located within the areas slated for mechanical muck removal, while the majority of deeper classes (135 – 205 cm) were never dried enough or did not contain vegetation communities targeted for restoration. Random coordinates were used to locate samples in the field with a GPS (Global Positioning System) on each collection. The shallowest areas sampled coincided with the approximate shoreward extent of muck removal activities, which was roughly the 30 cm depth contour at maximum lake stage. Three locations per depth class were sampled at each site for a total of 15 samples per site, 75 total. Aboveground vegetation was clipped from 0.25 m^2 circular quadrats at each location, sorted by species, stems counted, and biomass recorded after excess water was shaken off. Samples were collected each year during the summer (June) and winter (December) seasons from June 2002 - June 2008, to account for any seasonal variations in response and to increase the temporal intensity of sample events. This resulted in 13 repeated measures for each location.

Lake-stage data were collected from a South Florida Water Management District gauge located on the southern end of the lake, recording average daily water levels

since January 1942. Average water depths from three points at each sampling location were referenced to lake stage data to approximate shoreline elevations across sites.

Historical vegetation data were referenced from agency studies conducted in 1956, eight years prior to water regulation (Sincock et al. 1957) and in 1971, seven years after (Holcomb and Wegener 1971). These studies used intercept methods to calculate frequency of occurrence along transects perpendicular to shore, with several locations overlapping the sites in this study. While their methods vary considerably from the sample techniques used in this study, they represent the only estimates of dominant species and their distributions along shoreline elevations prior to stage regulation.

Analyses

Pre/post restoration comparison

Plant species density and biomass were summed across sub-samples within depth classes for each sample event, resulting in five samples per site and 25 per sampling occasion. While each depth class represented a subsample within a study site, they were analyzed separately to determine water depth influences on vegetation response. The December 2002 and June 2003 sample events were used to represent pre-restoration conditions, and December 2007 and June 2008 samples were used as post-restoration representatives. These times were chosen to capture littoral conditions immediately prior to restoration and after vegetation communities re-colonized mechanically-scraped areas. Importance Values (IV) were computed for each species from the summed sub-samples by averaging the relative biomass and density of each species in those sub-amples, and converting to a percentage value

$$IV = (\text{Relative Biomass} + \text{Relative Density})/2 * 100$$

Importance values were used to estimate species importance within a given depth class and site as they are not biased towards large, few-stemmed species or small, numerous-stemmed species. This calculation also relativized the dataset, eliminating the need for transformations typically applied to density or biomass data that can vary by orders of magnitude between species and samples (McCune and Grace 2002).

To reduce noise from rare species, only those with cumulative IV's composing 99% of the total were retained for this analysis. Many studies eliminate species that occur in < 1% of samples, but I used 1% of the total IV instead. This method is more representative of the actual abundance of a species for the same reason IV's are more representative of a species' abundance than frequency.

The resultant matrix consisted of 100 (50 pre and 50 post) samples and 21 species of the 37 encountered, and included a summer and winter sample event for both the pre- and post-restoration periods. Although only 5 of these 100 samples were independent (sites = 5), each depth class (5) and sampling occasion (4) were analyzed separately in order to account for gradient responses and seasonal variation within study sites. All analyses for the pre/post comparisons were performed on this matrix and unless otherwise specified, were performed using PCORD software (McCune and Mefford 1999).

Shannon-Weiner diversity indices were calculated from species biomasses prior to eliminating rare species. The index was converted to effective numbers of species (exponential of the diversity index), which is useful when comparing across groups due to the non-linear nature of diversity indices (Hill 1973, Peet 1974). The effective number

of species in this case is essentially a measure of how many species were consistently abundant relative to other species during that period.

Groups with similar species compositions were identified using a hierarchical, agglomerative cluster analysis with flexible beta (-0.25) linkage and Sorenson distance measures. These were chosen for their space conserving properties, compatibilities with each other, and their advantages with non-normal data (McCune and Grace 2002). Samples were grouped based on species IV's, using multiple species as a basis for deciding on the fusion of additional groups.

An Indicator Species Analysis (ISA) determined the optimum number of clusters for further analysis and defined those clusters in terms of representative species. This analysis uses the proportional IV and frequency of a particular species in a particular cluster relative to its IV and frequency in all other clusters (Dufrene and Legendre 1997). The optimum number of clusters was determined by which level produced the most species with p-values < 0.05 in the indicator species analysis (McCune and Grace 2002). Species with low p-values (< 0.05) and high indicator values (> 40) were used as community descriptors (cluster labels) in future analyses.

A Classification and Regression Tree (CART) model (S-Plus Tree Library, De'ath 2002) classified samples into the groups identified by the cluster analysis using the measured environmental variables alone. We used the Gini index to measure impurity (Breiman et al. 1984), cross-validation to select the best tree size (Vaysieres et al. 2000), and 1-Cross Validated Error as a more conservative estimate of variation explained by the model (De'ath 2002). CART models were built using the combined matrix of pre- and post-restoration communities in order to determine how muck-

removal effects varied temporally, spatially, and with water depth. Several combinations of the variables water depth (at full pool) and hydroperiod were used as continuous predictors, while site, scraping (for the post-restoration period), dominant land use (cattle grazing, yes/no), and whether the sample occurred on a floating mat were used as categorical variables.

A Multivariate Regression Tree (MRT) was built to identify communities based on species IV's and where they occurred along environmental gradients, and to compare the results with those from the cluster analysis and CART model. This method uses the sum of squared Euclidian distances about the multivariate mean of samples as an impurity measure of each node, and each split is made to maximize the sum of squares between nodes and to minimize it within nodes (De'ath 2002). Each leaf is then characterized by the multivariate mean of its samples, the number of samples within that leaf, and their defining environmental variables. The percent of variation explained by the tree is reported as 1 - Relative Error, or more strictly 1 - Cross Validated Error.

In short, this technique partitions the samples into communities using both species IV's as well as the associated environmental variables, and provides the threshold values for each partitioning variable. The resultant communities are defined not just by species compositions (as in the cluster analysis) but where they occurred on the environmental gradients as well, providing a different approach to community delineation than the combined cluster and CART model methods. This method was used as a confirmatory procedure, to verify groupings and distributional thresholds identified in the previous analyses.

Nonmetric Multidimensional Scaling (NMS) ordinations were used to graphically display community shifts from pre- to post-restoration periods using IV's (McCune and Grace 2002). Pearson correlations were calculated for species biomass and water depths for each of the ordination axes. Vectors were used to track species composition changes over time within sample units (sample position in species space), and approximate boundaries were drawn onto ordination results to represent changes from one community type to another, based on the afore-mentioned cluster analyses. Depth classes were graphically separated from a single ordination to ease interpretation.

Temporal analyses

In order to track change in species biomass over time, I combined sub-samples of biomass within each depth class, and then followed changes in species composition by site, for two periods prior to restoration and for the last two periods of the study. Each sampling period (pre = December 2002 and June 2003, post = December 2007 and June 2008) consisted of 25 samples, five depth classes at each site of five sites. These data were ordinated using NMS to graphically display changes in species abundances throughout the period of study. Results were graphically separated after the ordination by depth class for ease of interpretation.

Results

Hydrological Comparisons to Historical Record

Following regulation in 1964, annual fluctuations were managed between 15.9 and 16.8 meters NGVD, with flood events reduced by approximately 1.0–1.5 m (Ch. 1, Figure 1-2). Average monthly water levels were similar when comparing pre- and post-regulation periods, except for the early growing season (Figure 2-2). February and

March water levels were held higher and for longer duration after 1965, and dropped more quickly to low pool by the end of the dry season (June).

The 10 year pre- (1944–1954) and post-regulation (1992–2002) periods had similar mean, annual lake stages (16.45 and 16.40 m, respectively) and within-year variation (0.61–1.91 St Dev and 0.63–1.01 St Dev respectively) (Figure 2-3). However, inter-annual variations were considerably lower in the post-regulation period, with the standard deviation of annual means falling from 1.09 prior to regulation, to 0.22 after. The largest reduction in between-year variation occurred for the months of September and October, where pre-regulation water levels for these months varied by 2 standard deviations. From 1992 to 2002, standard deviations for these fall months were 0.26 and 0.34, respectively.

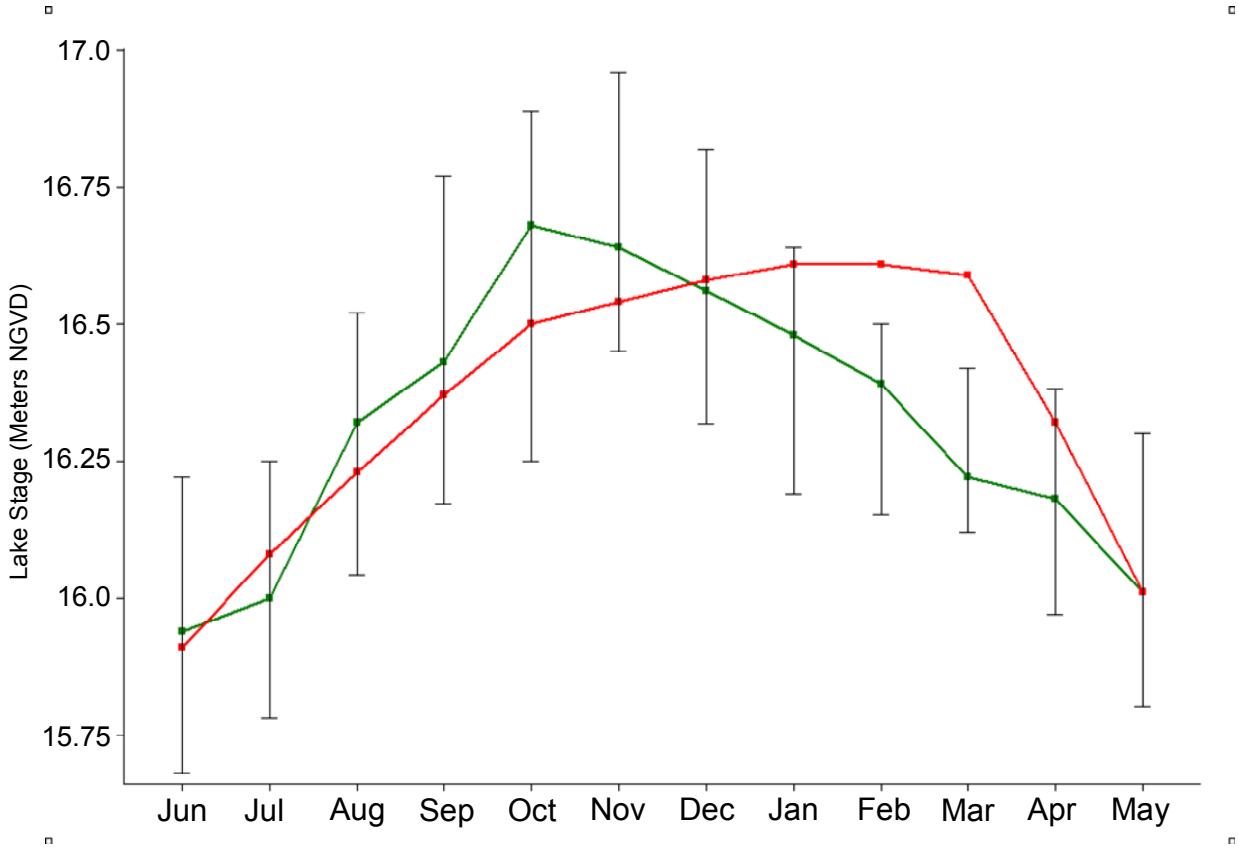

Figure 2-2. Monthly lake stage (Meters NGVD) for the pre-regulation period 1942–1964 (green), and post-regulation period 1965–2008 (red). The 75th percentiles are shown for the pre-regulation period.

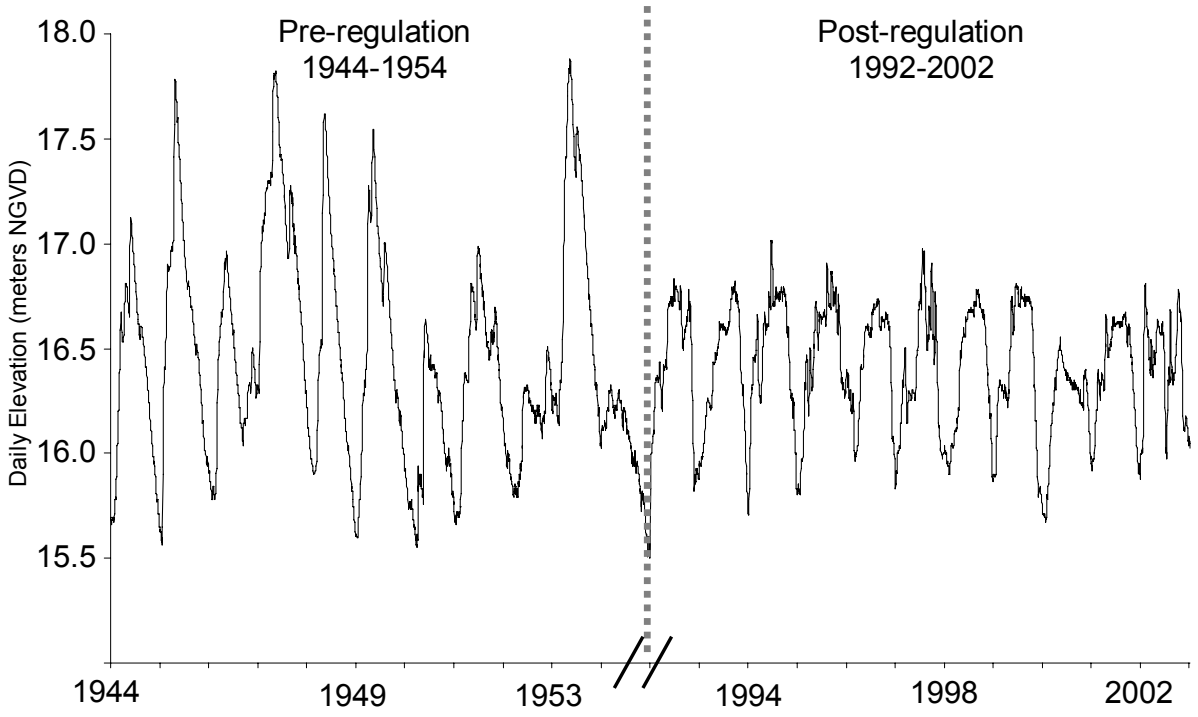

Figure 2-3. Daily lake stage (Meters NGVD) for a pre-regulation (1944–1954) and post-regulation period (1992–2002).

Vegetation Response

Total numbers of species encountered in the two pre- and two post-restoration samples were 32 and 27, respectively, with frequency histograms showing similar distributions among samples between the two periods (Figure 2-4). The majority of samples had 2–3 species in each quadrat, regardless of sample period.

A histogram of scraped samples showing species changes over time displayed a similar pattern, with the majority of quadrats having no change or a loss/gain of only one species (Figure 2-5). When deeper water, unscraped samples (still exposed to artificial

dry-down) were included in the histogram there was a slight left skew, but no strong pattern in overall species richness was evident throughout the study period.

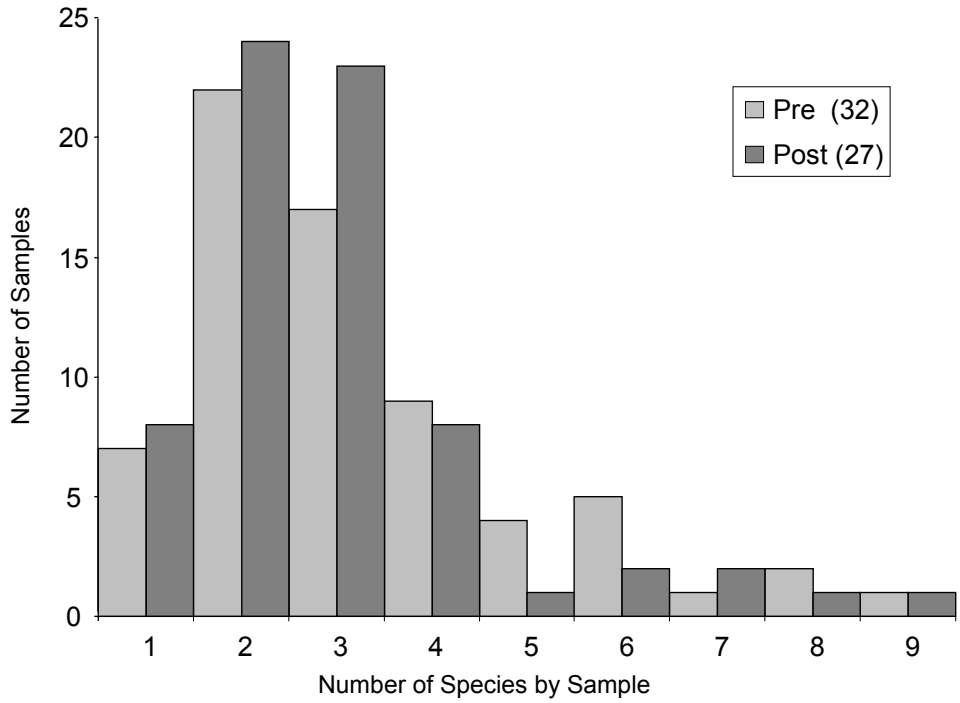

Figure 2-4. Frequency histogram displaying number of species per quadrat for all samples before and after restoration.

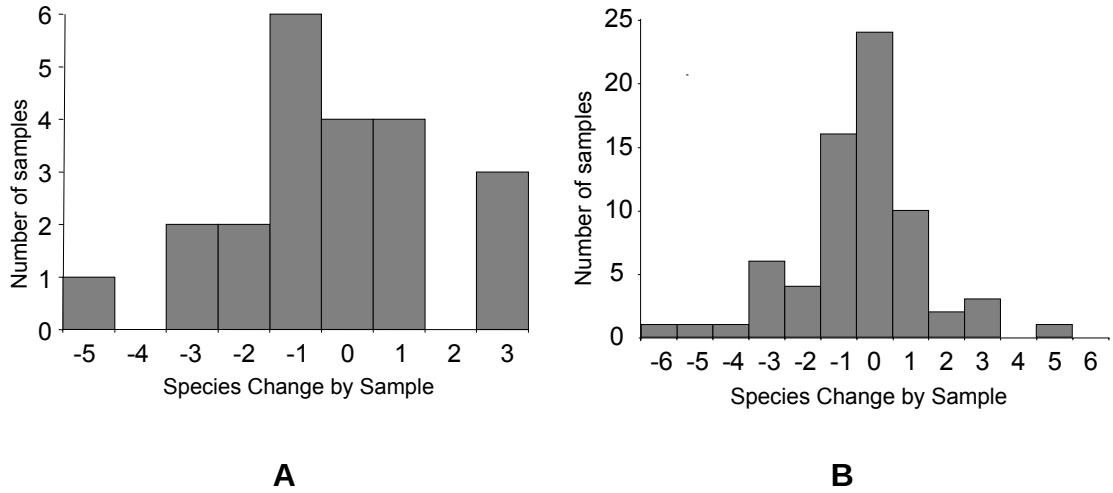

Figure 2-5. Frequency histogram of species gain or loss by quadrat after restoration. A) Only those samples that were mechanically scraped, roughly 30–135 cm in depth. B) All samples, including those too deep for scraping but still exposed during the drawdown.

Shannon-Weiner diversity indices showed an increase in the number of effective species in the scraped areas, from 5.3 to 6.2 after restoration. However, when including those samples too deep for mechanical removal, there was a decline in diversity from 7.9 to 5.5 effective species, highlighting a loss from those areas that were only subject to drawdown.

The cluster analysis revealed six distinct groups based on the number of indicator species at each level of clustering, which resulted in approximately 50% of the information remaining based on a scaled Wishart's objective function (McCune and Grace 2002). Groups were labeled with species that had indicator scores of roughly 50 or greater in a given cluster (Table 2-1). These groups were 1) *Pontederia cordata,* 2) *Typha* spp., 3) *Hydrilla verticillata*, 4) *Paspalidium geminatum,* 5) *Panicum repens* and *Eleocharis* spp., and 6) *Vallisneria americana*.

Table 2-1. Indicator values (0–100) of species in the six groups identified by the cluster analysis. Those species with values of approximately 50 and greater were chosen as representatives of the corresponding group, or community. Species are coded as the first 3 letters of genus and first 2 of specific epithet (*Pontederia cordata* = PONCO).

P-value	Species	Group 1	2	3	4	5	6
0.0002	**PONCO**	**71**	12	0	0	0	0
0.0002	**TYPSP**	0	**95**	0	0	0	0
0.0002	**HYDVE**	0	4	**50**	25	0	9
0.0002	**PASGE**	0	0	17	**73**	0	3
0.0002	**PANRE**	8	0	0	0	**81**	0
0.0002	**ELESP**	1	1	0	0	**48**	0
0.0002	**VALAM**	0	0	0	0	2	**92**

Community correlations to measured environmental variables were determined by CART models. The best model was pruned to nine leaves based on the 1 - cross validated error method, and used water depth at maximum lake stage, muck removal (y/n), sample period (pre/post-restoration), and whether the sample was on a grazed

shoreline (Figure 2-6). The CART model had a cross validated error of 0.36, and a misclassification rate of 17%, explaining 64% of the variation in the dataset. Water depth at maximum lake stage was the most important predictor variable, followed by muck removal, sample time, and cattle grazing (yes or no). Sample time was incorporated into this analysis as a surrogate for the artificial dry-down that all samples experienced, regardless of whether or not their water depths allowed mechanical removal of soil and vegetation. Samples that changed community types following the restoration but did not actually get scraped were considered to exhibit dry-down effects.

Each of the six communities identified in the Cluster and ISA analyses were classified in the CART model, with *Typ*ha and *P. geminatum* having the smallest number of samples (4) and *Vallisneria* having the most (22 & 4). While water depth explained more of the variation in the model, muck removal was responsible for the primary division of the data. *Vallisneria* was predicted to occur in scraped areas of shoreline at depths > 98 cm, up to approximately 135 cm, or the maximum scraped depths. *P. repens* and *Eleocharis* spp. dominated the shallowest scraped samples (approx. 30–98 cm).

As expected, unscraped communities (no muck removal) were much more variable, as they included pre-restoration samples as well as post-restoration samples too deep for mechanical scraping. Water depth differentiated the two, as the maximum depth scraped was approximately 135 cm. Seven of the leaves in the tree were classified as unscraped, with the majority of samples predicted as *Pontederia* (18) dominating 30–109 cm in depth.

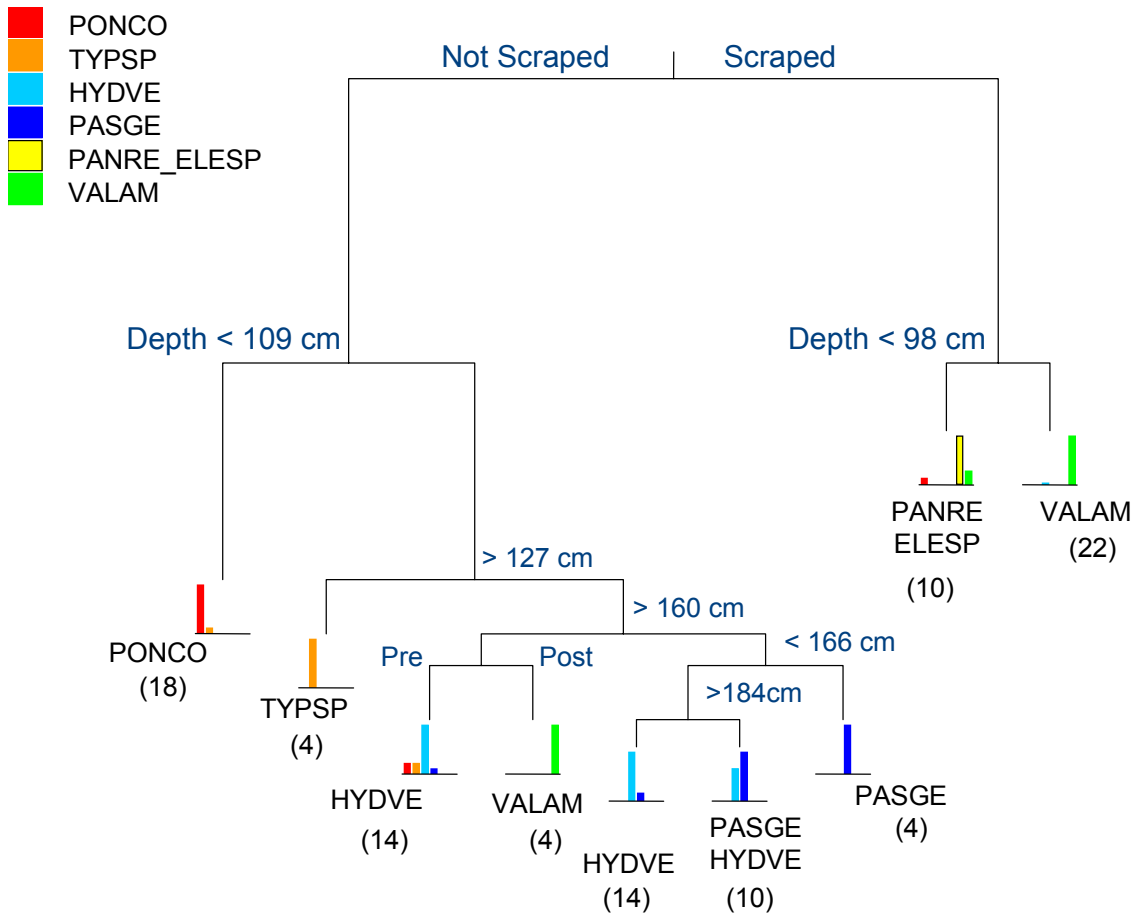

Figure 2-6. CART model of pre-post restoration periods (9 groups, CV error = 0.36, Misclass rate = 17%). Bargraphs under leaves represent proportion of samples in that leaf classified as the corresponding community. Numbers in parentheses under the leaves indicate how many samples are in each leaf. Rank of variable importance was water depth, muck removal, sample period, and grazing.

