LITTORAL VEGETATION OF LAKE TOHOPEKALIGA: COMMUNITY DESCRIPTIONS PRIOR TO A LARGE-SCALE FISHERIES HABITAT-ENHANCEMENT PROJECT

By

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An extreme dry-down and muck-removal project was conducted at Lake Tohopekaliga, Florida, in 2003-2004, to remove dense vegetation from inshore areas and improve habitat degraded by stabilized water levels. Vegetation was monitored from June 2002 to December 2003, to describe the pre-existing communities in terms of composition and distribution along the environmental gradients. Three study areas (Treatment-Selection Sites) were designed to test the efficacy of different treatments in enhancing inshore habitat, and five other study areas (Whole-Lake Monitoring Sites) were designed to monitor the responses of the emergent littoral vegetation as a whole. Five general community types were identified within the study areas by recording aboveground biomasses and stem densities of each species. These communities were distributed along water and soils gradients, with water depth and bulk density explaining most of the variation. The shallowest depths were dominated by a combination of
Eleocharis spp., Luziola fluitans, and Panicum repens; while the deeper areas had communities of Nymphaea odorata and Nuphar luteum; Typha spp.; or Paspalidium geminatum and Hydrilla verticillata. Mineralized soils were common in both the shallow and deep-water communities, while the intermediate depths had high percentages of organic material in the soil. These intermediate depths (occurring just above and just below low pool stage) were dominated by Pontederia cordata, the main species targeted by the habitat enhancement project. This emergent community occurred in nearly monocultural bands around the lake (from roughly 60–120 cm in depth at high pool stage) often having more diverse floating mats along the deep-water edge. The organic barrier these mats create is believed to impede access of sport fish to shallow-water spawning areas, while the overall low diversity of the community is evidence of its competitive nature in stabilized waters. With continued monitoring of these study areas long-term effects of the restoration project can be assessed and predictive models may be created to determine the efficacy and legitimacy of such projects in the future.
CHAPTER 1
INTRODUCTION

Florida Lakes

Historically, Florida was once much wetter than it is today, with as much as 25% of the peninsula covered with freshwater during wet years (Tebeau 1971). Low elevation, flat topography, and poorly drained soils support a landscape pockmarked with swamps, lakes, and marshes, many of which were once connected. In fact, over 7700 lakes occur in the state of Florida; most formed from gradual dissolving and collapsing of subsurface limestone (solution processes) or from relict sea-bottom depressions that were filled with freshwater as the oceans receded (Edmiston and Myers 1983). These lakes generally have a large area:volume ratio as a result of the formation processes and lack of topography in the landscape.

The largest lake in the state and third largest in the country, Lake Okeechobee, is an example of a depression lake, with an area of 1732 km$^2$ and an average depth of only 2.7 m. Large, shallow lakes of this nature have considerable stretches of shoreline capable of supporting vegetation, with sections of the 400 km$^2$ of Lake Okeechobee marsh so large that the interior is hydrologically isolated from the lake itself. The maximum depth to which vegetation extends into the lake generally depends on light availability, but is closely related to water chemistry (Spence 1967, Heegard et al. 2001), lacustrine topography (Duarte & Kalffe 1986), fluctuations in water level and depth (Hudon et al. 2000), substrate composition (Power 1996), and interactions with other flora and fauna (Leslie et al. 1983, Wilson and Keddy 1985). The vegetated portion of
the lake, including either emergent or submersed communities, is loosely referred to as the littoral zone, and in many shallow lakes may include the entire water body. For the remainder of this thesis, the littoral zone is defined as the portion of