Prior to restoration, the *Hydrilla* and the *P. geminatum* communities were predicted to occur intermittently at > 127 cm of water depth, either as individual communities or grouped as one. Following the restoration, *Hydrilla* distributions were somewhat reduced, with *Vallisneria* replacing that community in 127–160 cm of water, regardless of whether or not samples were scraped. *Typha* was classified in just four unscraped samples, at 109–127 cm in depth, all of which were later scraped. Essentially, the 18 samples classified as *Pontederia*, 4 as *Typha*, and 14 classified as *Hydrilla* (36 total), all

became *Vallisneria* (22 & 4) or *P. repens* and *Eleocharis* (10) after restoration, depending on water depth.

These same data were used to track changes in species compositions of individual sample units over time using an NMS ordination (Figure 2-7). The final solution was three dimensional, accounting for 68% of the variance with 54% in the primary two axes. Total biomass per sample was correlated with Axis 2 (R^2 = -0.41) and water depth with Axis 1 (R^2 = 0.72), having a final stress of 16.8 and an instability of 0.002. These values lie within the ranges typically seen with ecological community datasets (McCune and Grace 2002).

The ordination results were graphed in the two primary dimensions, and approximate community boundaries were drawn in to highlight shifts in community type over time. Water depth classes were pulled apart into separate graphs to ease visual interpretation of 25 different sample units moving through four time periods (Figure 2-8). Due to the Pearson correlations with ordination axes, Axis 1 can be approximated with water depth (R^2 = 0.72) and Axis 2 with decreasing total biomass (R^2 = -0.41).

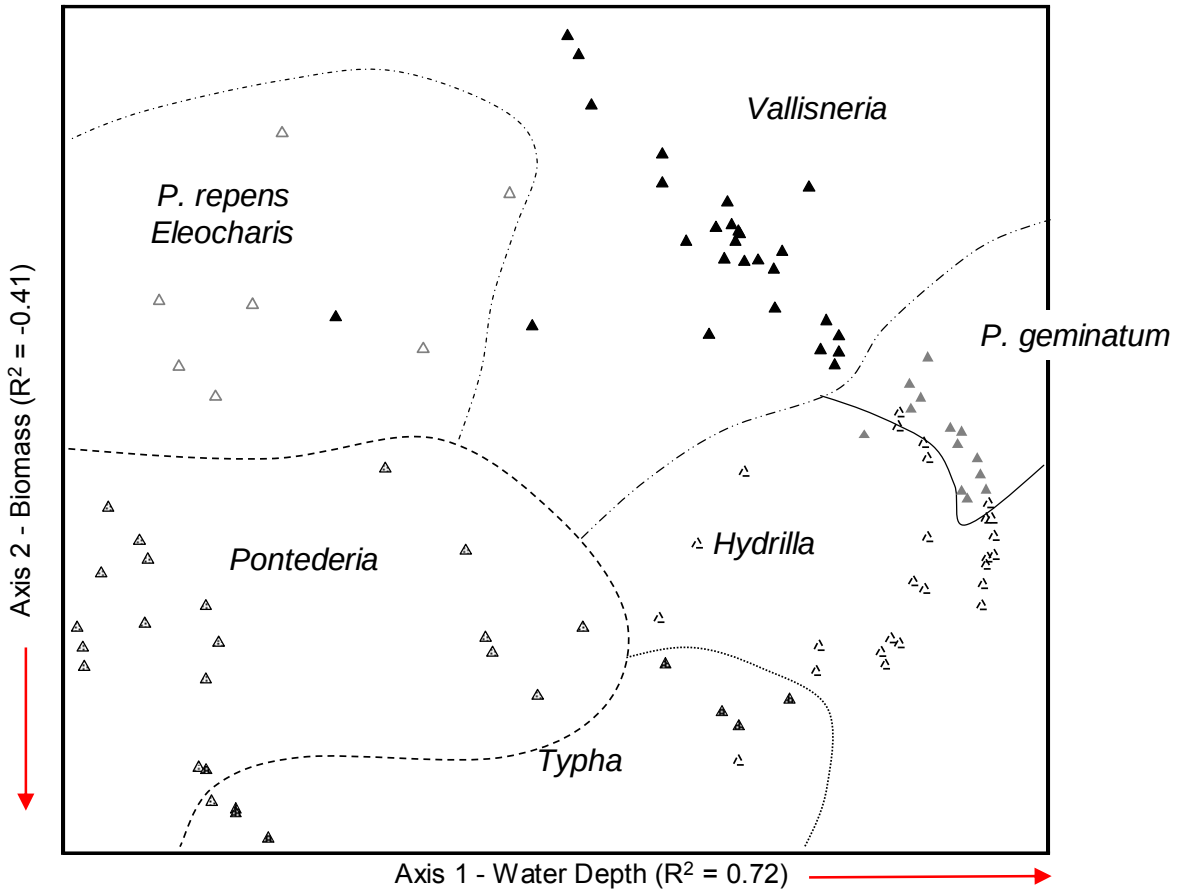

Figure 2-7. NMS ordination of two pre- and two post-restoration sample periods. Approximate community boundaries based on cluster groupings were outlined on the ordination for ease of interpretation. Pearson correlations (R^2) with axes were: Water depth = 0.72 to Axis 1, Total biomass = -0.41 to Axis 2.

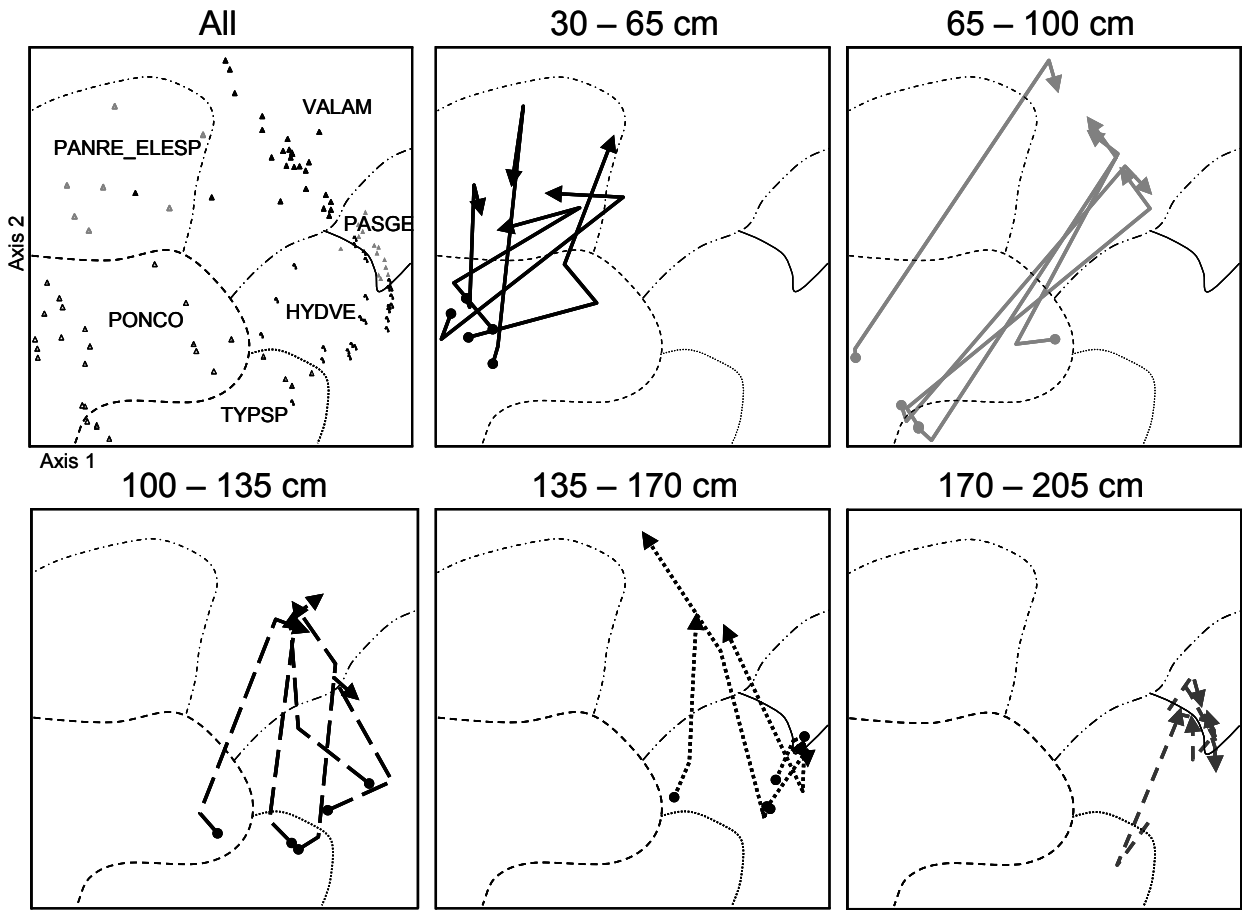

Figure 2-8. NMS ordination of two pre- and two post-restoration sample periods. Approximate community boundaries based on cluster groupings were overlayed onto the ordination, and arrows show movement of samples through species space over time. Large movements indicate large changes in species compositions, and vice versa. Depth classes were pulled from the same ordination to ease interpretation. Pearson correlations (R^2) with axes were: Water depth = 0.72 to Axis 1, Total biomass = -0.41 to Axis 2.

Similar to the CART model, the shallowest depth class went from a *Pontederia* community to *P. repens* following restoration, while the second depth class moved from either *Pontederia* or *Typha* to *Vallisneria*. This depth class saw the largest change in species composition, as evidenced by the amount of distance between the pre- and post-restoration samples.

The 3rd depth class contained several community types prior to the muck removal, including *Pontederia*, *Typha*, and *Hydrilla*; all but the *Hydrilla* community changed to

Vallisneria following restoration. The fourth depth class was beyond muck-removal depths, but also shifted primarily to *Vallisneria* from either *P. geminatum* or *Hydrilla* after restoration. The deepest samples remained largely unchanged, grouped as either *Hydrilla* or *P. geminatum* communities.

The MRT had a higher error rate than the CART model (CV error = 0.55) explaining only 45% of the variation in the dataset (Figure 2-9). Including site location and sample season improved the fit slightly, but I was more interested in isolating how mechanical scraping and dry-down varied by water depth, and wanted to simplify the tree (minimize number of leaves) in order to ease interpretation. Site differences that were delineated in alternative models were not attributed to obvious anomalies (grazing pressure, shoreline slope, dominant wind directions, etc.) and so were considered as local variations and not included as a variable in the final model.

Even without accounting for more than 50% of the variation in species abundances, the MRT still showed very similar results to the CART model and cluster analysis. Most of the dominant species in the final nine groups were listed as indicator species, and their positions along the gradients were very similar to the CART model. There were essentially seven groups identified in the nine leaves of the tree, with the primary differences between the MRT and CART being the absence of *Typha*, the addition of *Nuphar advena*, and the splitting of the *Pontederia* group to include a shallower *Luziola fluitans* community.

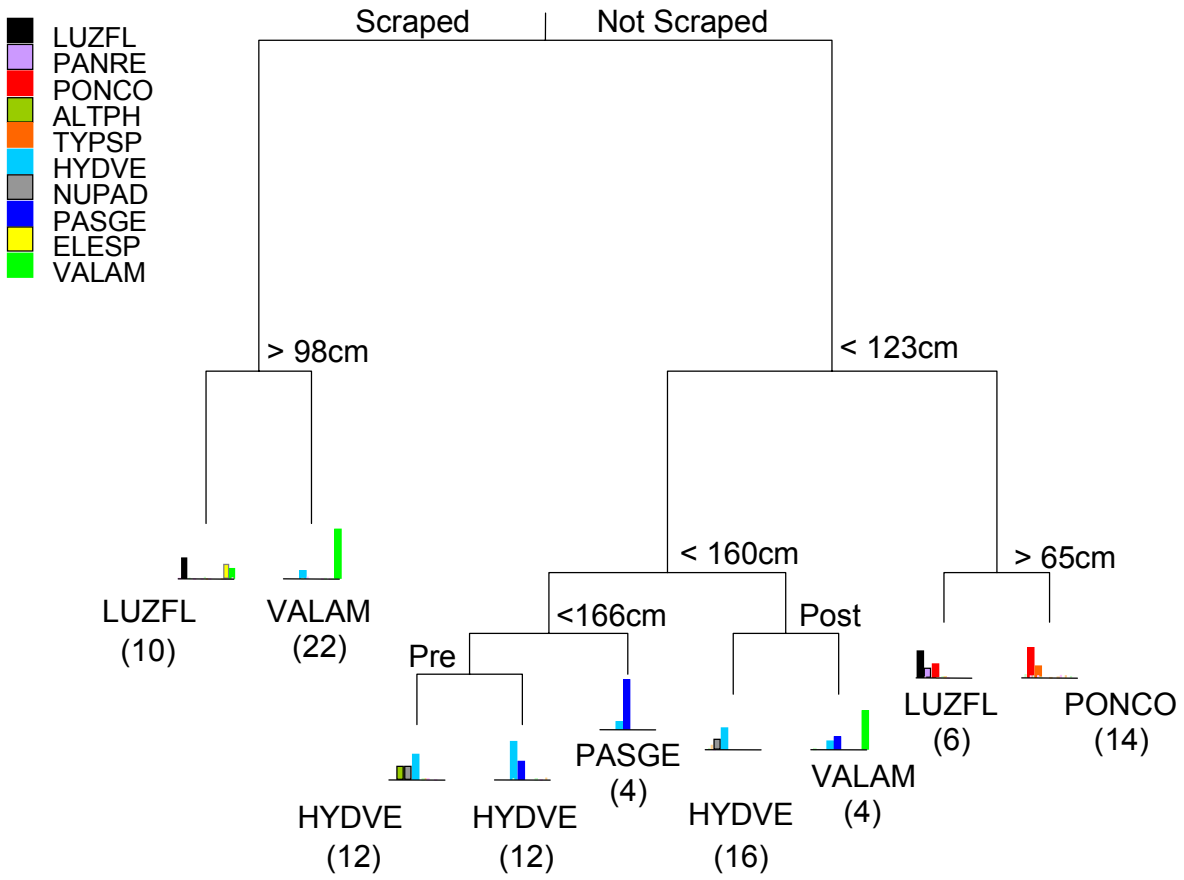

Figure 2-9. MRT model of pre-post restoration periods (9 groups, CV error = 0.55). Bargraphs under the leaves represent the proportion of each species in that group. Numbers in parentheses under the leaves indicate how many samples are in each leaf. Rank of variable importance was water depth, sample period, muck removal, and grazing. Only the most common of the 21 species are shown.

The primary division was attributed to muck removal, with the scraped samples again dominated by *P. repens* and *Eleocharis* spp. at < 98 cm in depth, while everything in 98–135 cm was dominated by *Vallisneria*.

There were also similar groups among the unscraped samples, with the next division occurring at 123 cm in the MRT, as compared to 109 cm in the CART model. The unscraped samples at < 123 cm were dominated by either *Pontederia* or *Luziola*,

the same as the CART model, but were further divided at 65 cm in depth with the shallowest community classified as *Luziola*.

The deep water communities were also quite similar to the CART model, with *Hydrilla*, *P. geminatum*, and *Vallisneria* all dominating at varying depths > 123 cm. The MRT again identified temporal shifts from *Hydrilla* to *Vallisneria* even in the unscraped samples, but also revealed a loss of *Nuphar* over time as well. Samples > 160 cm in depth were again dominated by either *P. geminatum* or *Hydrilla*, as in the CART model.

Biomass plots showed similar patterns in dominant species change after restoration, and highlighted the dramatic loss of floating leaf aquatics and *Typha* that were subtle in the analyses based on importance values (Figure 2-10). These communities were relatively infrequent in study samples, but both lost 100% of their sampled biomasses after restoration. *Pontederia*, the most common species and primary target of the mechanical removal project, lost 88%. Similar to the importance value analyses, *Vallisneria* had by far the largest increase in biomass among the species (from 0 to 14.6 kg), but *Hydrilla* and *P. repens*, both exotics, increased biomasses 137% and 58%, respectively. *P. geminatum* was very prevalent in the deepest samples and as evident in the ordination tracks, showed very little change in biomass between time periods.

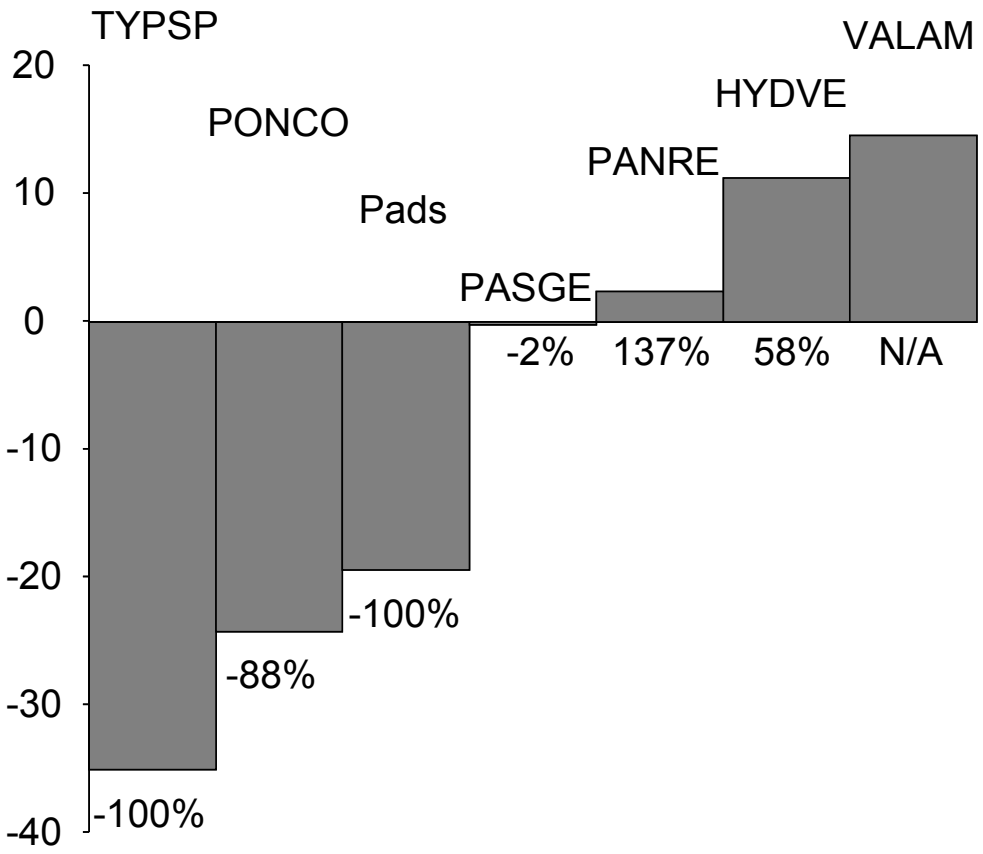

Figure 2-10. Changes in biomass of common species (in kilograms wet weight), including *Nuphar advena* and *Nymphaea odorata* grouped as lily pads. Biomass gain or loss is also expressed as a percentage of pre-restoration biomass, unless a species was not recorded previously (*Vallisneria*).

Discussion

Historical Comparisons

The primary goal of this restoration project was to replace robust communities that became established after years of elevated nutrient levels and stabilized water schedules, with communities more typical of the dynamic, lower-nutrient system that occurred historically (sparse macrophyte coverage and sandy substrates). Ideally, this would be accomplished by re-establishing the range of environmental variation, including nutrient levels (Moss et al. 1996), hydrological regime (Middleton 1999), and species pools (Cole 1999). While point-source nutrient reductions (James et al. 1994)

and selective species removals (Moyer et al. 1989) have been the focus of past management activities on the lake, annual water regulation schedules have been unchanged for over 40 years. As early as 1969, managers recognized the need to incorporate larger fluctuations into annual schedules (Wegener 1969) but, like many ecosystems today, this was hindered by flood control and water use demands in the changing watershed. Instead, management efforts focused on species removal, rather than addressing changes in processes that may have led to their establishment.

For example, over a 10 yr period just prior to restoration (1992–2002), the shoreline elevation occupied by the dominant *Pontederia* community was flooded 78–99.9% of the period. The deepest edge of this community essentially never dried, and the shallowest edge was flooded by up to 83 cm of water during high water events. During a typical 10 yr period prior to regulation (1944–1954), however, this shoreline elevation was flooded only 66–96% of that period, with water receding 18 vertical cm below the deepest edge of the community during low water events, and flooding the shallowest edge by up to 1.7 meters of water during high water events.

Besides a reduction in the magnitude of water level variations, there was also a substantial difference in the timing of annual fluctuations after water-level regulation. Historically, high water events consistently occurred in early winter (October and November), and shifted to early spring (February and March) after stabilization. Additionally, the early spring levels are now higher than they were historically, and drop more suddenly to match annual lows in May and June.

Water levels in the early growing season can have a big influence on species compositions (Weiher et al. 1996), limiting germination to more flood tolerant species, or

promoting vegetative growth from established perennials. Likewise, the timing (van der Valk 1981, Seabloom et al. 1998), frequency, and duration of flooding (Squires and van der Valk 1992) largely influences species compositions in wetland systems. The dramatic change in magnitude, seasonality, and frequency of flooding/drying events are likely the primary reason for a shift in dominant vegetation type since stage regulation.

Under the dynamic lake-levels of the 1950's, the shoreline elevations in this study were dominated by grassy species, namely *P. repens, Paspalum spp.,* and *Luziola* (Sincock et al. 1957). While this period and habitat was often referenced as the target for shoreline restoration on this lake (sandy substrate, sparse emergent grasses), the dominant species prior to regulation was an invasive exotic grass (*P. repens*) that was originally introduced for grazing cattle (Tarver 1979). This same species has had dramatic impacts in other Florida lakes (Smith et al. 2004) and is continually regulated with herbicides by the Bureau of Invasive Plant Management (Schardt 1994). During the 1950's, however, *P. repens* was not considered a nuisance on Lake Toho, and was described as an important species that provided cover during higher water (Holcomb and Wegener 1971).

This a good example of the difficulty in defining the ‘natural’ or historical state of systems (Landres et al. 1999), as well as how restoration targets can often be biased or value-laden perceptions of what a system should resemble rather than what it was prior to human-induced changes (Zweig and Kitchens *in press*). In this particular case, the restoration target appeared to resemble the habitat *structure* (sparse emergent grasses) that was established in the 1950’s, but there is no record of a similar, native-dominated community having ever occurred on the lake.

Prior to restoration activities in 2004, a grassy community like that described in the 1950's was found in my study areas, but was restricted to narrow bands near the annual high water lines (< 58 cm) and was dominated by *P. repens* and *Luziola*. The lower elevations that it occupied historically were dominated by more competitive emergent species, primarily *Pontederia* and the invasive exotic *Alternanthera philoxeroides*, neither of which were identified in the 1950's (Sincock et al. 1957). Four years after restoration, there was a marked decrease in the *Pontederia* community but it was not replaced by the grassy communities that existed historically. Instead there was a dramatic expansion of submersed aquatics, whose composition and abundance were unprecedented in this system.

Vallisneria, a native, submersed species, dominated scraped sections of shoreline four years after restoration, although it was extremely rare prior to restoration. While this plant had been recorded in the 1950's, it was at lower elevations (deeper water) and at very low frequencies (0–3%) in comparison to this study (Sincock et al. 1957). By 1970–1971 *Vallisneria* had moved shoreward nearly 60 vertical centimeters, expanding into elevations similar to where it was found at the end of this study, but its frequency of occurrence was still only around 3% (Holcomb and Wegener 1971). *Hydrilla*, another dominant submersed species in this study, expanded in both the scraped and unscraped areas following restoration, and was never recorded on Lake Toho prior to 1972.

Historically, Lake Toho was described as having low alkalinity and was not considered to support many submersed plants, and water-level stabilization was predicted to have little impact on their abundance (Sincock et al. 1957). Since that

period, nutrient pollution, water stabilization, and the introduction of the “Perfect Aquatic Weed” *Hydrilla* (Langeland 1996), submersed species have occupied large portions of the lake, and have hindered navigation and even flood control (BIPM 2004). This is another indication of the magnitude of change since water level regulations took place, and how dissimilar post-restoration communities remained from those in historical records.

Management Implications

The muck removal application conducted on Lake Toho was the largest and most intensive removal event to date, and was used as a substitute for the loss of historic flood/drought cycles that would have naturally flushed/oxidized accumulated organic materials or floating mats during such events. This unique approach was an attempt to reset decades of succession by removing the species, seedbanks, and soils associated with degraded shorelines. Initial colonization was regulated with selective herbicide applications, in an effort to force historical patterns on the sandy, exposed shorelines without the historical processes that maintained the system originally.

Ecosystem restoration will increasingly involve finding new methods or mechanisms to produce desired pattern where key drivers have been lost (Williams 2007). Global warming and human population growth is pushing many systems outside of their historical range of variability, and many lost processes may not be restorable. The prevalence of novel ecosytems, or the existence of new communities evolving under changing environmental conditions and altered disturbance regimes (Suding et al. 2004), may require shifting restoration targets from focusing on historical states to finding new, potentially more beneficial ecosystem conditions (Chapin et al. 2006).

This study is a good example of the difficulty in applying traditional, removal-based management approaches with increasing efforts, attempting to maintain historical patterns under degraded conditions. After 30 years of gradually intensifying management techniques (Wegener and Williams 1974, Moyer et al. 1989), the largest-scale muck removal project ever implemented still failed to restore historical littoral patterns on Lake Toho. The dense, monocultural *Pontederia* community that dominated for at least 20 years after hydrologic and nutrient changes in the system promoted its expansion, was replaced by yet another novel, submersed community that was previously only documented at very low frequencies (Sincock et al. 1957, Holcomb and Wegener 1971, Moyer et al. 1989).

While the objective of establishing the historical pattern of sparse, emergent grasses was not realized, the community that did establish along the treated shorelines had similar desirable attributes as the target habitat. For example, organic soils were replaced with sandy substrates, the submersed communities provide important habitat for fish (Barnett and Schneider 1974) and waterfowl (McAtee 1939, Sculthorpe 1967), and the removal of floating mats and dense emergent vegetation allows for better recreational access.

When system degradation cannot be reversed at an acceptable cost, managers should strive for the biotic structure and ecosystem services that stakeholders desire, while promoting communities that are both feasible and resilient (Seastedt et al. 2008). This project has been successful at the former, but the resilience or longer-term establishment of a submersed community at these lake elevations is unknown. The vertical range of shoreline occupied by the submersed community will likely compress to

only those areas with 100% annual hydroperiods under normal regulations (see Ch. 4), and aggressive emergent species have already been re-established in the shallow regions of this study. A regional drought could expose most of the shoreline occupied by the newly established submersed community, allowing rapid invasion by emergent species like *Pontederia*, or perhaps more likely, *P. repens*; this species has previously displaced thousands of hectares of native marsh after low water events on other Florida lakes (Smith et al. 2004). Without substantial changes in water regulation schedules, it is likely that *Pontederia* will continue to expand lakeward from its narrow bands along the shore, as happened under similar conditions from 1979 to 1987 (Moyer et al. 1989).

The importance of hydrological conditions to wetland control and structure is widely recognized (National Research Council 1996), and restoration of these systems must begin with hydrology (Hunt 1999). The communities established on Lake Toho following restoration may be dependent on consistent herbicide applications, which are increasingly regulated and dependent on currently declining state budgets (BIMP 2004). While restoring the variability of the natural hydrological regime is not possible in this or many other aquatic systems, it is possible that partial improvements to hydroperiods could be of value (Zedler 2000). For example, Lake Toho is consistently managed between 15.9 to 16.8 meters (NGVD) annually, with little to no inter-annual variability (excluding infrequent drawdowns). Year to year fluctuations are known to increase plant diversity, and can essentially double the number of vegetation types on a shoreline (Keddy and Fraser 2000). Managing lake levels with 0.5 m of inter-annual variation, for example, may reduce the amount of herbicides needed to keep robust, resilient communities from dominating the zone of intra-annual variation.

In many cases, the sequence of disturbances (including floods and droughts) and their timing, intensity, and spatial pattern have greater impacts than single, intensive, large-scale events (Barlow and Peres 2006). Since the 1970's, intensive, managed drawdowns were conducted on Lake Toho at approximately 10 year intervals to counteract effects of water stabilization. It is possible that incorporating year-to-year fluctuations would have a greater impact on littoral communities than infrequent, drastic drawdowns. The dense emergent communities established between these rare events proved too robust to be displaced by periodic droughts, and appear well adapted to the degraded environmental conditions of the lake.

Additionally, large-scale, intensive disturbances may have profound impacts (Turner et al. 2003), but their outcomes are difficult to predict and are risky to implement. The first drawdown implemented on the lake in 1971, for example, was followed by a substantial drought, keeping lake levels below normal for nearly two years (Wegener and Williams 1974). Even if results similar to this study could be expected from large-scale, muck-removal treatments among other shallow, subtropical systems, they would likely vary considerably depending on environmental conditions during and directly after application. Had this treatment been followed by a prolonged drought, for example, we might expect shorter hydroperiod communities to have colonized treated areas, instead of the submersed species found in this study.

Ecosystem restoration should stay focused on key structuring processes and promoting desired ecosystem functions under future conditions. The large-scale muck-removal project implemented in this study did not re-establish littoral vegetation patterns that occurred prior to water-level regulation, but resulted in an unprecedented

expansion of submersed species instead. While the novel, submersed community that became established is preferred by managers over the pre-restoration habitats, it is unclear whether it will persist under degraded environmental conditions and unchanged water regulation schedules. This study will hopefully serve as an example of the need to focus management and restoration efforts on establishing communities that will persist under current and projected conditions with minimal maintenance and effort. Even as recent studies have called for accepting new communities instead of historical states (Seastedt et al. 2008) and promoting new approaches to managing under novel conditions (Holling 2001), we must keep the basic premise of successful restoration efforts. Restoring or at least partially implementing key structuring processes (Landres et al. 1999) should remain at the forefront of pattern restoration, and will minimize management contributions and costs (Mitsch and Wilson 1996). Hydrological regimes will become increasingly difficult to restore with population growth and changing precipitation patterns, and with it the temptation to maintain pattern with herbicides, species removals, and bulldozers.

CHAPTER 3
MUCK REMOVAL AS A TOOL FOR RESTORATION OF LITTORAL VEGETATION ON A SUBTROPICAL LAKE

Introduction

Much of the literature on shallow lake restoration typically involves reducing water column turbidity and reestablishing aquatic macrophytes, either through reducing planktivore biomass, stocking piscivores (top-down approach), or reducing nutrient loads, thereby reducing phytoplankton and increasing light penetration to the sediments (Jeppeson et al. 1990, Moss et al. 1996). These studies are based on the phenomenon of alternative stable states, where shallow, eutrophic lakes can occur in either a degraded state (turbid water, phytoplankton-dominated) or in a clear-water, macrophyte dominated state, under the same environmental conditions (Scheffer et al. 1993). Transitions between these states can occur rapidly, switching from plant to algae-dominated conditions after water fluctuations (Blindow et al. 1993), plant removal (van Donk and Gulati 1995), or changes in the food-web structure (Carpenter and Pace 1997).

However, in warm temperate (Romo et al. 2005) and subtropical lakes (Bachmann et al. 2002) the correlation between high plant density and clear water is much weaker. In Florida lakes, for example, turbid water can still support high macrophyte coverage, and lake restoration projects typically involve vegetation removal, rather than establishment. This approach is seemingly at odds with much of the shallow lake restoration literature, but controlling aggressive and dense growth of littoral vegetation is a primary goal in this region.

Florida lakes are subject to the same pressures facing most waterbodies near urban development, including modified lake stages (Havens 2005), elevated nutrient

levels (Bachmann et al. 1999), exotic species invasions (Smith et al. 2004), and shoreline modification (Light and Dineen 1994). Usually, such conditions result in degraded, turbid systems, but strict environmental regulations and relatively large aquatic management budgets in the USA have improved conditions over the last few decades; eliminating point-source pollution, implementing fish harvest plans, promoting management of sport fish habitat, and continually removing invasive exotic plants (Moyer et al. 1989, Williams 2001, Allen et al. 2003). Much of Florida lake management has moved beyond reestablishing macrophytes in degraded systems, and focuses now on regulating the abundance, distribution, and composition of the established littoral vegetation (FFWCC 2003).

There are several factors contributing to prolific littoral vegetation growth in Florida's lakes: 1) Nutrient concentrations have been reduced from their highest levels, but non-point source pollution (Havens 1995) and internal loading mechanisms (Bachmann et al. 1999) can maintain higher levels than occurred historically, 2) Strictly regulated water schedules maintain predictable, relatively stable hydrological conditions (HDR Engineering 1989), 3) Aggressive exotic species, including emergent (e.g. *Panicum repens*), floating (e.g. *Eichhornia crassipes*), and submersed (e.g. *Hydrilla verticillata*) genotypes, are capable of rapid expansion in these warm-water, eutrophic systems, and 4) Large area:volume ratios (large photic zones) can result in up to 100% of the lake bottom capable of supporting rooted aquatic vegetation (Canfield and Hoyer 1992).

Lake restoration in this region has shifted from vegetation establishment to removal, because without dynamic water schedules, dense emergent vegetation can

form floating mats around the annual low-pool elevation of the shorelines (Hoyer and Canfield 1997), possibly leading to a loss of sport fish spawning habitat, recreational access, open water area or functional lake size, plant diversity, and lower oxygen levels (Moyer et al. 1989). Typical management responses include mechanical harvest of floating mats (Mallison et al. 2001), regular herbicide control of aggressive species (Schardt 1997), and implementation of managed droughts (drawdowns), which expose organic mats to oxidation and subsidence (Wegener et al. 1973). However, the short-term benefits of these procedures (Moyer et al. 1995) and the increasing difficulty of implementing drawdowns in urban watersheds have led managers to search for new approaches, including mechanical scraping to remove muck and vegetation (hereafter referred to as muck removal).

Muck removal involves scraping (with bulldozers) vegetation and accumulated organic materials from exposed portions of the littoral zone during drawdowns, and may include regulating initial plant succession with herbicides. This technique has been applied to several lakes in Florida, and has been considered successful in improving short-term juvenile sport-fish abundance (Moyer et al. 1989, Allen et al. 2003). Although no long-term faunal or vegetation monitoring was conducted on early projects, increasingly larger applications have been attempted since its inception. The largest of these applications took place on Lake Tohopekaliga in central Florida, where approximately seven million cubic meters of shoreline vegetation and underlying soils were removed from roughly 1500 ha of the perimeter in 2004.

The goal of this study was to determine the efficacy of this procedure by comparing pre- and post- restoration vegetation communities, in both scraped and

unscraped treatment plots. Specifically, I tested whether muck removal resulted in different vegetation communities than a typical managed drawdown, and if so, how those responses varied by water depth and recovery rates. These results are important to lake restoration practitioners and aquatic plant managers, especially as goals shift beyond simply re-establishing vegetation and begin managing for specific habitat types.

Methods and Analyses

This project was conducted on Lake Tohopekaliga (hereafter referred to as Lake Toho), one of several large lakes in the Upper Kissimmee River Basin in central Florida, USA. Each of these lakes is successively connected and jointly regulated to collectively drain thousands of square kilometers into the Kissimmee River and ultimately Lake Okeechobee (Ch. 1, Figure 1-1). Toho is located near the top of this system, and covers 8,176 ha with an average depth of 2.1 m (at maximum stage regulation of 16.75 m NGVD). This volume of water effects systems downstream when stage levels are manipulated (e.g. Lake Okeechobee, Kissimmee River), specifically since the entire chain of lakes must be lowered in order to gravitationally drawdown lakes in the northern region of the chain (HDR Engineering 1989, Remetrix LLC 2003).

Water control structures were installed on the Kissimmee Chain and Lake Toho in 1964 (Blake 1980), reducing the range of water level fluctuations by approximately 1.5 m to an intra-annual variability of 1.1 m (Ch. 1, Figure 1-2). Sewage effluent from up to three treatment facilities was discharged into the lake from roughly 1940 to 1988, reaching a maximum of 113 million liters per day in 1986 (Wegener et al. 1973). The combined impacts of stage regulation and nutrient loading were blamed for decreases in water quality and fisheries production in the late 1960's, leading to a series of artificial dry-downs in 1971, 1979, 1987, and 2004 to improve fish habitat.

The largest muck removal project to date was implemented on Lake Toho in 2004. Water levels were dropped from 16.8 m to 14.9 m from November 2003 until June 2004, during which time roughly 6.5 x 10^6 m^3 of muck and vegetation were removed from roughly 1500 ha of shoreline lake bottom. Spoil was deposited at several upland sites and in 29 locations within the lake (FFWCC 2004). Water levels returned to normal by August 2004.

Sample Locations

Three study sites spanning 1600 m (approx. 1 mi) of shoreline each were located in areas with similar depth contours, vegetation communities, and shoreline use, in order to minimize inter- and intra-site variation that might confound treatment results. Sites were selected to represent the habitat targeted by muck removal projects, which in this case was primarily a band of dense pickerelweed (*Pontederia cordata*) and floating mats of vegetation (tussocks), which occurred roughly within the range of annual water level fluctuation. Plot sizes also had to be of functional value to avian and herpetofaunal communities for concurrent studies monitoring their responses to treatment. Each study site was therefore split into four treatment blocks of 400 m each, the size of which severely limited the amount of replicate sites available (Figure 3-1). The spatial extent of each study plot and the reluctance of lake managers to reserve multiple control sites throughout the lake resulted in just three locations isolated for experimental treatment.

These sites were originally structured as a randomized complete block design, with three treatments and a control randomly assigned to four blocks at each site. However, two of the planned treatments were dropped by managers after pre-sampling was completed, so a control and treatment were randomly assigned twice within each

study site. This complicated the sample design as treatments and controls were replicated within and between sites. Due to the efforts in minimizing inter-site variation during site selection and the dearth of replicates, I used each treatment as an independent sample to increase the sample size. Ideally, additional control sites would have been established on adjacent, similar lakes, but due to linked hydrologies and gravitational drawdown, other lakes of similar size and region were also lowered during this application. Therefore, the design of this project was limited by cost, logisitics, and treatment restrictions, and I feel the best sampling protocol was established given the constraints. The maximum water depth of the plots, or the lakeward extent, was delimited by the approximate water depths mechanical scraping could be applied, from roughly 35 - 135 cm water depth at maximum lake stage.

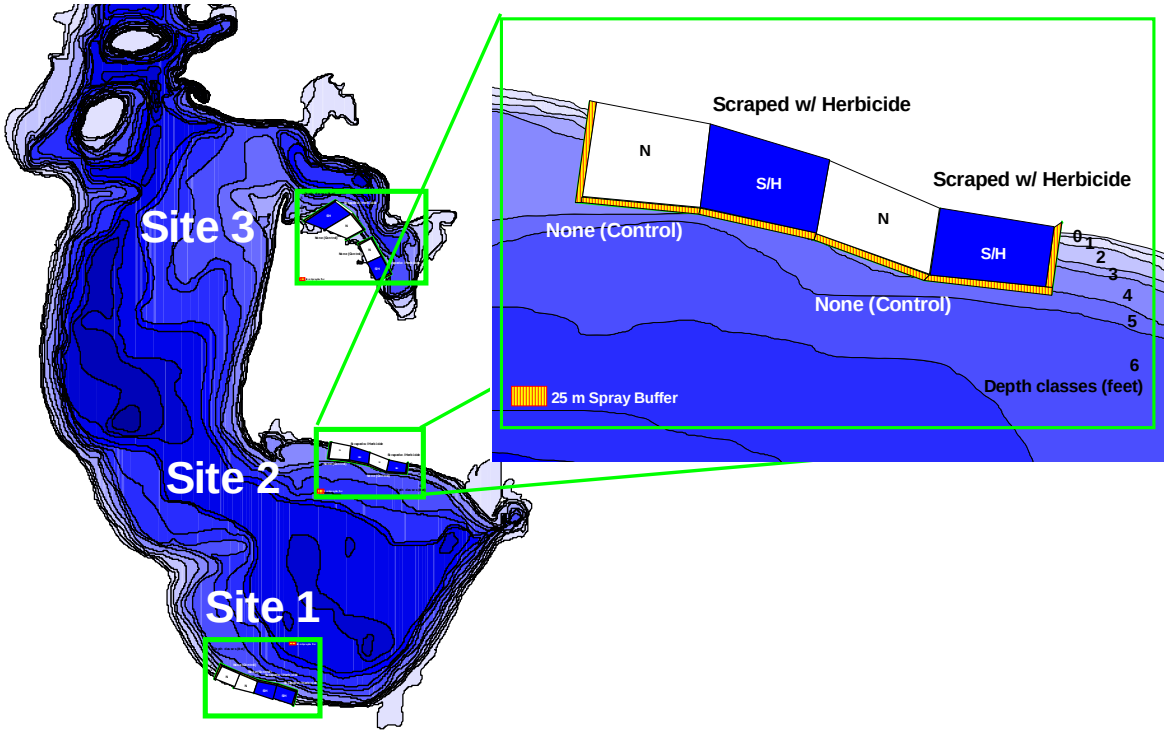

Figure 3-1. Location of experimental study sites on a bathymetric map of Lake Toho (0–13 ft, or ~ 2 m). White plots were designated controls, while blue plots were treated with mechanical muck removal and periodic herbicide applications.

Sampling locations were stratified by three depth classes (One = 35–68 cm, Two = 69–102 cm, Three = 103–135 cm) and were located on maximum slopes of 30 cm change over 30 m in distance, so as to avoid unusual shoreline contours. This was accomplished by placing 30 x 30 m grids onto a GIS bathymetry layer (Remetrix 2003) and randomly selecting grid numbers from each depth category. Centroid coordinates were used to locate samples in the field with a GPS (Global Positioning System) on each sampling occasion. Two locations per depth class were sampled from each treatment plot for a total of six samples per treatment, and 12 total treatment plots.

Aboveground vegetation was clipped from 0.25 m^2 quadrats at each location, sorted by species, stems counted, and biomass recorded after being oven-dried to a constant weight (70 deg C). Samples were collected each year during the summer (May-June) and winter (December) seasons from June 2002 to June 2008, resulting in 13 repeated measures for each location.

Soil cores were collected from the top 10 cm of substrate from each sampling location in June 2003 and June 2008, using cylindrical aluminum corers measuring 7 cm in diameter. Samples were placed on ice until moved to a freezer at the University of Florida, Gainesville, FL. After being oven dried to constant weight, bulk densities were determined (Blake and Hartge 1986) and percent organic content was calculated by loss on ignition (Chapman and Pratt 1961, Jacobs 1971).

Lake-stage data were collected from a South Florida Water Management District gauge located on the southern end of the lake, recording average daily water levels since January 1942. Indicators of Hydrologic Alterations (IHA) software was used to analyze pre (1942–1964) and post water-level regulation (1965–2008) periods, defined by the completion of water control structures in 1964. Both periods were analyzed for 30, 60, and 90 day maximum and minimum water levels, average monthly levels, and quartiles. Two 10 year periods before and after regulation, 1944–1954 and 1992–2002, were selected for further comparison between pre- and post-regulation periods. This was done to exclude some of the more extreme events in either period, including historical highs and lows experienced in the early 1960s, as well as managed drawdowns in the latter period. Water level structures were not completed on the Kissimmee Chain of lakes until 1964, but it seems reasonable that substantial changes

were occurring in the watershed up to several years prior (beginning of construction), possibly contributing to the historical highs (1960) and lows (1962) recorded just prior to completion. Rather than use these events as representative of typical pre-regulation fluctuations, the 10 year period characterized by more modest events and that occurred just prior to early vegetation studies (1956) was chosen. These two periods allowed comparison of relatively stable events, rather than just looking at differences in maximum and minimum stage levels, which would also be affected by rare climatic events. Water years were defined as June through May of the following year, corresponding with the beginning of the wet season and end of the dry season, respectively.

Historical vegetation data were referenced from management agency studies conducted in 1956, eight years prior to water regulation (Sincock et al. 1957), and in 1971, seven years after (Holcomb and Wegener 1971). These studies used intercept methods to calculate frequency of occurrence along transects perpendicular to shore, with several locations overlapping the sites in this study. These methods vary considerably from the sample techniques used here but are the only estimates of dominant species and their distributions along shoreline elevations prior to stage regulation. While not specifically referenced as restoration targets by managers, these early data served as representatives of the pre-stabilization, pre-nutrient pollution, sandy substrate communities that were often invoked by proponents of this project.

Analyses

Pre/post-restoration comparison

To determine vegetation responses to the 2004 muck removal project, plant species density and biomass were summed in each quadrat from December 2002 and

June 2003 to represent pre-restoration communities, and December 2007 and June 2008 samples as post-restoration representatives. Importance Values (IV) were computed from these summed values by averaging the relative biomass and density of each species in each quadrat, and converting to a percentage value.

$$IV = (\text{Relative Biomass} + \text{Relative Density})/2 * 100$$

Importance values were used to estimate species importance within a given quadrat as they are not biased towards large, few-stemmed species or small, numerous-stemmed species. This calculation also relativized the dataset, eliminating the need for transformations typically applied to density or biomass data that can vary by orders of magnitude between species and samples (McCune and Grace 2002).

To reduce noise from rare species, only those with cumulative IV's composing 95% of the total were retained for this analysis. Many studies eliminate species that occur in less than 1–5% of samples, but I used 5% of the total IV instead. This method was more representative of the actual importance of a species throughout the sample for the same reason IV's are more representative of a species' abundance than frequency. Analyses were limited to more common species as the dominant community responses to treatment were of primary interest, and not necessarily the loss or addition of rare species. Final matrices consisted of 72 samples by 18 species for the pre- and post-enhancement periods, reduced from the 37 species encountered over the four combined sample periods. All analyses for the pre-post comparisons were performed on these matrices and unless otherwise specified, performed using PCORD software (McCune and Mefford 1999).

A hierarchical, agglomerative Cluster Analysis was used to find groups of similar species compositions, termed here as communities. Flexible beta (-0.25) linkage and Sorenson distance measures were chosen for their space conserving properties, compatibilities with each other, and their advantages with non-normal data (McCune and Grace 2002). This analysis grouped similar sample units based on species IV's, using multiple species as a basis for deciding on the fusion of additional groups.

An Indicator Species Analysis (ISA) was performed for two reasons: 1) to determine the optimum number of clusters for further analysis and 2) to define those clusters in terms of representative species. This analysis uses the proportional IV and frequency of a particular species in a particular cluster relative to its IV and frequency in all other clusters (Dufrene and Legendre 1997). The optimum number of clusters was determined by the level of clustering that produced the most species with p-values < 0.05 in the indicator species analysis (McCune and Grace 2002). Species with low p-values (< 0.05) and high indicator values (> 50) were used as community descriptors (cluster labels) in future analyses.

A Classification and Regression Tree (CART) model (S-Plus Tree Library, De'ath 2002) was used to classify samples into the groups identified by the cluster analysis using measured environmental variables alone. The Gini index was used to measure impurity (Breiman et al. 1984), cross-validation to select the best tree size (Vayssieres et al. 2000), and 1-Standard Error as an estimate of variation explained by the model (De'ath 2002). By building CART models for pre- and post-enhancement communities, species distributions could be compared across environmental, spatial, treatment, and temporal gradients. Several combinations of the variables water depth, soil organic

content, and bulk density were used as continuous predictors, while site, treatment, and whether the sample occurred on a floating mat were used as categorical variables.

Temporal analyses

In order to track changes in species biomass over time, I combined sub-samples within each depth class and site by treatment and sample occasion, resulting in six samples over 13 time periods, each representing a depth class and treatment in a site.

Nonmetric Multi-dimensional Scaling (NMS) ordinations were run for each site to graphically display changes in species abundances throughout the period of study (McCune and Grace 2002). Joint plots of correlated variables ($R^2 > 0.20$) were overlayed onto the ordination diagrams, with length and direction representative of their correlation to the axes. The sample units were color coded by treatment and consecutive samples were connected by vectors to track their movements. Within each site, ordinations were graphically separated by depth class for ease of interpretation.

Results

Soils

Soil percent organic matter was plotted by treatment and time period, i.e. before and after the lake restoration project, using all subsamples and depth stratifications (Figure 3-2). The mean percent organic was 33% across all samples prior to treatment, and the median was 11%. After muck removal, the mean and median of scraped plots were both less than 2%, and were 15% and 4%, respectively, in the control plots. After averaging across all subsamples (resulting in n = 6), Wilcoxon signed rank tests showed significant differences between the pre- and post-enhancement periods in both the control (P = 0.031) and the treatment plots (P = 0.016) at the 0.05 alpha level. However, I was unable to detect a significant difference between treatments in the

amount of percent organic matter lost after restoration, using a Wilcoxon rank sum test (P = 0.09). The amount of organic material lost was more variable in the control sites, but not significantly less overall than the treated areas.

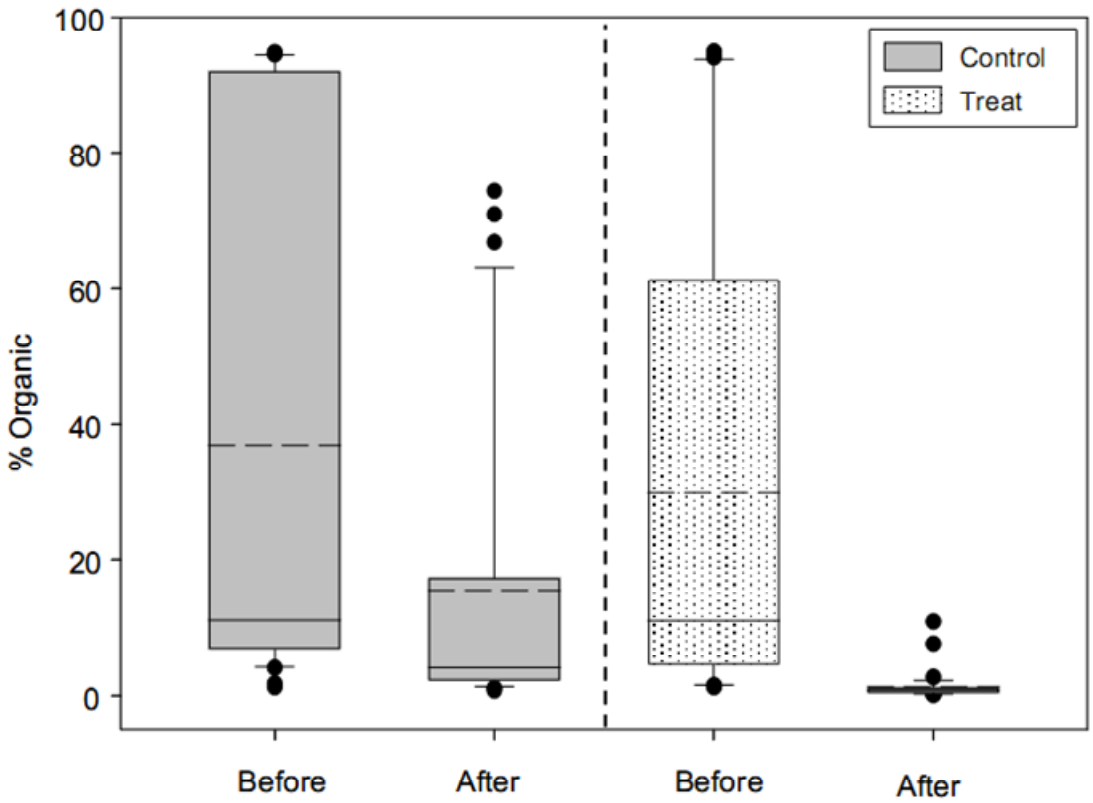

Figure 3-2. A boxplot of percent organic content in all soil cores from treatment and control plots, before (2002) and after (2008) the dry-down and muck removal project (before averaging sub-samples). Shaded boxes represent the 25th and 75th percentiles, whisker bars are the 10th and 90th percentiles, and solid circles are outliers. The means (dashed lines) and medians (solid lines) are shown within each shaded box.

Vegetation

Species richness was lowest in the shallowest depth class prior to treatment, with the second and third depth class having more species in both the control and treated plots. After the dry-down and scraping, however, both plots reversed patterns and had more species in the shallowest depth class than in the deepest (Figure 3-3).

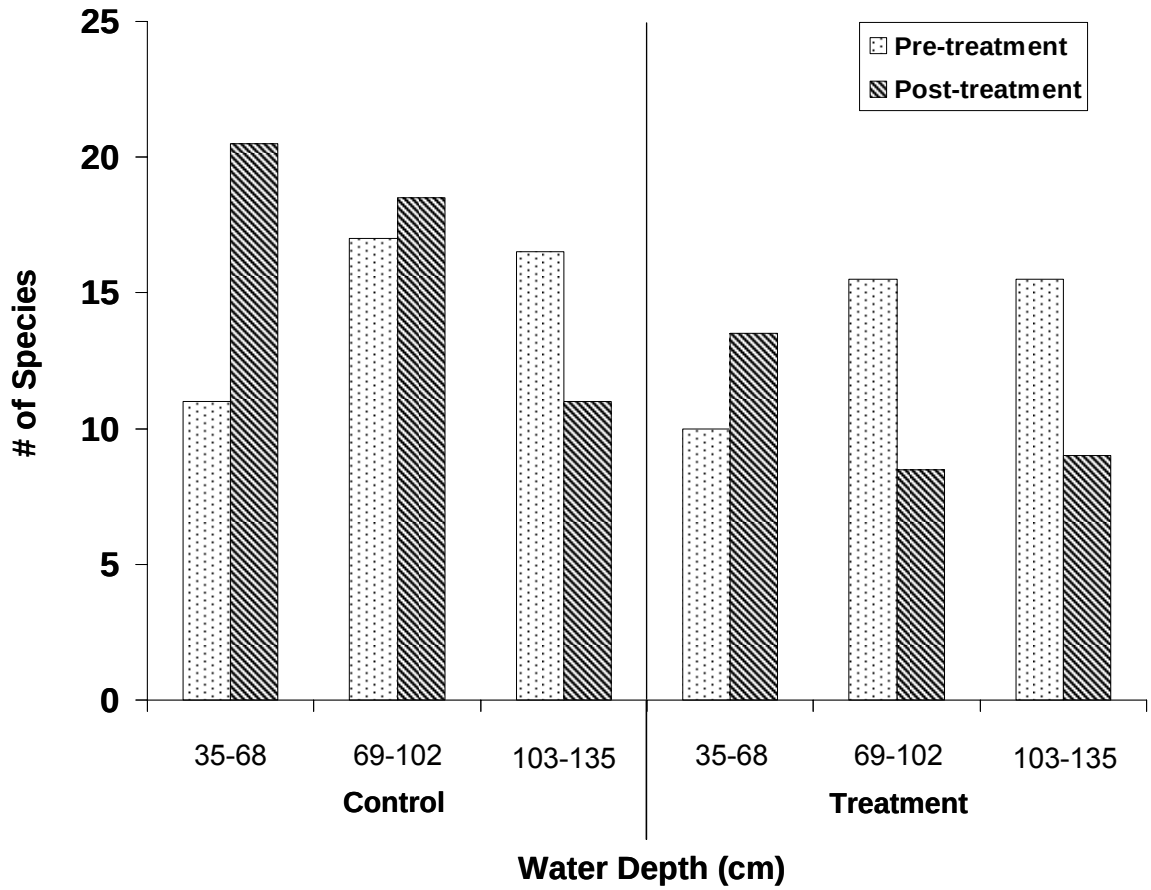

Figure 3-3. Species richness by depth category and treatment, before and after restoration.

Changes in biomass after treatment application were tallied for several of the most common species (Table 3-1). These tallies were indicative of total change, including all depth, site, and subsamples for each treatment type. Several species had substantial declines in biomass regardless of treatment, including *Pontederia cordata* and water lilies (*Nuphar advena, Nymphaea odorata,* and *Nymphoides aquatica*). Species that had substantial increases in biomass in control plots included *Luziola fluitans*, *Polygonum hydropiperoides*, *Hydrilla verticillata,* and *Vallisneria americana*. The few species that benefited from the mechanical scraping were *Vallisneria, Panicum repens, Hydrilla,* and *Eleocharis* spp. *Vallisneria* was not recorded prior to the treatment, and

had over 1.3 kg (dry weight) totaled across the last two sample periods. *P. repens* had a 29% increase in biomass in scraped plots, vs. a 35% decrease in controls.

Table 3-1. Change in total dry biomass (g) from two pre- and two post-treatment sample periods of common species. Percent change could not be calculated if no biomass was recorded before treatment.

Species	Control Biomass (g)	% Change	Treat Biomass (g)	% Change
P. cordata	- 3356	- 66%	- 3966	- 83%
L. fluitans	1037	124%	- 171	- 83%
Water lilies	- 350	- 72%	- 150	- 82%
P. hydropip.	520	522%	- 32	- 97%
P. geminatum	16	23%	45	500%
Eleocharis spp.	63	112%	200	1100%
H. verticillata	497	43%	320	68%
P. repens	- 84	- 35%	320	29%
V. americana	270	N/A	1316	N/A

Time Series

The NMS ordinations tracking species biomass through time suggested varying stages of recovery depending on depth and site. Treatment effects were evident when the end point of the control and treatment trajectories were 1) in different locations relative to each other, indicating different compositions between treatments, and 2) when the treatment trajectory was stabilized in a different species space at the end of the study (new community established), and the control trajectory was near its origin (recovery in control plots).

Pearson correlations were calculated for each environmental variable and axis, and those with $R^2 > 0.20$ were displayed on the two axes with the highest amount of variance explained in the three dimensional solution (McCune and Mefford 1999). Axes had at least a weak correlation to either soil organic matter, water depth, or both in all

ordinations. These correlations were portrayed with a red arrow next to the corresponding axis, with directionality indicating increasing values of organic matter percentage or water depth. The three depth figures for each site were separated from one ordination to ease interpretation.

The ordinations for Site 1 suggest the shallowest depth class control (dashed lines) and treatment (solid lines) plots had recovered to near pre-treatment compositions by the end of the study, as evidenced by the proximity of the beginning and end points of the arrow trajectories (Figure 3-4). The treatment plot in the second depth class (69–102 cm), however, actually appeared to be closer to the 2003 compositions than the control plot did, indicating further recovery in the treated area. The deepest samples at this site appeared to show less change overall and also seemed to be near the pre-treatment conditions in both control and treated plots.

Site 2 ordinations suggested substantial recovery in the shallowest depth class, again with no striking difference in either trajectories or degree of recovery between treatments (Figure 3-4). The second depth class at this site, however, had a different composition in the treated plots by the end of the study, and an apparent recovery in the control plots. Both plots seemed to have stable communities, with very little distance (dissimilarity) between the last two sample periods. This was indicative of a strong treatment effect. Both the treatment and control plots remained different from pre-treatment conditions in the deepest class, though the last sample in the control plot indicated recovery may be taking place as it moved nearer its origin.

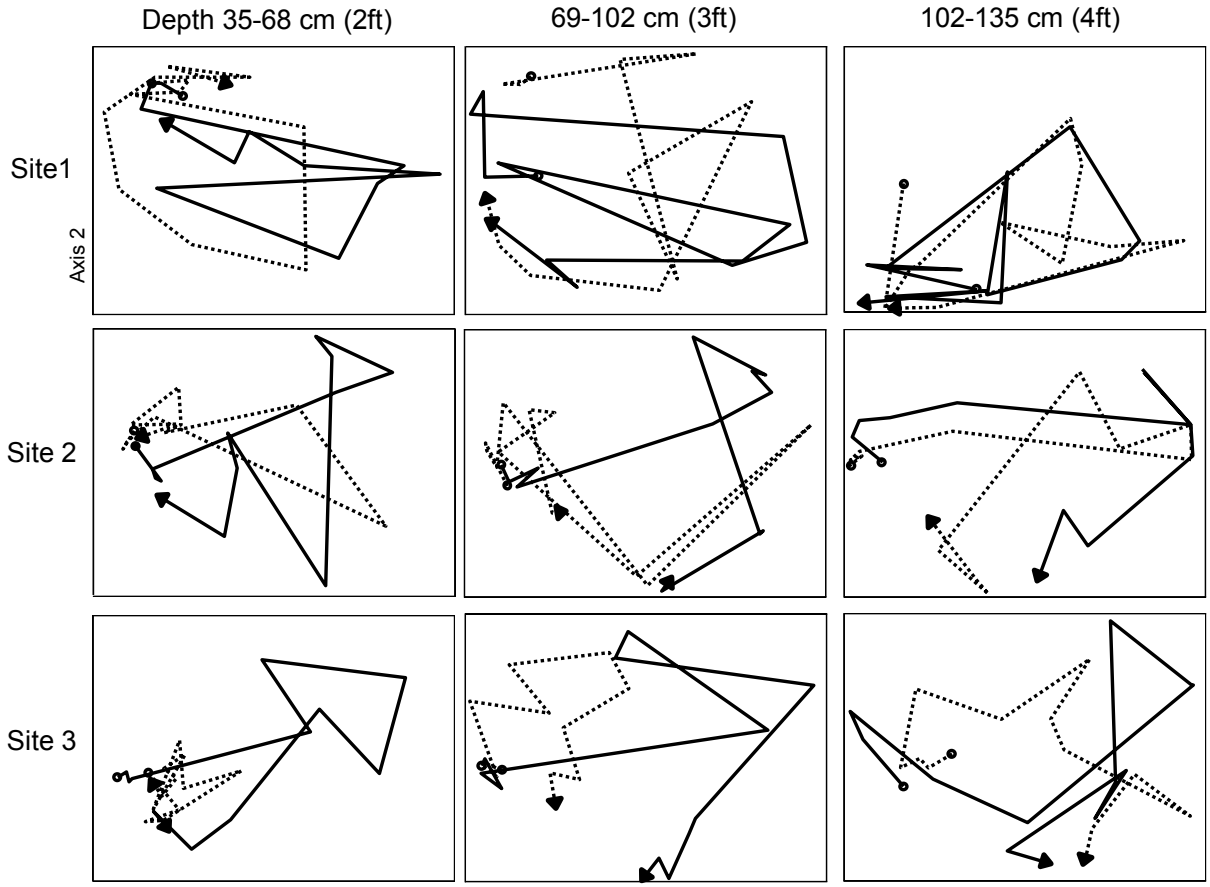

Figure 3-4. NMS ordinations of each site, with depth categories graphically separated. Dashed lines show control plot trajectories and solid lines indicate treated plots. Axes 1 and 2 are horizontal and vertical, respectively, for all of the graphs. Site 1: Water depth weakly negatively correlated with Axis 2 (R^2 -0.34) while soil percent organic matter positively correlated (R^2 0.21). Site 2: Percent organic negatively correlated with Axis 1 (R^2 -0.32). Site 3: Percent organic negatively correlated with Axis 1 (R^2 -0.48).

Site 3 had similar patterns, with the shallowest samples having recovered in both the control and treated plots, while the second depth class showed a remarkable difference in recovery between the treatments (Figure 3-4). The scraped plot at this depth remained very dissimilar in terms of species composition and biomass than it was prior to treatment, while the control plot had recovered. Again, this was indicative of a strong treatment effect. The deepest samples, however, showed substantially different communities in treatment and control plots, indicating both areas remained

compositionally changed after restoration, regardless of whether or not they were mechanically scraped.

Community Changes

The four samples from the pre- (December 2002 and June 2003) and post-treatment (Dec 2007 and Jun 2008) periods had 37 species, 18 of which comprised the top 95% of the cumulative importance values. The pre- and post-treatment summed datasets resulted in matrices of 72 samples by 18 species, which were divided into six communities (clusters) for the pre- (3.5% chaining, 55% information remaining) and post-restoration (2.6% chaining, 55% information remaining) periods. Species with indicator values of approximately 50 or greater from the ISA were used to define clusters as community states (Table 3-2), and were labeled accordingly. The pre-restoration indicators were: 1) *Luziola fluitans* and *Panicum repens*, 2) *Pontederia cordata* and *Alternanthera philoxeroides*, 3) *Hydrocotyle* spp., 4) *Hydrilla verticillata*, 5) *Lymnobium spongia* and *Eichhornia crassipes*, and 6) *Utricularia spp*., *Nuphar advena*, and *Nymphaea odorata*.

The post-treatment period also had six communities identified by the cluster and ISA, which were 1) *Eleocharis spp*. and *P. repens*, 2) *Luziola*, *Polygonum*, and *Paspalidium acuminatum*, 3) *Pontederia*, 4) *Typha* spp. and *Nuphar*, 5) *Hydrilla,* and 6) *Vallisneria* (Table 3-3).

Table 3-2. Indicator values of species in the pre-enhancement period (Dec 2002, Jun 2003), with values ranging 0–100.

P_value	Species	Group 1	2	3	4	5	6
0.001	**EICCR**	49	0	0	0	0	0
0.000	**LYMSP**	63	0	1	2	0	0
0.000	**LUZFL**	0	98	0	0	0	0
0.007	**PANRE**	2	46	0	0	4	0
0.000	**HYDSP**	7	0	57	0	0	0
0.000	**HYDVE**	3	0	1	88	0	0
0.000	**PONCO**	1	11	28	0	53	0
0.001	**ALTPH**	3	11	13	0	46	0
0.000	**UTRSP**	0	0	0	0	0	94
0.001	**NUPAD**	0	0	0	0	0	64
0.000	**NYMOD**	0	0	0	0	0	48
0.697	POLHY	9	0	4	0	7	0
0.170	UNPAS	11	21	0	0	5	0
0.044	CERSP	1	0	0	20	0	32
0.047	PANHE	0	0	0	0	0	31
0.090	SAGLN	0	0	21	0	0	0
0.229	TYPSP	0	0	14	0	1	0
0.010	ELESP	0	36	0	0	0	0

Species with high indicator values are highlighted accordingly and are used as community descriptors for each group.

Table 3-3. Indicator values of species in the post-enhancement period (Dec 2007, Jun 2008), with values ranging 0–100.

P_value	Species	Group 1	2	3	4	5	6
0.000	**LUZFL**	76	0	0	13	3	0
0.000	**POLHY**	63	0	0	3	3	0
0.000	**PASAC**	61	0	0	10	4	0
0.000	**VALAM**	0	92	3	0	0	0
0.000	**HYDVE**	0	5	75	0	0	9
0.000	**PANRE**	5	0	0	68	2	0
0.000	**ELESP**	4	0	1	61	9	0
0.000	**PONCO**	1	0	0	1	89	1
0.006	**TYPSP**	0	0	0	0	0	40
0.016	**NUPAD**	0	0	2	0	0	37
0.183	ALTPH	22	0	0	14	19	1
0.068	HYDSP	0	2	0	25	4	0
0.039	SAGLN	0	0	0	0	25	0
0.302	PANHE	4	0	0	0	11	0
0.456	CERSP	0	0	10	0	0	0
0.844	NYMOD	0	4	1	0	0	0
0.241	CHASP	0	5	16	0	0	0
0.301	UTRSP	3	0	13	0	1	0

Species with high indicator values are highlighted accordingly and are used as community descriptors for each group.

Five of the six communities were predicted by water depth, soil percent organic matter, site location, and whether the sample was categorized as a floating mat (Figure 3-5). The *Eichhornia* and *Lymnobium* community identified by the cluster and ISA analyses was not delineated at this level of pruning, and only contained 3 of the 72 samples in the analysis.

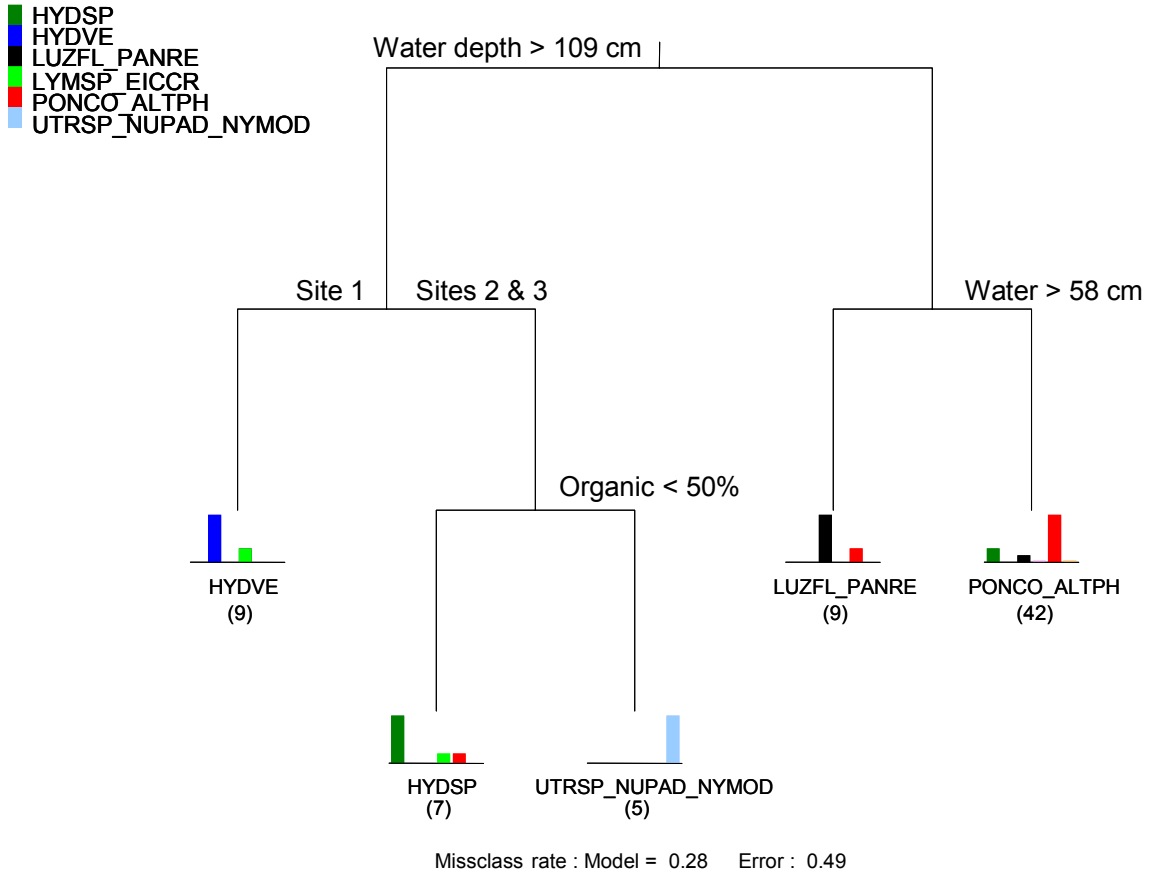

Figure 3-5. CART model of pre-treatment community distribution along the measured environmental gradients. The numbers of samples in each leaf are shown in parentheses below bargraphs, which show the compositions of communities within each leaf. Species abbreviations are the first three letters of genus and first two of specific epithet (PONCO = *Pontederia cordata*).

The biggest difference in community types occurred at 109 cm in water depth. The most abundant community of the pre-treatment period was *Pontederia* and *Alternanthera*, with 58% of all samples classified as such. This community was predicted to occur in 58–109 cm of water depth at full pool, and represented the habitat type targeted by restoration efforts. The shallowest community was *Luziola* and *P. repens*, occurring at < 58 cm. Deeper communities differed primarily by site. The *Hydrilla* community dominated at Site 1 at > 109 cm in water depth, while Site 2 and 3 had a *Hydrocotyle* community, or *Utricularia, Nuphar,* and *Nymphaea*. The *Hydrocotyle*

community was indicative of a floating mat, or tussock, as evidenced by the high soil organic content (> 50%) and the fact that *Hydrocotyle* cannot survive in > 109 cm in water without a buoyant substrate.

The best CART model for the post-treatment period was pruned to seven leaves, with five of the six communities again represented (Figure 3-6). The misclassification rate was 33%, with 53% of the variation explained (1-Standard Error). Soil percent organic matter was omitted from the final model, primarily to ease interpretation of treatment effects. When soil organic matter was included, several tree splits were attributed to soil differences, rather than treatment type. The soil differences were directly related to whether or not samples were treated, and the final groups only varied by three samples between models. I chose the model without soils type included so as to emphasize the difference in treatment type rather than having to infer treatment from soil organic matter content.

Contrary to the pre-treatment period, the main break between community types in the post period occurred at 69 cm in water depth, rather than 109 cm. The majority of samples in the post period were identified as *Hydrilla* rather than *Pontederia*, with all control samples at > 69 cm in water depth classified as such. The treated sites varied between *Vallisneria* or *Hydrilla* at > 69 cm in depth.

The *Pontederia* group that was so prominent in the pre-treatment period was reduced to 8 samples in the post period, down from 58, and no longer had *Alternanthera* as a co-indicator. This community was classified in both treated and control areas, but was restricted to a very narrow water depth, occurring at 61–69 cm. There were also treatment differences in the shallowest samples, with control plots

having *Luziola*, *Polygonum*, and *P. acuminatum*. at < 61 cm in water depth, while treated plots had an *Eleocharis* community at < 66 cm.

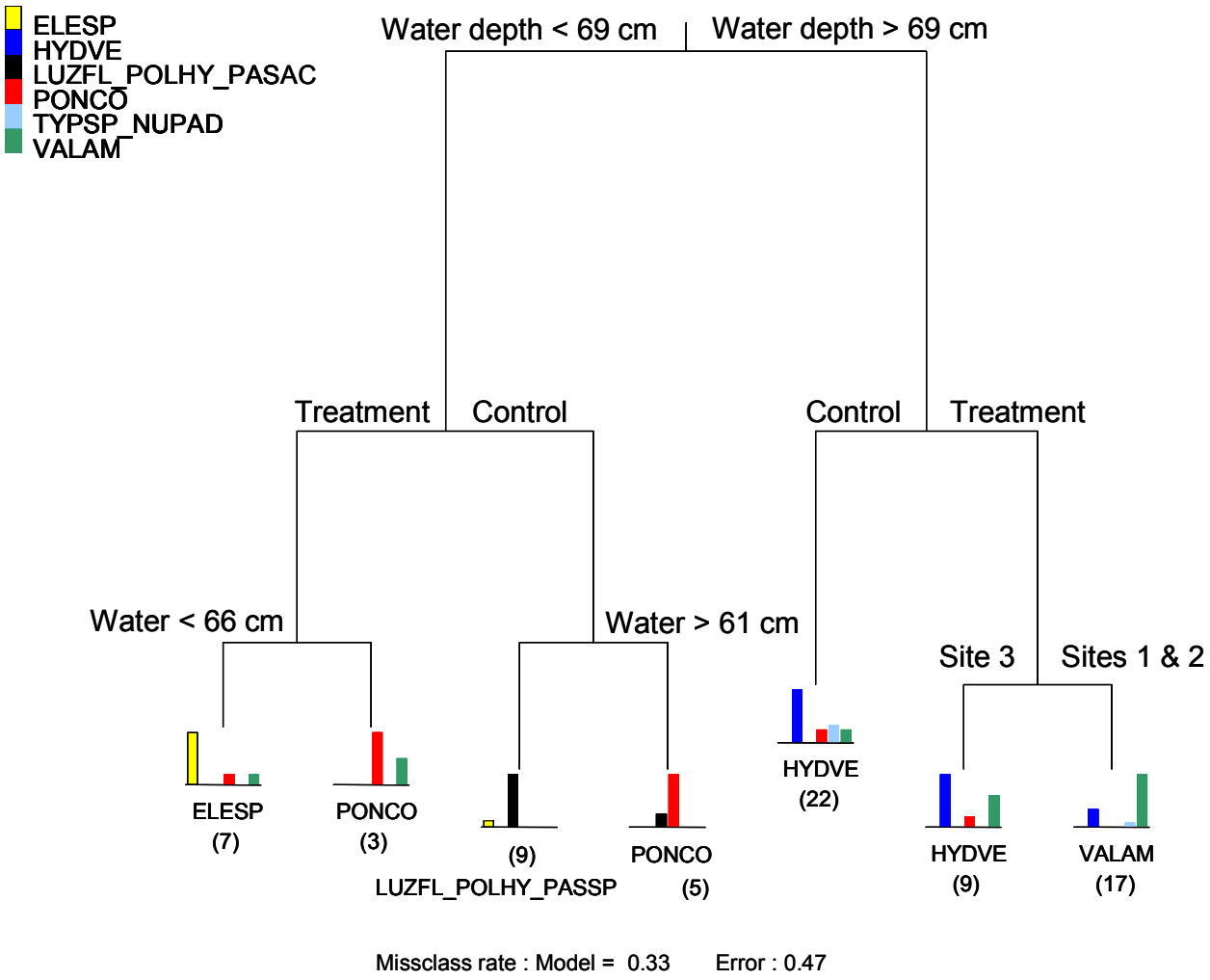

Figure 3-6. CART model of post-treatment community distribution along the measured environmental gradients. The numbers of samples in each leaf are shown in parentheses below each bargraph, which shows the compositions of communities within each leaf. Species abbreviations are the first three letters of genus and first two of specific epithet (PONCO = *Pontederia cordata*).

Discussion

Muck Removal

This project is the first to document littoral vegetation community responses to a mechanical muck removal project, particularly one of this scale. Previous studies have

monitored short-term (two years) changes in species frequencies in treated areas (Moyer et al. 1989), but this paper details vegetation community responses over a longer time frame (four years), establishes recovery rates, and showed how treatment effects vary by water depth. In as little as four years after restoration, I documented that submersed vegetation had replaced dense emergent and floating leaf communities in treated areas, and that the newly established communities showed signs of stabilization, evidenced by smaller changes in community composition between sample periods.

The primary community in the zone targeted for restoration was *Pontederia*, which dominated littoral environments in roughly 30–122 cm in depth prior to treatment. *Typha* stands were scattered at the deeper edge of the *Pontederia* community, and both of these species have been considered to support low diversity, monocultural stands that rapidly accumulate leaf litter, or organic sediment (Hoyer and Canfield 1997). Interestingly, this study found no consistent change in species richness after the treatment, and an actual decrease in the total number of species encountered from 32 to 27. This was primarily due to a loss of rare species or those associated with floating mats of vegetation (*Eupatorium* spp*, Bidens laevis, Scirpus cubensis*), which have been shown to increase species richness in wetlands by providing variably inundated substrates (Cherry and Gough 2006).

Water lilies (*Nuphar, Nymphaea*) were not specifically targeted by the mechanical scraping, but they were largely absent following the several month drawdown, presumably due to drought intolerance. These species and *Typha* are known to be susceptible to periodic drying events (Li et al. 2004, David 1996), and may rebound if

water depths remain similar to pre-treatment levels for a long enough period of time. While not evident here, some populations of water lilies were established by the end of the study outside of sampled areas.

The three communities most affected by the restoration project, *Pontederia*, *Typha*, and water lilies, were completely replaced by submersed communities in all but the shallowest of treated areas. Four years after restoration, *Vallisneria* and *Hydrilla* dominated the deeper scraped sites, with *Vallisneria* forming dense carpets (an average of 634 plants per square meter) on the sandy substrates. This species was present prior to muck removal but was infrequent (Sincock et al. 1957, Moyer et al. 1989), raising concerns about whether its rebound will be limited and if it will be out-competed under sustained pre-restoration hydrologic conditions.

In the shallowest of the study areas, a grassy community dominated by the exotic species *P. repens* replaced *Pontederia*, which resulted in a more similar shoreline to what was described in the 1950's (Sincock et al. 1957). During that period, water levels fluctuated more than two meters during some years, and these large oscillations likely favored the highly invasive exotic, *P. repens*. This species frequently invades disturbed shorelines, and has become problematic in many of Florida's water bodies (Schardt 1997, Smith et al. 2004). The mechanical and drawdown disturbances caused by this restoration project increased *P. repens* biomasses by 140% over a four year period, and expanded its distribution from < 65 cm to < 98 cm in water depth. Future drawdowns or regional droughts might extend the lakeward range of *P. repens* further, which is known to expand during droughts and can tolerate flooding depths > 1m when established (Smith et al. 2004).

Overall, muck removal treatments were most effective in deeper-water communities (70–130 cm), and had longer-lasting impacts on dense emergent or floating mat communities than submersed. For example, emergent species like *Pontederia* that may have been dependent on buoyant, organic mats to survive at these depths will take longer to re-establish than submersed species, and no such recoveries were documented after four years in this study. Control plots were also slow to recover at these depths, but several plots had regained similar species compositions and biomasses within four years of drawdown. The shallowest areas (35–68 cm) studied, however, showed temporary treatment effects at best, with dense emergent communities recovering within three years after muck removal.

Management Implications

Mechanical muck removal is used as a method of setting back soil or shoreline succession; by removing organic substrates and associated nutrients, re-establishing sparse communities of macrophytes, and essentially creating a habitat more indicative of high disturbance conditions. This technique has been used to restore other peatlands where accumulated organics have raised nutrient levels and resulted in losses of diversity (Jacquemart et al. 2003). However, in a lake the size of Tohopekaliga, mechanically removing soils and associated plant communities from 1500 ha of shoreline may not realistically change nutrient concentrations. Half of the seven million cubic meters of material scraped from Toho was redeposited directly within the lake on spoil islands, and water column nutrient levels were unchanged two years after treatment (Hoyer et al. 2008).

In reality, muck removal projects on shallow, eutrophic lakes are likely to cause shifts in the compositions or distributions of dominant vegetation types (at least

temporarily), rather than lower littoral productivity or nutrient concentrations. In order to maintain a diversity of vegetation types and limit the eventual reformation of floating tussock communities, changes in lake stage regulations must be considered. Keddy and Fraser (2000) suggested introducing inter-annual variability in water schedules to maximize shoreline diversity, which would more closely mimic historical conditions on Lake Toho. Even though shoreline developments have lowered the maximum allowable lake stages by almost one meter, incorporating a half-meter of variability between water years might increase the littoral diversity. Generally, lakes with high fertility and low levels of disturbance (stable, predictable water schedules) are dominated by low diversity littoral zones, supporting large stands of nearly monocultural, highly competitive species (Grime 1979), like *Pontederia*. Shoreline diversity can be increased by either lowering fertility or increasing disturbance events, the latter of which could be accomplished through inter-annual stage fluctuations. Point-source pollution was eliminated on Lake Toho in the late 1980's (James et al. 1994), and further reductions in fertility would likely involve addressing non-point source runoff through watershed changes; an extremely difficult task in an urbanized and agricultural landscape. Disturbance related to flooding and drying of littoral communities remains a viable tool in managing shoreline vegetation, and may reduce the need for such large-scale, intensive management projects in the future.

Before applying the results of this project to other large, shallow lakes where muck removal is being considered, several caveats should be addressed. Lake Toho has a significant population of the submersed exotic species *Hydrilla* in deeper areas of the littoral zone, beyond the depths sampled in this study. Without submersed species

stabilizing deeper sediments, drawdowns might increase wind-induced turbulence of the lake bottom; releasing nutrients, decreasing water clarity, and perhaps limiting macrophyte establishment even upon reflooding (Blindow et al 1993). If a large lake already has unconsolidated sediments and deep-water portions that do not support submersed vegetation, low water levels and the removal of shoreline vegetation may cause a shift to a phytoplankton-dominated state (Scheffer et al. 1993). Lake Toho had the lowest amount of submersed vegetation since the 1980's (BIPM 2005) immediately following this restoration, and lower water quality measures for nearly two years. These changes were attributed to tropical disturbances during the reflooding phase of treatment, another caveat in the application of these results to other systems (Ch. 4). Several conditions will likely affect the outcome of mechanical muck removal projects, including lake size, water depth, maximum fetch, nutrient concentrations, and sediment stability, any of which may affect water quality/turbidity and vegetation establishment in treated areas.

Finally, water levels after treatment should be a major focus by management agencies, as hydrology is the primary factor in determining wetland and littoral vegetation (Pearsal 1920, Walker and Coupland 1968, van der Valk and Welling 1988). The treatments in this study were immediately followed by the passing of three major hurricanes, which resulted in high water events for several months following muck removal. Had lake levels risen at a slower rate or oscillated during the early recovery period, entirely different communities may have been established in treated areas (van der Valk 1981). In the case of this study, short-term responses were positive (though different than expected) in that the dense, robust communities that dominated the

shallow littoral zone for over 20 years were replaced with *Vallisneria*, an important species for waterfowl (McAtee 1939, Sculthorpe 1967) and sportfish (Barnett and Schneider 1974), and which allows for better recreational access. Longer-term monitoring is needed in order to asses the persistence or longevity of these treatment effects.

CHAPTER 4
HURRICANE EFFECTS ON A LARGE-SCALE LITTORAL HABITAT RESTORATION PROJECT

Introduction

The importance of water levels in regulating wetland and littoral vegetation communities has long been recognized (Pearsall 1920, Segal 1971). Hydrology is typically the strongest environmental factor controlling wetland plant community composition (Walker and Coupland 1968, van der Valk and Welling 1988), through influencing seed viability (Poiani and Johnson 1989), recruitment (Seabloom et al. 1998), and the growth and survival of adult plants (Squires and van der Valk 1992). The frequency, duration, and seasonality of flooding are therefore critical processes in determining wetland and littoral plant communities (Gasith and Gafny 1990, Keddy 1983), affecting specific diversity and structural complexity of vegetation (Wilson and Keddy 1988, Wilcox and Meeker 1991).

Lake and wetland managers have used water levels to manipulate vegetation communities for decades (e.g. Wegener 1974), but hydrologic schedules are often regulated by anthropogenic needs (flood control, water supply) before ecological effects are considered (Havens and Gawlik 2005). In many temperate reservoir lakes, water levels fluctuate too widely and reduce shoreline diversity, often resulting in unvegetated portions of littoral zone (Hill et al. 1998). In Florida, USA, where many lakes are used for flood control and water supply purposes, water levels can be stabilized from their natural range and often have higher nutrient concentrations as well. A general decrease in specific diversity or structural complexity of communities after water-level stabilization (Keddy 1983) or eutrophication (Seddon 1972, Lachavanne 1985, Harper 1992) has been well documented, and such degradation is often countered with

periodic, infrequent drawdowns in hopes of reestablishing desirable submersed or emergent vegetation communities (Wegener 1974, Havens 2004). Some lakes, most recently and notably Lake Tohopekaliga (hereafter Lake Toho) in central Florida, also have organic sediments and associated vegetation mechanically removed during the drawdown period to aid colonization of desirable species in the absence of competitive dominants (FFWCC 2003). While this effort on Toho was successful in establishing a previously undocumented, novel community in treated areas (see Ch's 2 and 3), the results may have been largely influenced by natural hydrological events following the multi-million dollar project.

Immediately after muck removal was completed and the lake began to fill, three major hurricanes passed within 65 kilometers of Toho, raising water levels 2.5 meters over a four month period to the highest lake stage since 1960 (0.5 m above maximum pool). This prolonged and deep flooding event on the heels of the restoration project likely affected early colonization and subsequent succession in treated areas. For example, without abiotic stressors (e.g. flooding), community composition is determined by dispersal and colonization events (Seabloom et al. 1988), and the order of species arrival at sites has been shown to affect species distributions for some time (Tilman 1997, Grace 1987). If the rate, depth, and duration of flooding caused by hurricanes was sufficient to regulate or even eliminate early colonizers, initial succession would have occurred after normal lake stages were restored, which may have favored the originally established communities that were removed during restoration. Without any knowledge of how these hurricanes may have affected succession and the overall outcome of this project, it would be difficult to apply these results to other projects on

similar lakes. The goal of this paper was to determine the impacts that natural disturbances may have had on this intensive restoration effort. Specifically, I asked: 1) Whether initial colonization compositions differed from those after the hurricanes, and 2) Whether the eventual dominant species were a result of the high-water events. These results are important for managers to understand the efficacy of this relatively new restoration approach, and serve as an important reminder that outcomes of large-scale projects may depend heavily on uncontrollable, external influences.

Methods

Mechanical muck removal began in late spring of 2004 after water levels reached a low of 14.9 m (NGVD), or approximately 1.0 m below normal low pool stage. The project was completed by June 2004, at which point water depths were slowly increased to regular stage levels. Standing, above ground, vegetation biomass and stem density measurements were collected from 0.25 m^2 quadrats in late August 2004, December 2004, and in the summer and winter of each year after until June 2008. Samples were collected late in the summer of 2004 (August), anticipating water levels would be near normal lake stages and initial succession or colonization would have taken place in scraped areas prior to sampling.

One hurricane passed over the lake in mid August (2004), which doubled the rate of water level rise over the second half of the month and brought the lake close to maximum stage by the time of the first sample (Figure 4-1). Two more major hurricanes passed in September and October of 2004, further increasing lake stages to 0.5 m above full pool, the highest level recorded since 1960. Lake levels remained at or above maximum stage for seven months, from September 2004 until the end of March 2005. Lake stage data were collected from a South Florida Water Management District

gauge located at the south end of the lake (S-61H). Visual assessments of wind/wave damage were conducted after the last hurricane passed, and other studies documented changes in water quality (Hoyer et al. 2008).

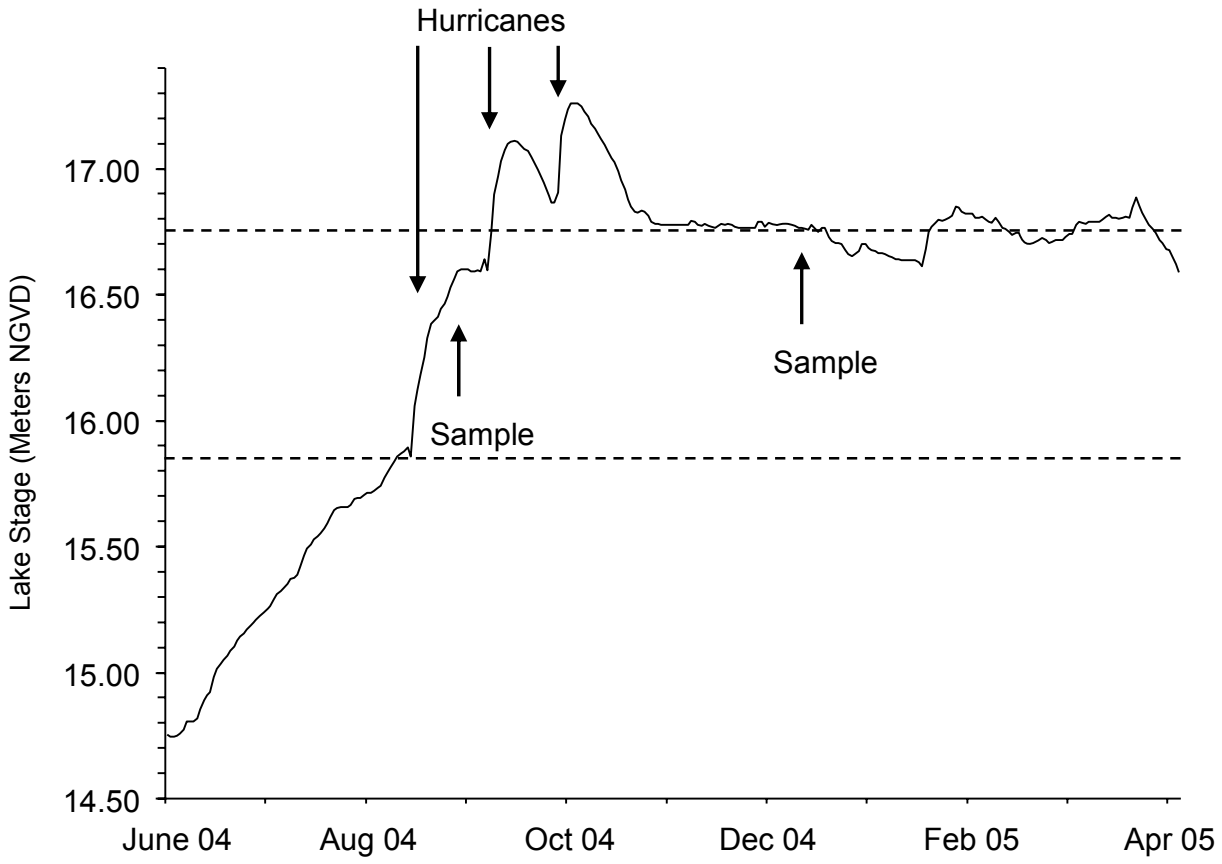

Figure 4-1. Lake stages (meters above sea level NGVD) following the managed dry down in summer of 2004. Dotted lines indicate normal maximum and minimum lake regulation schedules, and the first two sample periods of early colonizers are depicted on the graph.

Vegetation data were used from two other studies designed to assess littoral vegetation responses to the muck removal project. They were: 1) an experimental study where sampling was restricted to water depth zones that were mechanically scraped, and study sites consisted of treated (scraped) and control (unscraped) plots (see Ch. 3), and 2) a lake-wide study where sampling occurred throughout the range of

emergent littoral zone, including areas too deep for bulldozers to access (145–200 cm) (see Ch. 2). Sampling methodologies in these studies differed only in that oven-dried biomasses were recorded in the former and wet biomasses in the latter. Sampling was stratified by depth category at each site, and several subsamples were collected within each stratification. Species data were summed across subsamples within each stratification, and unless otherwise noted, averaged across sites for each time period. Bare ground (empty) samples were counted individually across all stratifications. Biannual samples were also collected for two years prior to muck removal.

Hydroperiods were calculated for samples based on the average number of days flooded per year from 1993 through 2002, a ten year period of hydrologic record immediately preceding sampling. This period was representative of the typical annual lake stage regulation schedules, absent artificial dry-downs that occurred in 1987 and 2004.

Results

Dominant species biomasses were averaged across sites for the first four sample periods following muck removal to evaluate initial site colonization. In the experimental study sites, *Paspalidium geminatum* had the highest biomass and stem counts of all species in treated plots immediately after reflooding in August 2004 (Figure 4-2). Other prominent species in scraped areas were *Pontederia cordata, Panicum repens, Polygonum hydropiperoides*, and *Alternanthera philoxeroides*. These same species were recorded in the control sites but with different relative abundances, with *Pontederia, Polygonum*, and *Alternanthera* dominating unscraped sections of shoreline (Figure 4-3). Following the hurricanes, all biomass was severely reduced in both control

and treated plots, and only *Pontederia* and *P. repens* had recovered to initial levels in either plot by the following December (2005).

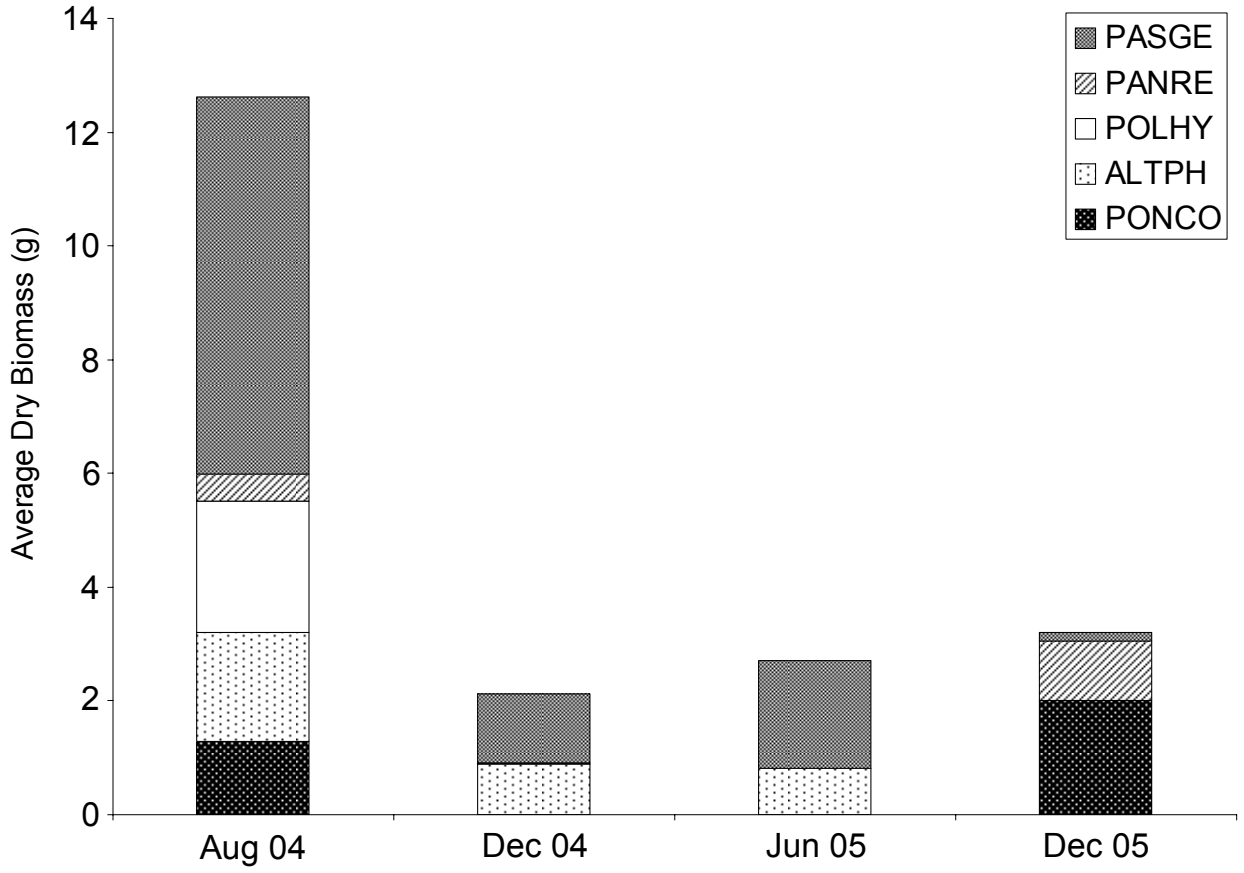

Figure 4-2. Initial relative abundances of dominant species in scraped experimental plots. Dry biomasses (g) were averaged across water depths and sites for each species. Species were coded as the first three letters of genus and the first two of specific epithet (e.g. ALTPH = *Alternanthera philoxeroides*).

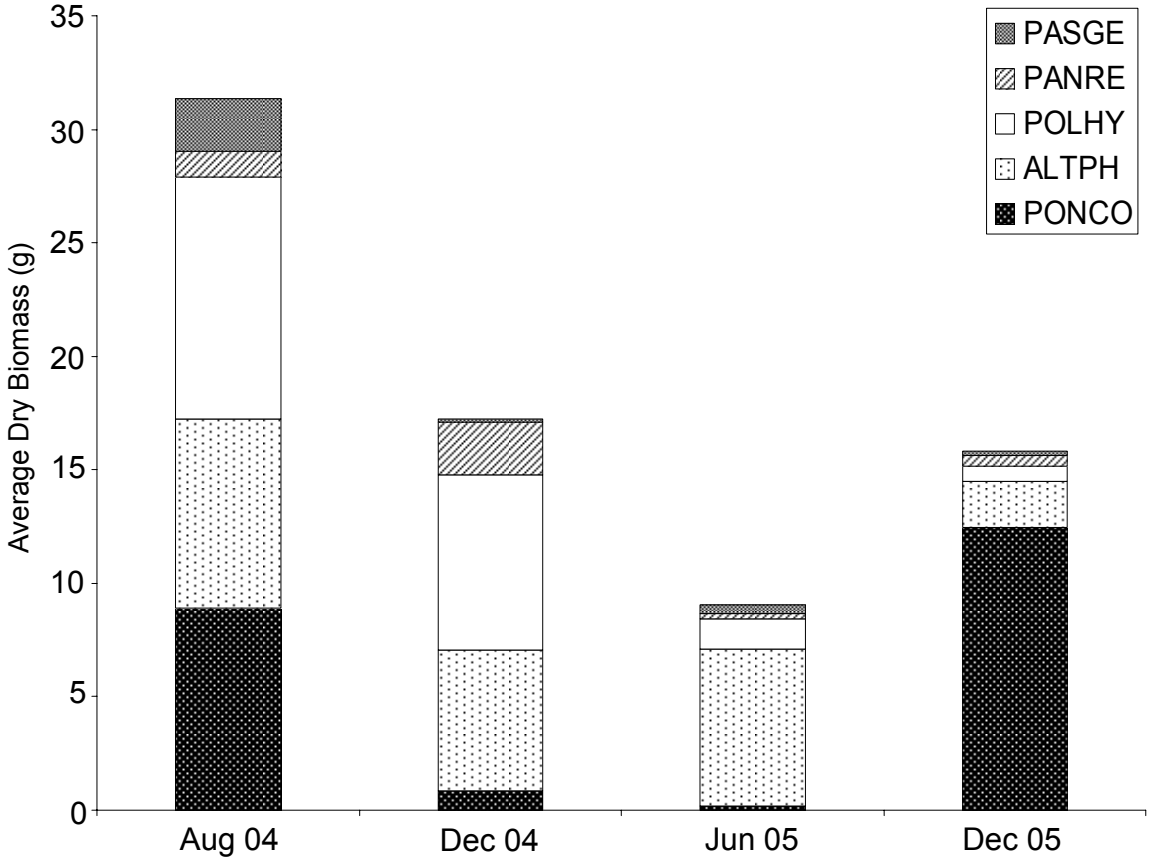

Figure 4-3. Initial relative abundances of dominant species in control (unscraped) experimental plots. Dry biomasses (g) were averaged across water depths and sites for each species. Species were coded as the first three letters of genus and the first two of specific epithet (e.g. PANRE = *Panicum repens*).

The shallower, scraped sections of the lake-wide study sites responded similarly to the experimental treatment plots, with original colonizers including *P. geminatum* and *Pontederia*. Other dominant species differed, however, with these sites having *Hydrilla verticillata*, *Eleocharis* spp., and *Paspalum acuminatum* (Figure 4-4). Following the hurricanes, there were massive declines in all biomasses, and only *Pontederia, P. geminatum*, and *Hydrilla* had recovered in the scraped areas by the following December (2005).

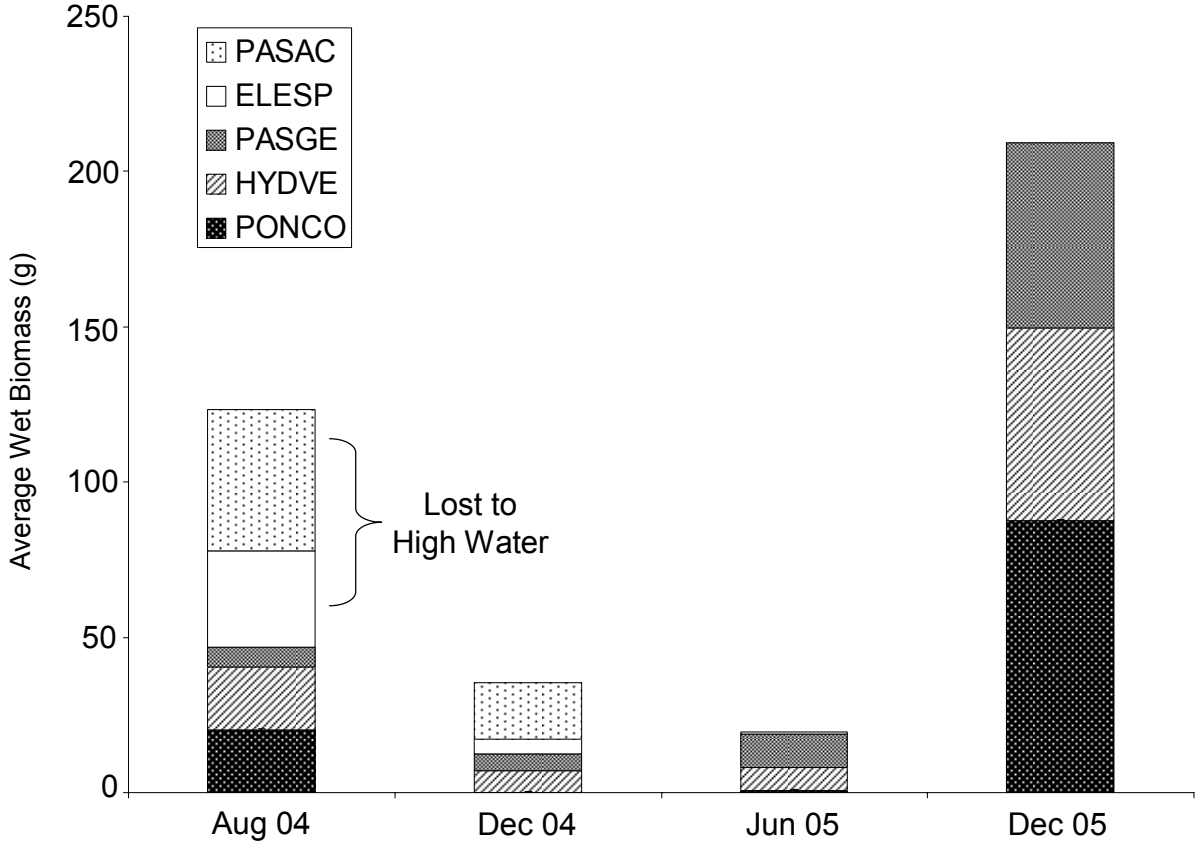

Figure 4-4. Initial species compositions of dominant species in scraped sections of lake-wide study sites. Wet biomasses (g) were averaged across water depths and sites for each species. Species were coded as the first three letters of genus and the first two of specific epithet (e.g. PASAC = *Paspalidium acuminatum*).

Total species biomass across all lake-wide sites declined considerably after the hurricanes as well, particularly in the shallower scraped areas (Figure 4-5). However, even the deeper-water, unscraped sections of littoral zone had massive losses in biomass, reaching their lowest levels of the study between June and December of 2005.

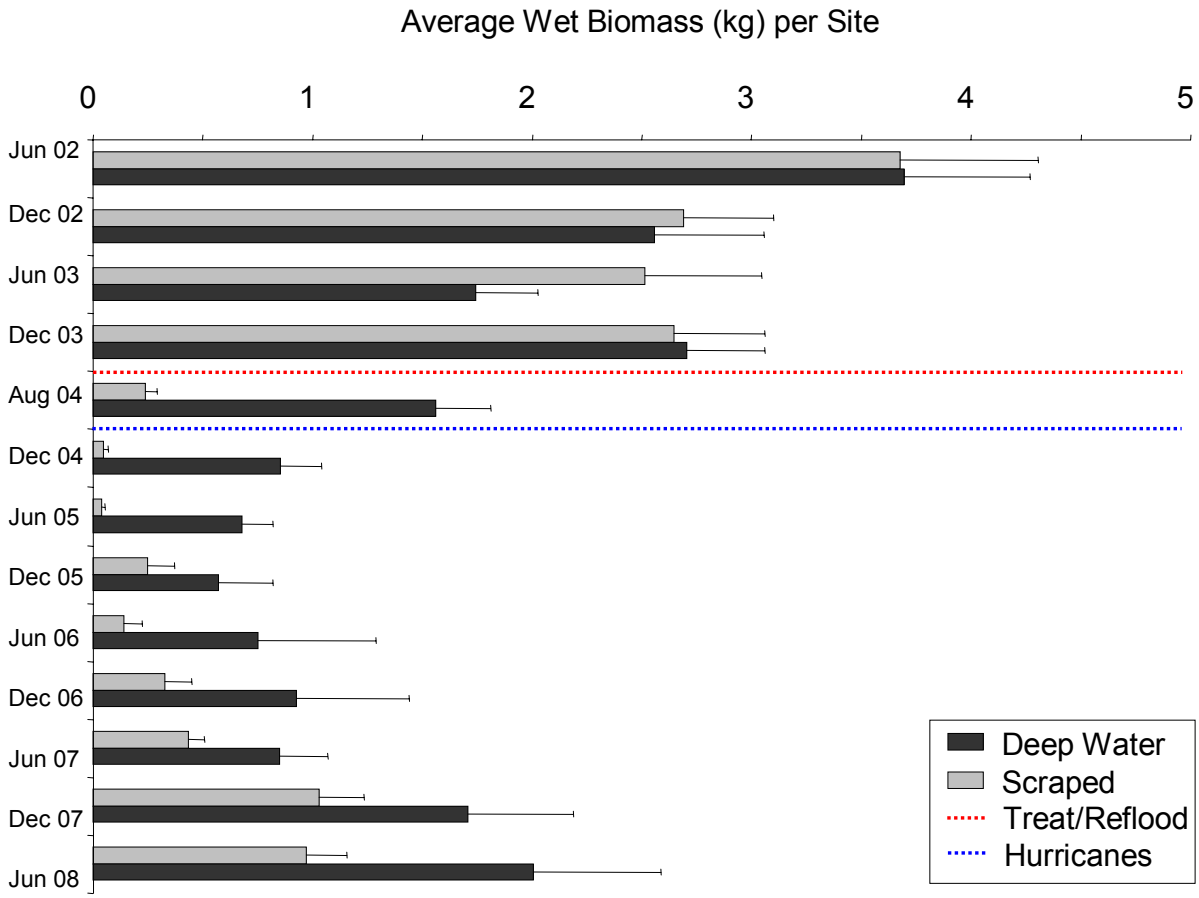

Figure 4-5. Average wet biomass per site (kg) of all species in the shallow, scraped (gray) and deeper water, unscraped (black) sections of the lake-wide study sites. Standard errors of the means are shown above each bar, and the cessation of treatment and resumption of water levels is indicated in red.

Most species were reduced in biomass either from the mechanical removal or desiccation during the dry down, except for *P. geminatum* and *P. acuminatum.* The latter increased in biomass and abundance considerably before the hurricanes, though it was never found at high abundance prior to treatment (Figure 4-6). *P. geminatum* was abundant throughout the study, and also had its highest biomass immediately following treatment. The vast majority of the increased biomass was from deeper-water areas where mechanical scraping did not occur, where *P. geminatum* was already well established (Figure 4-6).

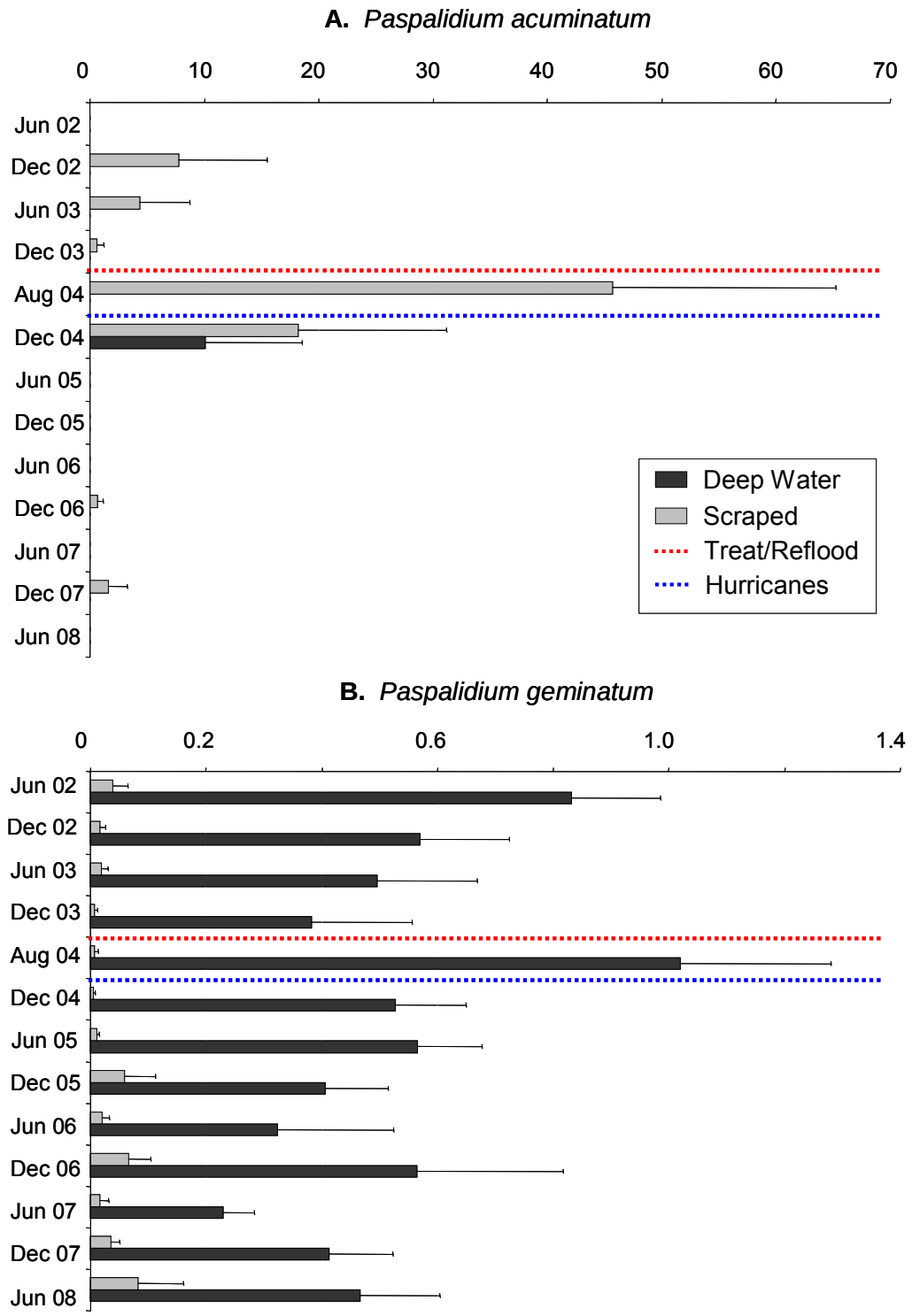

Figure 4-6. Average wet biomass per site of A) *P. acuminatum* (grams) in the shallow, scraped (gray) and deeper water, unscraped (black) sections of the lake-wide study sites, and B) *P. geminatum* (kilograms). Standard errors of the means are shown above each bar, and the cessation of treatment and resumption of water levels is indicated in red.

Following the hurricanes and high water, *P. acuminatum* was never recorded in the deeper, unscraped sections of the lake-wide study again, and was only occasionally found at low levels in the shallower, scraped areas. This species was found in low abundances both before and after treatment in the scraped sections of experimental plots, however, and at occasionally higher abundances throughout the study in control plots (Figure 4-7).

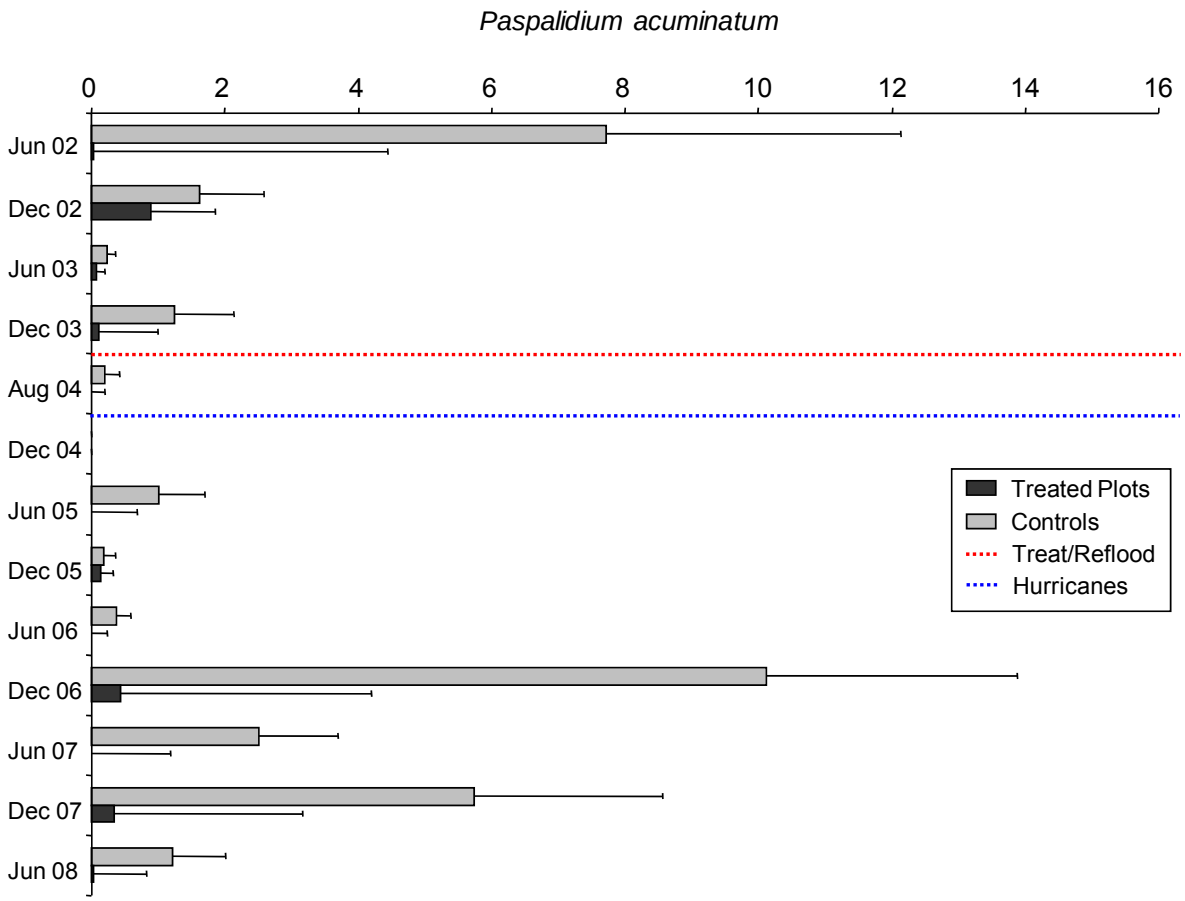

Figure 4-7. Average dry biomass per site (g) of *P. acuminatum* in control (gray) and treated (black) sections of experimental plots. Standard errors of the means are shown above each bar, and the cessation of treatment and resumption of water levels is indicated in red.

P. geminatum lost considerable biomass in the unscraped, deeper-water sections after the hurricanes, essentially all that was gained during the brief dry down. Biomass remained very similar to pre-treatment levels throughout the study period, however. In

the shallower, scraped sections, *P. geminatum* was at higher levels by the end of the study than occurred pre-treatment, but still well below its deep water populations.

The only species that was not recorded after initial colonization in the scraped plots of experimental study sites was *Polygonum hydropiperoides*, though its biomass increased in the control plots. All other species that initially colonized the treated plots were found later in the study period. *Polygonum* was found throughout the study in the shallower, scraped sections of lake-wide sites.

The number of empty samples (no species) increased dramatically after the hurricanes in all sites, including the control plots in the experimental study (Figure 4-8). Generally, the number of empty quadrats was low in all control and treated plots in August 2004, even though scraping had occurred and the lake had been reflooded. Following high water and two additional hurricanes, however, the number of empty samples increased in all sites and depth zones, including the controls. Empty quadrats reached a high in all study areas roughly one year after the hurricanes (December 2005), with the exception of the 102–135 cm depth zone in experimental plots. Both the treated and control plots had the highest number of un-occupied samples in June of 2006, (83% and 67% respectively) two years after treatment.

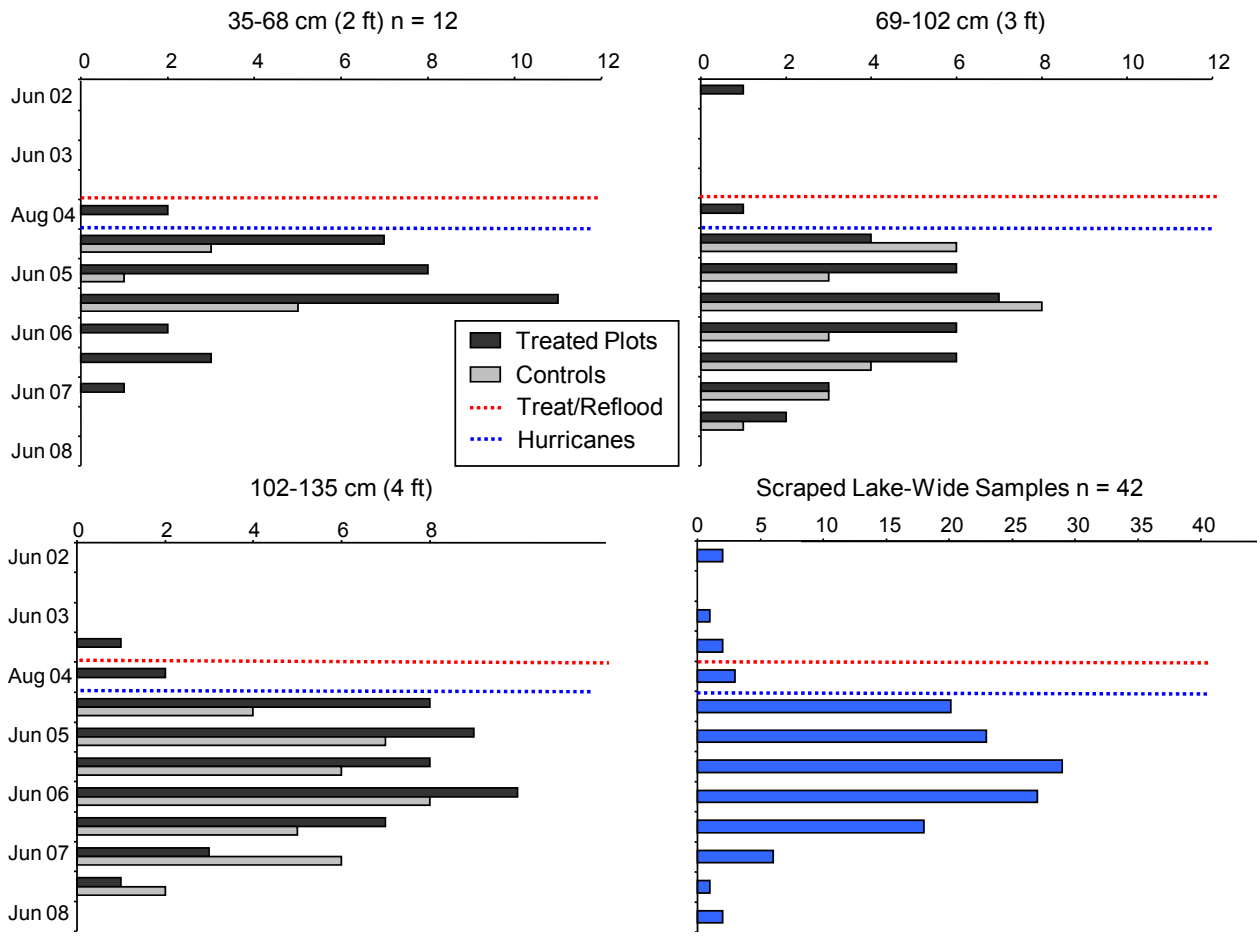

Figure 4-8. Number of empty samples in experimental plots (gray and black) and lake-wide study sites. Cessation of treatment and resumption of normal water levels are indicated in red.

Re-colonization of scraped areas (after hurricanes) in the lake-wide study generally did not take place until after December 2006, more than two years after muck removal was completed. Total biomass of all dominant species increased dramatically beginning in June 2007, as did *Vallisneria americana* (Figure 4-9), the eventual dominant species in all scraped areas of the lake (Ch's 2 and 3). Together with *Hydrilla* and *P. repens*, these three species comprised 70–80% of the dominant species' total biomass from June 2007 through June 2008 (Figure 4-10) in treated areas, with *P. geminatum* and *Pontederia* rounding out the main dominants.

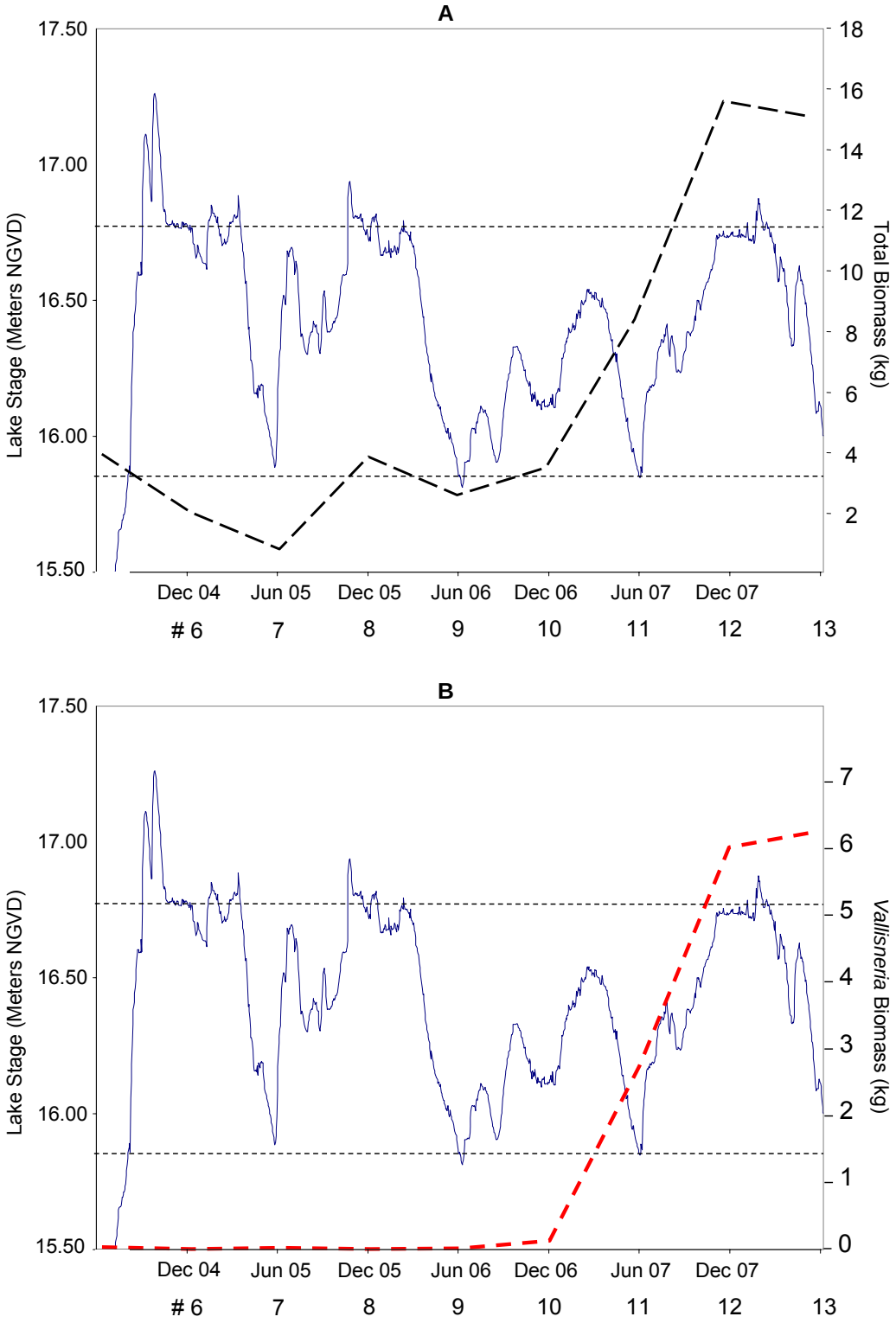

Figure 4-9. Average daily lake stage (meters NGVD) with horizontal dashed lines representing normal maximum and minimum lake stages. A) Total wet biomass (kg) of all species shown in dashed black line for each sample event B) *Vallisneria americana* biomass (kg) shown as red dashed line.

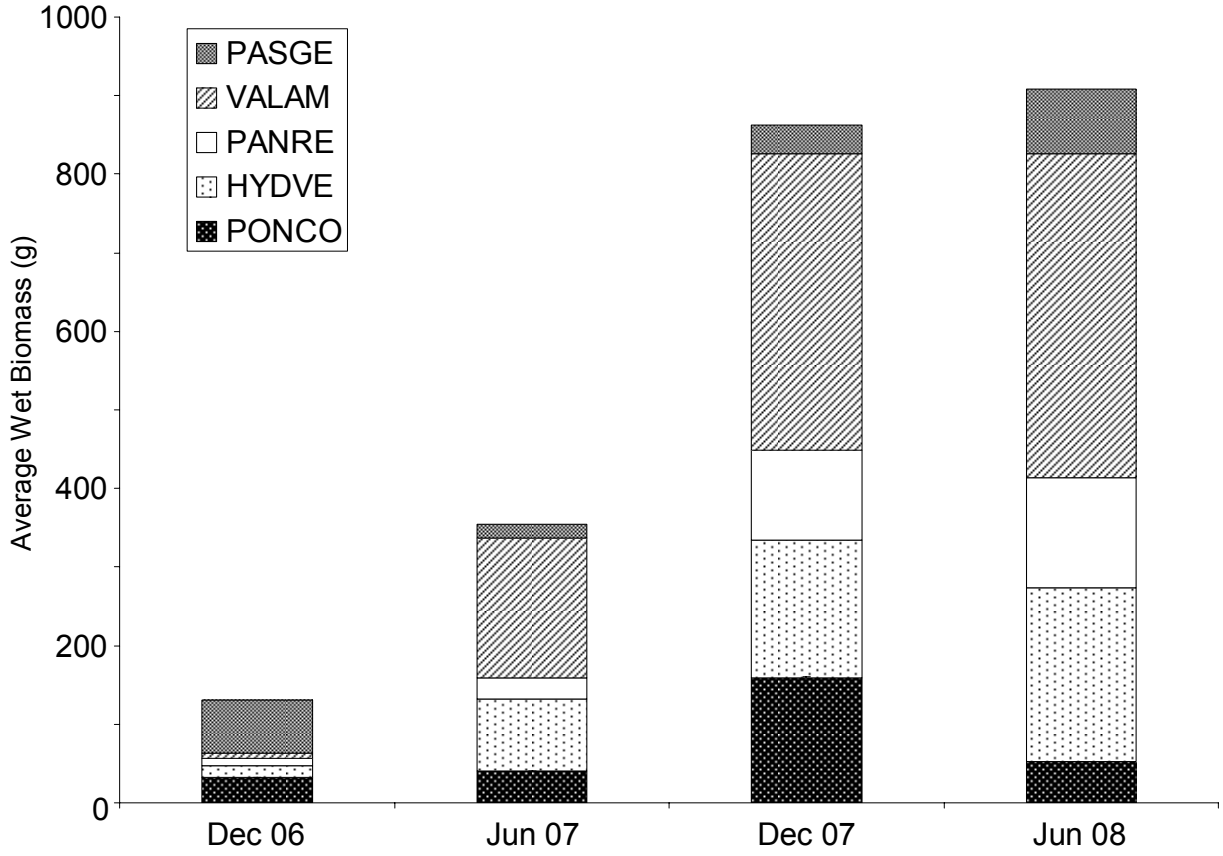

Figure 4-10. Average wet biomass (g) of the five dominant species at the end of the study in the lake-wide sites. Species were coded as the first three letters of genus and the first two of specific epithet (e.g. PASGE = *Paspalidium geminatum*).

Compositions in the experimental plots were very similar to the lake-wide sites by the end of the study, dominated by *Vallisneria*, *P. repens*, *Hydrilla*, and *Pontederia*, though *Eleocharis.* replaced *P. geminatum* in the top five at these sites (Figure 4-11). The control plots were quite different, with *Pontederia* and *Hydrilla* sharing dominance with *Typha*, *Luziola fluitans*, and *Polygonum* (Figure 4-11).

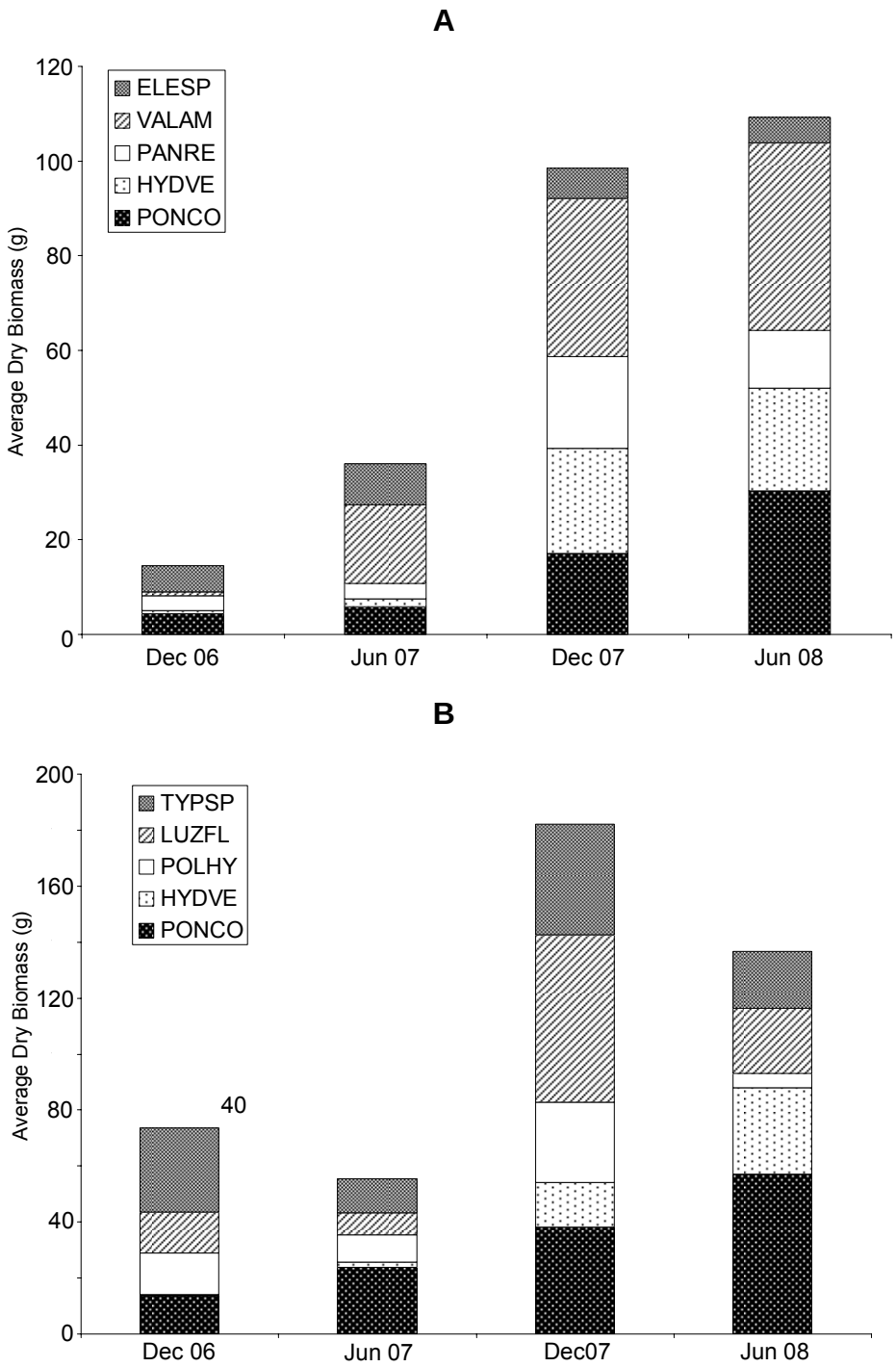

Figure 4-11. Average dry biomass (g) of the five dominant species at the end of the study in the A) treated plots and B) control plots of the experimental study sites. Species were coded as the first three letters of genus and the first two of specific epithet (e.g. ELESP = *Eleocharis* spp.).

The average number of *Vallisneria* plants per square meter during the last sample period was plotted against corresponding hydroperiods for various depth categories of samples. These hydroperiods were calculated based on the 10 year period of record from 1993 to 2002. Assuming lake stages return to the same schedule adhered to prior to restoration, the majority of the depths *Vallisneria* was found in would be flooded less than 95% of the year (Figure 4-12).

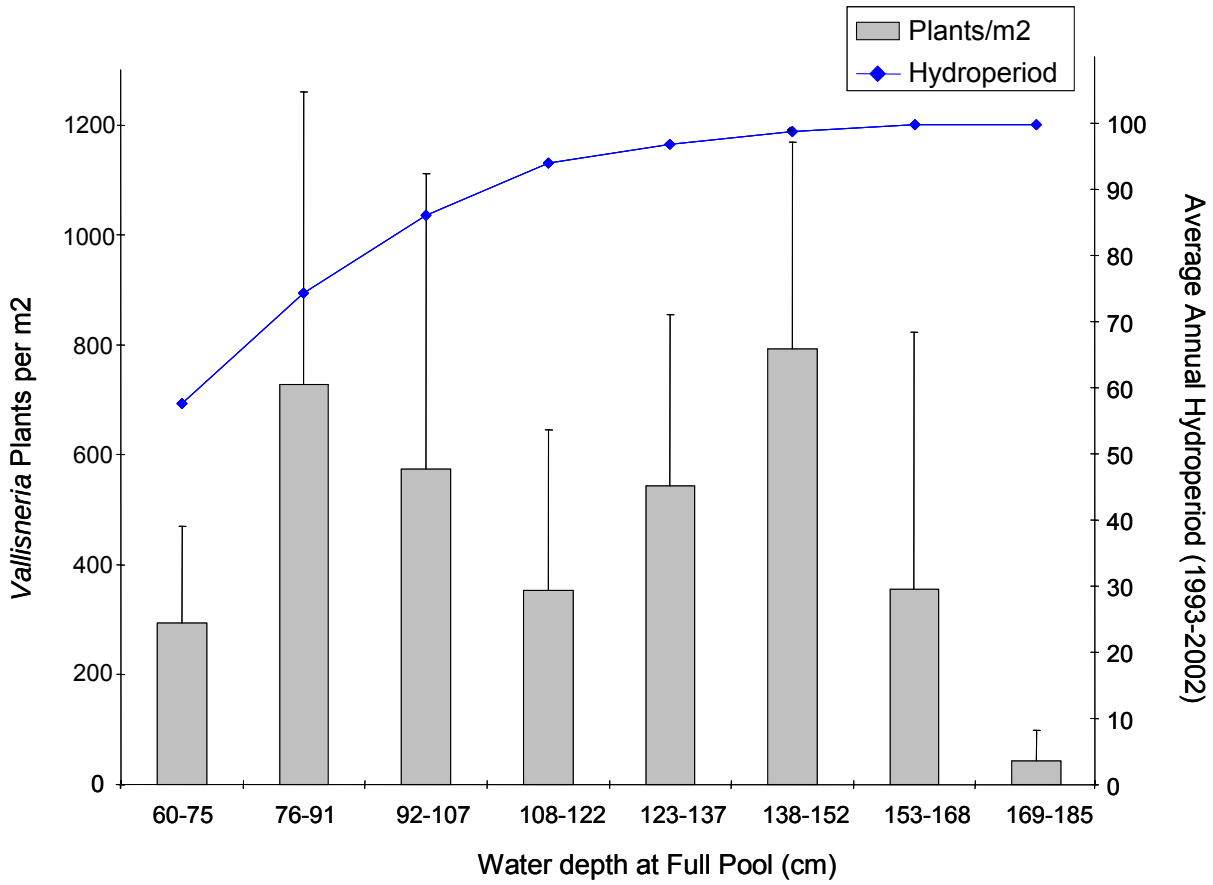

Figure 4-12. Average number of *Vallisneria* plants (per m^2) across all samples, including experimental and lake-wide study sites. The blue line represents the average annual hydroperiod from 1993 to 2002 for each depth bin.

Discussion

Generally, lakes with highly productive, stable environments promote high biomass, broad-leaf species with slow generation times and the capacity for vegetative spread (Day et al. 1988, Wisheu and Keddy 1992). These communities are typically dominated by a few competitive species and have lower diversity littoral zones, quite similar to the *Pontederia*-dominated shoreline that occurred on Lake Toho prior to treatment. Lake drawdowns in Florida are generally performed to allow germination and expansion of desirable grassy species into these mono-cultural habitats, which is important to their persistence under stabilized water levels (Moyer et al. 1989). After the treatment and reflooding of Lake Toho that took place in late summer of 2004, there was substantial colonization of several grassy and ruderal species in scraped areas, including *P. acuminatum*, *P. geminatum*, and *Eleocharis* spp. However, other species typically associated with the pre-treatment, degraded conditions were also present, including *Hydrilla, Pontederia*, *Alternanthera*, and *Polygonum.*

The hurricanes and associated high water essentially removed the earliest colonizers; there was an average of only 3 g of dry biomass and 40 g of wet biomass collected across entire scraped study sites the following growing season (June 2005). The species described as early colonizers were typically small, newly sprouted individuals that had low biomass and higher densities, though there was still an additional 80% biomass reduction in all scraped areas less than a year after the hurricanes passed. All of the first colonizing species were reduced in abundance or eliminated entirely within that period. However, those same species were found again at greater abundances later in the study period, with the exception of one; *P. acuminatum*. This species had the highest initial biomass of those found in the lake-

wide study sites, and a density of roughly 60 plants per square meter. After the hurricanes that density was reduced to 9 per square meter, and it was rarely collected from those sites after.

This species was also found in the experimental plots, but infrequently and with low abundance relative to common species. There was no increase in densities or biomass in treated plots like there was in the lake-wide studies, but its biomass was still reduced after the hurricanes. However, it was found later in both control and treated plots at the same low same low frequency and abundance that it had prior to treatment. This indicates that the increases recorded in the lake-wide sites were somewhat of a patchy event, and indeed occurred in only three of the five sites. At least one other study documented an increase in *P. acuminatum* following low water events in Florida lakes (Havens 2005), but this is generally not a dominant shoreline species in the region. Several local wetland flora books and regional plant I.D. websites do not list the species, further suggesting its local infrequency.

While it is unknown whether this species could have remained at least locally abundant in shallow, scraped sections of shoreline if the hurricanes had not passed, it seems probable that other regionally dominant species, specifically invasive exotic grasses like *P. repens*, would have replaced it. By the end of the study *P. repens* dominated all scraped plots in both the experimental and lake-wide study areas. This species typically colonizes disturbed sites and is very problematic in many of Florida's water bodies, having displaced thousands of acres of native marsh in other systems following droughts or low water events (Smith et al. 2004). Given the potential for *P. repens* to invade and persist in disturbed areas, as well as the fact it has been common

on Lake Toho since the earliest vegetation studies (Sincock et al. 1957, Holcomb and Wegener 1971, Moyer et al. 1989), it seems unlikely that *P. acuminatum*, a relatively infrequent species in the region would have remained abundant for long.

One of the biggest impacts of the hurricanes may have taken place at depths beyond where scraping took place, where *P. geminatum* was the most common and abundant species. Like most grasses, this species germinates during low water periods (Johnson et al. 2007.) and is typically found on Toho and other regional lakes at depths concurrent with previous drawdowns. It was predicted that *P. geminatum* would expand shoreward after organic substrates and dense competitors were removed (see http://aquat1.ifas.ufl.edu/guide/laketoho.html for project details), and *P. geminatum* was one of the few species to substantially increase in biomass immediately after the treatment (primarily in deeper, unscraped areas). It was also one of the early colonizers of treated shorelines and one of the first to recover following hurricane damage. However, the biomass increase from germination in deeper areas was immediately lost after the hurricanes, presumably because the dense, new growth could not withstand the high winds or water levels. Visual observations following the hurricanes confirmed the biomass reductions shown in the samples, as most shorelines had *P. geminatum* wrack deposited at the high water line.

Even after a nearly 50% reduction in biomass, *P. geminatum* abundance was still well within pre-treatment levels directly after the hurricanes and throughout the remainder of the study. There likely would have been much higher densities and possibly an expansion into previously uninhabited areas if the newly germinated plants could have survived rising water levels. For example, most of the lily pad communities

(*Nuphar advena* and *Nymphaea odorata*) were largely eliminated from the scraped and deeper water sections of shoreline, presumably due to desiccation and rapid water level increases (Ch. 2). It seems reasonable that the dry down expansion of *P. geminatum* into those areas previously occupied by dense floating leaf communities could have remained for some time.

Overall, the initial composition of early site colonizers did not appear to change much after the hurricanes. Early growth was severely limited due to high water, but the initially dominant species all recovered biomass after successive years of normal lake stages. The compositions found after nearly four years of post-treatment succession did not begin to take form until after the pre-hurricane colonizers had recovered. For example, *P. geminatum, Pontederia, Eleocharis, Hydrilla, Polygonum*, and *Alternanthera* were all dominant species initially, and were again dominant two growing seasons after the hurricanes passed (June 2006). Beginning in December of 2006, *Vallisneria* and *P. repens* became increasingly dominant. In other words, the 'final' composition documented at the end of the study formed after the initial colonizers were already in place.

It seems reasonable that if water levels had followed normal lake regulation schedules after the treatment, the same pattern of site colonization would have taken place, but most likely a year or two sooner. There most likely would have been more *P. geminatum*, particularly in the deeper unscraped areas, but given that fierce competitors like *Pontederia* and *P. repens* were among the early colonizers of scraped areas, it seems that the same succession pattern would have taken place at a more rapid pace. These were the results in a previous, small-scale muck removal on Lake Toho, where

within two years of treatment *Pontederia, Alternanthera*, *Hydrilla*, *P. repens* and *Eleocharis* were again among the most dominant species (Moyer et al. 1989).

These results also fit wetland community succession models, where, following drawdowns, perennial communities rapidly reestablish once original water levels are returned (Seabloom et al. 2001). Conversely, this rate of establishment has been linked to the level of flooding (deviation from normal) during the recovery period. If the normal annual lake stages had been restored immediately following restoration, it seems likely that the previously dominant species would have had the advantage.

The succession studies and models predicting rapid recovery assume adequate propagule availability, however, and this may not be the case in this study. When original communities fail to reestablish, dispersal capabilities or propagule availability are typically a limiting factor (Ellison and Bedford 1995), or conditions may have changed such that the original cohorts can no longer persist at the site (Turner et al. 1998). The restoration project on Lake Toho probably falls somewhere in between these two scenarios, as sediment characteristics were altered, water depths were slightly increased, and the seedbank was at least severely disturbed, if not relocated entirely. However, half of the sediment and/or vegetation that were removed form the shoreline was deposited back into the shallow littoral zone on spoil islands, and only about half of the emergent littoral zone was scraped (the shallower half, 45–135 cm). While seed availability and vegetative regeneration were surely limited following the treatment, it seems reasonable that all of the original species were still within dispersal range of the scraped sites. Given that adult plants were removed, initial succession would most likely have been driven by germination and dispersal limitations instead of

clonal or rhizomatous spreading. However, the close proximity of available propagules, similar species pool, and the inevitable return of stable hydrologic conditions will most likely favor reestablishment of the original communities eventually.

The major surprise in this project was the invasion and at least short-term persistence of a previously rare species on Lake Toho, *Vallisneria*. This submersed species rapidly expanded in areas of another regional lake (Okeechobee) following low water periods, and apparently is capable of displacing some submersed species under the right conditions (Havens et al. 2004). *Vallisneria* and most other species did not rapidly expand until unusually low winter water levels in 2006, after which the current dominant species increased dramatically. This may have been due to high turbidity and low water quality that persisted in the lake for up to two years following the hurricanes (Hoyer et al. 2008), presumably from flushing surrounding agricultural lands and a massive decline in macrophyte abundance after the treatment. While *Vallisneria* is fairly tolerant of low light conditions, it has higher light requirements for early growth than it does for germination (Kimber et al. 1995). It is possible that extended low winter water levels during 2006 aided in the expansion of *Vallisneria* from deeper water, unscraped habitats.

The communities found after four years of succession were likely a result of recent hydrological conditions, as well as dispersal capabilities. Two of the top four species were invasive exotics, apparently displacing slower growing, broad leaf emergents like *Pontederia* for the time being. However, the dominance of submersed species, both *Vallisneria* and *Hydrilla* in scraped areas, is likely due to higher water levels in general following the treatment. More than half of the areas occupied by *Vallisneria* have an

annual hydroperiod < 95% under current lake regulations, elevations typically occupied by emergent species. Had water levels been held below maximum or at minimum lake stage for a full growing season after the restoration, there likely would have been much less submersed species and a more rapid expansion of aggressive emergents, like *Pontederia* and *P. repens*. While prolonged high water and increased turbidity from the hurricanes undoubtedly affected early colonizers, the communities found at the end of this study seemed to be a result of several growing season hydrologies. Keeping water levels lower for a full growing season after the enhancement project likely would have promoted more *P. geminatum* in scraped areas, but substantially less *Vallisneria.* As many studies have shown, the hydrologic regime during colonization/germination of wetland soils will has a large impact on initial community composition (van der Valk 1981, Seabloom et al. 1998), but ultimately species distributions will be based on flooding tolerances (Squires and van der Valk 1992). Without changes to annual lake schedules, the communities that succeed after such large-scale lake restoration projects will likely be very similar to pre-treatment compositions once initial dispersal limitations are overcome.

CHAPTER 5
DISCUSSION

Review

This study was the most thorough documentation of littoral vegetation responses to mechanical muck removal, particularly on this scale of application. Previous studies monitored short-term (two years) changes in species frequencies in scraped areas after treatment (Moyer et al. 1989), but this paper details vegetation changes over a longer time frame (four years), includes pre-treatment descriptions, and monitors shifts in distributions along a water depth gradient.

The overall success of this restoration project was mixed, in that specified compositions were not achieved, but desired habitat characteristics were. The FFWCC predicted that over time healthy stands of knotgrasses (more commonly known as *P. geminatum*), bulrushes (*Scirpus californicus*), and eelgrass (*Vallisneria*), among other 'desirable species', would rebound from the seedbanks as workers managed against problematic species (http://aquat1.ifas.ufl.edu/guide/laketoho.html).

The primary community, or "problematic species" targeted by the restoration was *Pontederia*, which I found dominated in roughly 30–122 cm in water depth prior to treatment, with *Alternanthera* identified as another strong indicator for this community. Shoreward of this group was a mixture of *Luziola, P. repens,* and *Eleocharis*, all of which have been found at varying frequencies since the 1950's (Sincock et al. 1957, Holcomb and Wegener 1971, Moyer et al. 1989).

The deepest water edge of the *Pontederia/Alternanthera* community was bordered by occasional floating mats, including *Hydrocotyle*, *Lymnobium,* and *Eichhornia,* indicating an abrupt shift from dense emergent communities to deeper-water habitats.

These were the communities believed to form an organic, floating barrier to fish attempting to access shallow spawning areas (Moyer et al. 1989). Based on a 10 yr period of stage records (1993–2002) the lakeward extent of the dominant *Pontederia* zone extended just beyond the annual minimum water depths.

Typha stands were scattered along the deepest edge of this community, as cattails generally benefit from several centimeters of flooding for germination, but not complete exposure during annual lows (Johnson et al. 2007). Beyond the 100% hydroperiod zone there were water lily communities, primarily *Nuphar* and *Nymphaea*, while *Hydrilla* and *P. geminatum* dominated the deepest portions of the emergent littoral zone.

Soil organic content was highly variable before lake restoration, ranging anywhere from 2% to 96% in the top 10 cm of substrate, with a mean of 33% across plots and a median of only 11%. These numbers dropped to barely detectable levels four years after treatment (< 2%), but were even significantly reduced in control plots (mean 15%, median 4%). While peat depths were not actually measured, the soil corer generally reached a sand or silt substrate underneath the organic layer while sampling, which often occurred before 10 cm and made core retrieval more difficult. There were few instances where the amount of peat or organic material exceeded 10 cm, though samples from a cove and floating mat exceeded 20 cm on a few occasions.

Overall, the objective of removing existing plant monocultures and associated organic material was achieved, though there was only a slight rise in the effective number of species in scraped areas after restoration (5.3 to 6.2). However, given the loss of water lily communities from deeper, unscraped areas, the total effective species

for the emergent littoral zone dropped from 7.9 to 5.5 after restoration. It is unclear what role the hurricanes may have played in eliminating deeper water *Typha* and water lily communities.

The dense *Pontederia* community was primarily replaced by *P. repens* in the shallowest sections of shoreline (< 98 cm), and by *Vallisneria* in the deeper areas. Historically, *P. repens* was the most frequently occurring species along study transects, occupying nearly the same elevations *Pontederia* did due to greater shoreline fluctuations (Sincock et al. 1957). However, *Vallisneria* was very infrequent in early studies, and Lake Toho was described as having too low an alkalinity to support much submersed vegetation (Sincock et al. 1957).

While the replacement of *Pontederia* with *P. repens* in shallow water does more closely resemble pre-regulation (historic?) shorelines, the expansion of *Vallisneria* was unprecedented in this system. Havens et al. (2004) documented a recovery of *Vallisneria* following low water on Lake Okeechobee, but this presumably occurred from existing seedbanks and was accompanied by a rebound of *Potomageton* and *Hydrilla* as well. The seedbank was largely removed or at least severely disturbed on Toho following muck removal, and *Vallisneria* was rarely seen prior to treatment (Moyer et al. 1989), indicating a possible rapid expansion from isolated, deeper-water patches. This suggests that while *Vallisneria* remained on the lake for over 50 years, it was apparently a poor competitor under both historic and pre-treatment conditions, never being more than infrequently recorded. The question is, was establishment the only factor limiting its distribution, and can it continue to occupy large areas under the same environmental conditions and species associations as before?

P. geminatum was predicted to be the major benefactor of this restoration, including expansion into areas previously occupied by *Pontederia* (http://aquat1.ifas.ufl.edu/guide/laketoho.html). This species began establishing in scraped areas immediately after muck removal but was reduced in abundance following major hurricanes in 2004. There were substantial increases in deeper-water *P. geminatum* communities from the drawdown as well, but those gains were also lost during the hurricanes.

While water levels during initial colonization undoubtedly affected establishment rates and compositions, *P. geminatum* was still one of the few species present in scraped areas even a year after the hurricanes passed. While never dominant, *P. geminatum* remained one of the top five species in terms of total biomass in treated areas at the end of the study. This suggests that while *P. geminatum* was inhibited by the rapid water rise and prolonged flooding from the hurricanes, it faired better than other colonizing species and still was unable to dominate the scraped areas as predicted.

Overall, the short-term responses of this restoration were that the dense, robust communities that dominated the shallow littoral zone for over 20 years were replaced primarily with *Vallisneria*, an important species for waterfowl (McAtee 1939, Sculthorpe 1967) and sportfish (Barnett and Schneider 1974), and which permits better recreational access to restored areas. Whether *Vallisneria* can remain dominate at these depths and/or at what cost is unknown, as half of the zone occupied by this submersed aquatic was exposed annually from 1993 to 2002, and the invasive exotic *Hydrilla* is known to displace this species in fertile environments (Van et al. 1999). *Hydrilla* biomass

increased 58% after the restoration, and though this was primarily in deeper areas than where *Vallisneria* occurred, it still suggests the potential for invading scraped areas without continual intervention. As such, the *Vallisneria* community is likely to be compressed from emergent competition in areas with < 100% hydroperiod, and from *Hydrilla* and possibly recovering water lily communities at the deeper end of its gradient.

Management Implications

The muck removal treatment applied to Lake Toho was the largest and most intensive removal event to date, and was used as a substitute for the loss of historic flood/drought cycles that would have naturally flushed/oxidized accumulated organic materials or floating mats during such events. This unique approach was an attempt to reset decades of succession by removing the species, seedbanks, and soils associated with degraded shorelines. Recolonization was regulated with selective herbicide applications in an effort to force historical patterns on the sandy, exposed shorelines without the historical processes that maintained the system originally. After four years of post-treatment monitoring, these efforts appeared to have mixed results.

While the objective of establishing sparse emergent habitat was not realized, the communities that developed along the treated shorelines did have similar desirable attributes as the target habitat. Organic soils were replaced with sandy substrates, the submersed communities that were established provide important habitat for fish (Barnett and Schneider 1974) and waterfowl (McAtee 1939, Sculthorpe 1967), and the removal of floating mats and dense emergent vegetation allowed for better recreational access. When system degradation cannot be reversed at an acceptable cost, managers should strive for the biotic structure and ecosystem services desired by stakeholders, while promoting communities that are both feasible and resilient (Seastedt et al. 2008). This

project did accomplish the former, but the resilience or longer-term establishment of a submersed community at these lake elevations is doubtful. A regional drought could expose most of the shoreline occupied by the newly established submersed community, which would allow rapid invasion by emergent species like *Pontederia*, and especially *P. repens* (Smith et al. 2004). Without substantial changes in water regulation schedules, it is likely that *Pontederia* will continue to expand lakeward from its narrow bands along the shore, as happened from 1979 to 1987 (Moyer et al. 1989).

The importance of hydrological conditions to wetland control and structure is widely recognized (National Research Council 1996), and restoration of these systems must begin with hydrology (Hunt 1999). The communities established on Lake Toho following restoration may be dependent on constant herbicide applications, which are increasingly regulated and dependent on currently declining state budgets (BIMP 2004). While restoring the variability of the natural hydrological regime is not possible in this or many other aquatic systems, it is possible that partial improvements to hydroperiods could be of value (Zedler 2000). For example, Lake Toho is consistently held between 15.9 and 16.8 meters NGVD annually, with little to no inter-annual variability. Year to year fluctuations are known to increase plant diversity, and can essentially double the number of vegetation types on a shoreline (Keddy and Fraser 2000). Managing lake levels with 0.5 m of inter-annual variation, for example, may reduce the amount of herbicides needed to keep robust, resilient communities from dominating the zone of intra-annual variation.

Ecosystem restoration will likely become increasingly complex as more systems are exposed to novel conditions, but should continue to focus on key structuring

processes and promoting desired ecosystem functions under future conditions. Even as recent studies have called for accepting new communities instead of historical states (Seastedt et al. 2008) and promoting new approaches to managing under novel conditions (Holling 2001), the basic premise of successful restoration attempts should not be abandoned. Restoring or at least partially implementing key structuring processes (Landres et al. 1999) should remain at the forefront of pattern restoration, and will minimize external efforts and costs (Mitsch and Wilson 1996). Hydrologic regimes will become increasingly difficult to restore with population growth and changing climates, and with it the temptation to maintain pattern with herbicides, species removals, and bulldozers, instead of water level manipulation.

Before applying the results of this project to other large, shallow lakes where muck removal is being considered, several caveats should be addressed. Lake Toho has a significant distribution of *Hydrilla* populations in deeper areas of the littoral zone, beyond the depths sampled in this study. Without submersed species stabilizing deeper sediments, drawdowns might increase wind-induced turbulence of the lake bottom; releasing nutrients, decreasing water clarity, and perhaps limiting macrophyte establishment even upon reflooding (Blindow et al 1993). If a large lake already has unconsolidated sediments and deep-water portions unsupportive of submersed vegetation, low water levels and the removal of shoreline vegetation may cause a shift to a phytoplankton-dominated state (Scheffer et al. 1993).

Lake Toho had the lowest amount of submersed vegetation since the 1980's (BIPM 2005) immediately following this restoration, and lower water quality measures for nearly two years. These changes were attributed to tropical disturbances during the

reflooding phase of treatment, which is another important consideration when applying large-scale habitat modifications. Several conditions will likely affect the outcome of mechanical muck removal projects, including lake size, water depth, maximum fetch, nutrient concentrations, and sediment stability, any of which may affect water quality/turbidity and subsequent vegetation establishment in treated areas.

Finally, water levels after treatment should be a major focus in these restoration efforts, as they are instrumental in influencing seed viability (Poiani and Johnson 1989), recruitment (Seabloom et al. 1998), and the growth and survival of adult plants (Squires and van der Valk 1992) on the scraped shorelines. The hurricanes that occurred during this study resulted in a rapid increase of water levels that were held at maximum pool for nearly seven months. Had water returned at a slower rate or oscillated during the early recovery period, different communities may have been established (van der Valk 1981, Weiher et al. 1996).

Longer-term monitoring is recommended after such projects, as the treated areas were only beginning to stabilize by the end of this study. Several of the dominant species were still consistently increasing in biomass over the last few samples, including the target species *Pontederia* and its large-scale replacements, *P. repens* and *Vallisneria*. There is still valuable information about the long-term persistence of establishing communities or recovery of undesirable communities that has not yet been collected. Without adequate monitoring of management efforts, it will be impossible to learn from their long-term effects.

APPENDIX A
SPECIES LIST

Table A. Common species sampled over the period of study.

Species Code	Scientific Name	Common Name
ALTPH	*Alternanthera philoxeroides*	Alligator weed
BACCA	*Bacopa caroliniana*	Lemon Bacopa
BIDLA	*Bidens laevis*	Burrmarigold
BRAMU	*Bracharia mutica*	Para grass
CENAS	*Centella asiatica*	Coinwort
CERAT	*Ceratophyllum spp.*	Coontail
CHASP	*Chara spp.*	Musk grasses
CYPSP	*Cyperus spp.*	Sedges
DIOVI	*Diodia virginiana*	Buttonweed
EICCR	*Eichornia crassipes*	Water hyacinth
ELESP	*Eleocharis spp.*	Spikerushes
HABRE	*Habenera repens*	Water-spider orchid
HYDSP	*Hydrocotyle spp.*	Pennywort
HYDVE	*Hydrilla verticillata*	Hydrilla
LEESP	*Leersia spp.*	Cut grasses
LUDAR	*Ludwigia arcuata*	Piedmont primrose
LUDSP	*Ludwigia spp.*	Ludwigia/Water Primrose
LUZFL	*Luziola fluitans*	Water grass
LYMSP	*Lymnobium spongia*	Frog's bit
NAJGU	*Najas guadalupensis*	Southern naiad
NELLU	*Nelumbo lutea*	Water lotus
NITSP	*Nitella spp.*	Stoneworts
NUPLU	*Nuphar advena*	Spatterdock
NYMAQ	*Nymphoides aquatica*	Banana lily
NYMOD	*Nymphaea odorata*	Fragrant water lily
PANHE	*Panicum hemitomon*	Maidencane
PANRE	*Panicum repens*	Torpedo grass
PASGE	*Paspalidium geminatum*	Egyptian paspalidium (commonly knot grass or Kissimmee grass)
PASAC	*Paspalum acuminatum*	Canoe grass
POLDE	*Polygonum densiflorum*	Smartweed
POLHY	*Polygonum hydropiperoides*	Wild water-pepper
PONCO	*Pontederia cordata*	Pickerel weed
RHYNSP	*Rhyncospora spp*	Beakrushes
SAGLN	*Sagittaria lancifolia*	Duck potato
SAGLT	*Sagittaria lattifolia*	Arrowhead

Table A. continued.

Species Code	Scientific Name	Common Name
SCICA	*Scirpus californicus*	Giant bulrush
SCICU	*Scirpus cubensis*	Bulrush
SESPU	*Sesbania punicea*	Purple Sesban
TYPSP	*Typha spp.*	Cattails
UTRSP	*Utricularia spp.*	Bladderworts
VALAM	*Vallisneria americana*	Eelgrass

Nomenclature follows that of Tobe et al. 1998.

LIST OF REFERENCES

Abrahams, C. 2008. Climate change and lakeshore conservation: a model and review of management techniques. Hydrobiologia 613:33−43.

Allen, M. S., K. I. Tugend, and M. J. Mann. 2003. Largemouth bass abundance and angler catch rates following a habitat enhancement project at Lake Kissimmee, Florida. North American Journal of Fisheries Management 23:845−855.

Anderson, R. C., J. E. Scwegman, and M. R. Anderson. 2000. Micro-scale restoration: a 25-year history of a southern Illinois barrens. Restoration Ecology 8:296−306.

Bachmann, R. W., M. V. Hoyer, and D. E. Canfield. 1999. The restoration of Lake Apopka in relation to alternative stable states. Hydrobiologia 394:219−232.

Bakker, J. P., and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology and Evolution 14:63−68.

Barlow, J., and C. A. Peres. 2006. Consequences of cryptic and recurring fire disturbances for ecosystem structure and biodiversity in Amazonian forests. Pages 225−240 *in* W. F. Laurance and C. A. Peres, editors. Emerging threats to tropical forests. University of Chicago Press, Chicago.

Barnett, B. S., and R. W. Schneider. 1974. Fish populations in dense submersed plant communities. Hyacinth Control Journal 12:12−14.

Blackman, W. F. 1973. History of Orange County. Mickler House Publishers, Chulota, FL.

Blake, G. R., and K. H. Hartge. 1986. Bulk density. Pages 464−475 *in* A. Klute, editor. Methods of soil analysis: Part 1. Physical and mineralogical methods. American Society of Agronomy, Madison, WI.

Blake, N. M. 980. Land into water – water into land. University Presses of Florida, Tallahassee, FL.

Blindow, I., G. Anderson, A. Hargeby, and S. Johansson. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. Freshwater Biology 30:159−167

Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. The Wadsworth Statistics/Probability Series, Chapman & Hall, New York, NY.

Bureau of Invasive Plant Management. 2004. Status of the Aquatic Plant Maintenance Program in Florida Public Waters. Annual Report to Florida State Legislature. Department of Environmental Protection.

Bureau of Invasive Plant Management. 2005. Status of the Aquatic Plant Maintenance Program in Florida Public Waters. Annual Report to Florida State Legislature. Department of Environmental Protection.

Canfield, D. E., and M. V. Hoyer. 1992. Aquatic macrophytes and their relation to the limnology of Florida Lakes. Final Report. Bureau of Aquatic Plant Management, Tallahassee, FL.

Carpenter, S. R., and M. L. Pace. 1997. Temporal variation in a paleolimnological record arising from a trophic cascade. Ecology 72:277−285.

Chapin III, F. S., A. L. Lovecraft, E. S. Zavaleta, J. Nelson, M. D. Robards, G. P. Kofinas, S. F. Trainor, G. D. Peterson, H. P. Huntington, and R. L. Naylor. 2006. Policy strategies to address sustainability of Alaskan boreal forests in response to a directionally changing climate. Proceedings of the National Academy of Sciences USA 103:16637−16643.

Chapman, H. D., and P. F. Pratt. 1961. Methods of analysis for soils, plants and waters. University of California, Riverside, CA.

Cherry, J. A., and L. Gough. 2006. Temporary floating island formation maintains wetland plant species richness: The role of the seed bank. Aquatic Botany 85:29−36.

Cissel, J. H., F. J. Swanson, and P. J. Weisberg. 1999. Landscape management using historical fire regimes: Blue River, Oregon. Ecological Applications 9:1217−1231.

Davis, S. M., and J. C. Ogden. 1997. Everglades: the ecosystem and its restoration. St. Lucie Press, Boca Raton, FL.

David, P. G. 1996. Changes in plant communities relative to hydrologic conditions in the Florida Everglades. Wetlands 16:15−23.

Day, R. T., P. A. Keddy, J. McNeil, and T. Carleton. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. Ecology 69:1044−1054.

De Angelis, D. L., L. J. Gross, M. A. Huston, W. F. Wolff, D. M. Fleming, E. J. Comiskey, and S. M. Sylvester. 1998. Landscape modeling for Everglades ecosystem restoration. Ecosystems 1:64−75.

De'ath, G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. Ecology 83:1105−1117.

Diehl, S. 1992. Fish predation and benthic community structure: The role of omnivory and habitat complexity. Ecology 73:1646−1661.

Dobson, A. P., A. D. Bradshaw, and A. J. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. Science 227:515−522.

Doren, R. F., and L. D. Whiteaker. 1990. Effects of fire on different size individuals of *Schinus terebinthifolius*. Natural Areas Journal 10:107−113.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345−366.

Ellison, A. M., and B. L. Bedford. 1995. Response of a wetland vascular plant community to disturbance: a simulation study. Ecological Application 5:109−123.

Fan, A., and S. Lin. 1984. Water budget for upper Kissimmee chain of lakes. Technical Memorandum. South Florida Water management District, West Palm Beach, FL.

Florida Fish and Wildlife Conservation Commission. 2003. 2004 Lake Tohopekaliga habitat enhancement project: a fishery management program. Fresh Water Fisheries Division, FFWCC.

Florida Fish and Wildlife Conservation Commission. 2004. Kissimmee Chain of Lakes Highlights, August 13, 2004. Aquatic Habitat Conservation and Restoration Section, Kissimmee, Florida, USA.

Gasith, A., and S. Gafny. 1990. Effects of water level fluctuation on the structure and function of the littoral zone. Pages 156–173 *in* M. M. Tilzer and C. Serruya, editors. Large Lakes: Ecological structure and function. Science-Tech Publication. Madison, Wisconsin

Giudicelli, J., and M. Bournaud. 1996. Invertebrate biodiversity in land-inland water ecotonal habitats. Pages 143−160 *in* J.-B. Lachavanne and R. Juge, editors. Biodiversity in land-inland water ecotones. Parthenon Publishing Group, New York, NY.

Grace, J. B. 1987. The impact of preemption on the zonation of two Typha species along lakeshores. Ecological Monographs 57:283−303.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, Chichester.

Harper, D. 1992. Eutrophication of freshwaters: principles, problems and restoration. Chapman & Hall, London, UK.

Havens, K. E. 1995. Secondary nitrogen limitation in a subtropical lake impacted by non-point source agricultural pollution. Environmental Pollution 89:241−246.

Havens, K. E. 2005. Aquatic vegetation and largemouth bass population responses to water-level variations in Lake Okeechobee, Florida (USA). Hydrobiologia 539:225−237.

Havens, K. E., N. G. Aumen, R. T. James, and V. H. Smith. 1996. Rapid ecological changes in a large subtropical lake undergoing cultural eutrophication. Ambio 25:150−155.

Havens, K. E., B. Sharfstein, M. A. Brady, T. L. East, M. C. Harwell, R. P. Maki, and A. J. Rodusky. 2004. Recovery of submerged plants from high water stress in a large subtropical lake in Florida, USA. Aquatic Botany 78:67−82.

Havens, K. E., and D. E. Gawlik. 2005. Lake Okeechobee conceptual ecological model. Wetlands 25:908−925.

HDR Engineering. 1989. Technical report of the development of a Surface Water Improvement and Management (SWIM) plan for Lake Tohopekaliga/East Lake Tohopekaliga. Final Report. South Florida Water Management District, West Palm Beach, FL.

Hill, M. 0. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427−432.

Hill, N. M., P. A. Keddy, and I. C. Wisheu. 1998. A hydrological model for predicting the effects of dams on the shoreline vegetation of lakes and reservoirs. Environmental Management 22:723−736.

Hobbs, R. J., and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4:93−110.

Hobbs, R. J., S. Arico, J. Aronson, J. S. Baron, P. Bridgewater, V. A. Cramer, P. R. Epstein, J.J. Ewel, C. A. Klink, A. E. Lugo, D. Norton, D. Ojima, D.M. Richardson, E. W. Sanderson, F. Valladares, M. Vila, R. Zamora, and Martin Zobel. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1−7.

Holcomb, D., and W. Wegener. 1971. Hydrophytic changes related to lake fluctuation as measured by point transects. Proceedings of the 25th Annual Conference of the Southeastern Association of Game and Fish Commissioners. Colombia, SC

Holling, C. S. 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems 4:390−405.

Holm, L.G., L.W. Weldon, and R. D. Blackburn. 1969. Aquatic weeds. Science 166:699−709.

Hoyer, M. V., and D. E. Canfield. 2007. Aquatic plant management in lakes and reservoirs. North American Lake Management Society, Madison, WI and Aquatic Plant Management Society, Lehigh, FL

Hoyer, M. V., R. W. Bachmann, and D. E. Canfield, Jr. 2008. Lake management (muck removal) and hurricane impacts to the trophic state of Lake Tohopekaliga, Florida. Lake and Reservoir Management 24:57−68.

Hunt, R. J., J. F. Walker, and D. P. Krabbenhoft. 1999. Characterizing hydrology and the importance of ground-water discharge in natural and constructed wetlands. Weltands 19:458−472.

Hunter, M. L. 1993. Natural fire regimes and spatial models for managing boreal forests. Biological Conservation 65:115−120.

Jacobs, H. S. 1971. Soils laboratory exercise source book. American Society of Agronomy, Madison, WI.

Jacquemart, A. L., D. Champluvier, and J. De Sloover. 2003. A test of mowing and soil-removal restoration techniques in wet heaths of the High Ardenne, Belgium. Wetlands 23:376–385.

James, R. T., K. O'Dell, and V. H. Smith. 1994. Water quality trends in Lake Tohopekaliga, Florida, USA: responses to watershed management. Journal of the American Water Resources Association 30:531−536.

Jeppeson, E., J. P. Jensen, P. Kristensen, M. Sondergaard, E. Mortensen, O. Sortkajaer, and K. Olrik. 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes. 2: Threshold levels, long-term stability, and conclusions. Hydrobiologia 200/201:219−227.

Johnson, K. G, M. S. Allen, and K. E. Havens. 2007. A review of littoral vegetation, fisheries, and wildlife responses to hydrologic variation at Lake Okeechobee. Wetlands 27:110−126.

Johnson, L. C., and J. R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377−3389.

Keddy, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. Ecology 64:331−344.

Keddy, P. A., and L. H. Fraser. 2000. Four general principles for the management and conservation of wetlands in large lakes: the role of water levels, nutrients, competitive hierarchies and centrifugal organization. Lakes and Reservoirs: Research and Management 5:177−185.

Kershaw, K. A., and J. H. H. Looney. 1985. Quantitative and dynamic plant ecology. Edward Arnold, Baltimore, MD.

Killgore, K. J., R. P. Morgan II, and N. B. Rybicki. 1989. Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac River. North American Journal of Fisheries Management 9:101−111.

Kimber, A., C. E. Korschgen, and A. G. van der Valk. 1995. The distribution of *Vallisneria americana* seeds and seedling light requirements in the upper Mississippi River. Canadian Journal of Botany 73:1966−1973.

Lachavanne, J. B. 1985. The influence of accelerated eutrophication on the macrophytes of Swiss Lakes: abundance and distribution. Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie 22:2950−2955.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1176−1188.

Langeland, K. A. 1996. *Hydrilla verticillata* (L.F.) Royle (Hydrocharitaceae), "The Perfect Aquatic Weed". Castanea 61:293−304.

Li, S., S. R. Pezeshki, and S. Goodwin. 2004. Effects of soil moisture regime on photosynthesis and growth of cattail (*Typha latifolia*). Acta Oecologica 25:17−22.

Light, S. S., and J. W. Dineen. 1994. Water control in the Everglades: a historical perspective. Pages 47−84 *in* S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie, Boca Raton, FL.

Lindig-Cisneros, R., J. Desmond, K. E. Boyer, and J. B. Zedler. 2003. Wetland restoration thresholds: can a degradation transition be reversed with increased effort? Ecological Applications 13:193−205.

Little, E. C. S. 1968. The control of water weeds. Weed Research 8:79−105.

Mallison, C. T., R. K. Stocker, and C. E. Cichra. 2001. Physical and vegetative characteristics of floating islands. Journal of Aquatic Plant Management 39:107−111.

McAtee, W. L. 1939. Wildfowl food plants. Their value, propagation and management. Collegiate Press, Ames, Iowa.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.

McCune, B., and M. J. Mefford. 1999. Multivariate analysis of ecological data, version 4.20. MjM Software Design, Gleneden Beach, OR.

Milleson, J. F. 1987. Vegetation changes in the Lake Okeechobee littoral zone: 1972 to 1982. Technical Publication. South Florida Water Management District, West Palm Beach, FL.

Mitsch, W. J., X. Wu, R. W. Nairn, P. E. Weihe, N. Wang, R. Deal, and C. E. Boucher. 1998. Creating and restoring wetlands. Bioscience 48:1019−1030

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands. Second edition. John Wiley & Sons, New York, NY.

Mitsch, W. J., and R. F. Wilson. 1996. Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications 6:77−83.

Moss, B., J. Madgwick, and G. Phillips. 1996. A guide to the restoration of nutrient-enriched shallow lakes. Borads Authority, Norwich, UK.

Moyer, E. J., M. W. Hulon, R. S. Butler, and R. W. Hujik. 1989. Kissimmee chain of lakes studies: study 1. Lake Tohopekaliga investigations. Florida Game and Freshwater Fish Commission, Tallahassee, FL.

Moyer, E. J., M. W. Hulon, and J. J. Sweatman. 1995. Fishery responses to habitat restoration in Lake Tohopekaliga, Florida. North American Journal of Fisheries Management 15:591−595.

National Research Council. 1992. Restoration of aquatic ecosystems: science, technology, and public policy. National Academy Press.

National Research Council. 1996. Weltands characteristics and boundaries. National Academy Press.

Niering, W. A. 1987. Vegetation dynamics (succession and climax) in relation to plant community management. Conservation Biology 1:287−295.

Parker, V. T. 1997. The scale of successional models and restoration objectives. Restoration Ecology 5:301−306.

Pearsall, W. H. 1920. The aquatic vegetation of the English Lakes. Journal of Ecology 8:164−201.

Peet, R. K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics 5:285−307.

Poiani, K. A., and W. C. Johnson. 1989. Effect of hydroperiod on seed-bank composition in semipermanent prairie wetlands.Canadian Journal of Botany 67:856−864.

Remetrix LLC. 2000. Bathymetric map of Lake Tohopekaliga. Remetrix LLC, Carmel, IN.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. St. Martin's Press, New York.

Schardt, J. D. 1997. Florida aquatic plant survey 1994. Technical Report. Florida Department of Environmental Protection, Tallahassee, FL.

Scheffer, M., S. H. Hosper, M-L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8:275−279.

Seabloom, E. W., A. G. van der Valk, and K. A. Moloney. 1998. The role of water depth and soil temperature in determining initial composition of prairie wetland coenoclines. Plant Ecology 138:203−216.

Seabloom, E. W., K. A. Moloney, and A. G. van der Valk. 2001. Constraints on the establishment of plants along a fluctuating water-depth gradient. Ecology 52:2216−2232.

Seastedt, T. R., R. J. Hobbs, and K. N. Suding. 2008. Management of novel ecosystems: are novel approaches required? Frontiers in Ecology and Environment 6:547−553.

Seddon, B. 1972. Aquatic macrophytes as limnological indicators. Freshwater Biology 2:107−130.

Segal, S. 1971. Principles on structure, zonation and succession of aquatic macrophytes. Hydrobiologia 12:89−95.

Sincock, J. L., J. A. Powell, R. K. Hyde, and H. E. Wallace. 1957. The relationship of the wintering waterfowl populations of the Kissimmee River Valley to the hydrology, topography, distribution of the vegetation and the proposed hydrological regulations. Technical Report. Florida Game and Freshwater Fish Commission, Tallahassee, FL.

Smith, D. H., R. M. Smart, and C. G. Hanlon. 2004. Influence of water level on torpedograss establishment in Lake Okeechobee, Florida. Lake and Reservoir Management 20:1−13.

Sorrell, B. K., H. Brix, H-H Schierup, and B. Lorenzen. 1997. Die-back of *Phragmites australis*: influence on the distribution and rate of sediment methanogenesis. Biogeochemistry 36:173−188.

Squires, L., and A. G. van der Valk. 1992. Water-depth tolerances of the Delta Marsh, Manitoba. Canadian Journal of Botany 70:1860−1867.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications 15:532−542.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution 19:46−53.

Surber, E. W. 1932. Controlling vegetation in fish ponds with sodium arsenite. U.S. Dept. of commerce, Investigational Report No. 2:1−39.

Tarver, D. P. 1979. Torpedo grass (*Panicum repens* L.). Aquatics 1:5−6.

Tobe, J. D., K. C. Burks, R. W. Cantrell, M. A. Garland, M. E. Sweeley, D. W. Hall, P. Wallace, G. Anglin, G. Nelson, J. R. Cooper, D. Bickner, K. Gilbert, N. Aymond, K. Greenwood, and N. Raymond. 1998. Florida wetland plants: an identification manual. Florida Department of Environmental Protection. Rose Printing, Tallahassee, FL.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81−92.

Tugend, K. I., and M. S. Allen. 2004. Changes in the plant and fish communities in enhanced littoral areas of Lake Kissimmee, Florida, following a habitat enhancement. Lake and Reservoir Management 20:54−64.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511−523.

Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and Environment 1:351−358.

U.S. Army Corps of Engineers. 1956. Central and southern Florida project for flood control and other purposes: part 2. Kissimmee River basin and related areas. General Design Memorandum, Kissimmee River Basin. Office of the District Engineer, Jacksonville, FL.

van der Nat, F-J. W. A., and J. J. Middelburg. 1998. Effects of two common macrophytes on methane dynamics in freshwater sediments. Biogeochemistry 43:79−104.

van de Koppel, J., M. Rietkerk, and F. J. Weissing. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. Trends in Ecology and Evolution 12:352−356.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 67:688−696.

van der Valk, A. G. 1998. Succession theory and restoration of wetland vegetation. Pages 657-667 *in* A. J. McComb and J. Davis, editors. Wetlands for the Future. Gleneagles Publishing, Glen Osmond, SA, Australia

van der Valk, A. G., and C. H. Welling. 1988. The development of zonation in freshwater wetlands: an experimental approach. Pages 145−158 *in* H. J. During, M. J. Werger, and J. H. Willems, editors. Diversity and pattern in plant communities. Academic, The Hague, Netherlands.

van Donk, E., and R. D. Gulati. 1995. Transition of a lake to turbid state six years after biomanipulation: mechanisms and pathways. Water Science and Technology 32:197−206.

Vayssieres, M. P., R. E. Plant, and B. H. Allen-Diaz. 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11:679−694.

Walker, B. H., and R. T. Coupland. 1968. An analysis of vegetation-environment relationships in Saskatchewan sloughs. Canadian Journal of Botany 46:509−522.

Wegener, W. L., and V. P. Williams. 1974. Extreme lake drawdown, a working fish management technique. Technical Memorandum. Florida Game and Freshwater Fish Commission, Tallahassee, FL.

Wegener, W. L., V. P. Williams, and D. Holcomb. 1973. Water level manipulation. Annual Progress Report. Federal Aid in Fish Restoration. Florida Game and Freshwater Fish Commission, Tallahassee, FL.

Wetzel, R. G. 1975. Limnology. Saunders College Publishing, Philadelphia, PA.

Whisenant, S. G. 1999. Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge University Press, Cambridge, MA.

Wilcox, B. A., and J. E. Meeker. 1991. Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. Canadian Journal of Botany 69:1542−1551.

Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences 104:5738−5742.

Williams, V. P. 2001. Effects of point-source removal on lake water quality: a case history of Lake Tohopekaliga, Florida. Journal of Lake and Reservoir Management 17:315−329.

Wilson, S. D., and P. A. Keddy. 1988. Species richness, survivorship and biomass accumulation along an environmental gradient. Oikos 53:375−380.

Wisheu, I. C., and P. A. Keddy. 1992. Competition and centrifugal organization of plant communities: theory and tests. Journal of Vegetation Science 3:147−156.

Zedler, J. B. 2000. Progress in wetland restoration ecology. Trends in Ecology and Evolution 15:402−407.

Zweig, C. L., and W. M. Kitchens. *In press*. The Semiglades: the collision of restoration, social values, and the ecosystem concept. Restoration Ecology

BIOGRAPHICAL SKETCH

Zach Welch began his college education at the University of Florida in 1994, coming from the small-town high school of Dunnellon, FL. Like most, he struggled to find an interest in the first year or two of undergraduate coursework, but was immediately hooked upon taking an introductory wetland ecology class, taught by Dr. Peter Frederick. He earned a Bachelor's degree in 1999 majoring in Wildlife Ecology and Conservation, and then began working for Dr. Kitchens at the Florida Cooperative Fish and Wildlife Research Unit.

He started as a research assistant in the summer of 2000, eventually earning his Master's degree in 2004 in Wildlife Ecology and Conservation. Having thoroughly enjoyed his experience with Dr. Kitchens and the Cooperative Research Unit, he eagerly started his PhD program with the same advisor, this time majoring in Interdisciplinary Ecology to allow greater emphasis on wetland studies. Throughout his graduate career, wetland ecology and vegetation modeling were among his favorite study topics, and he earned his Doctoral degree in the fall of 2009 after a long and gratifying experience.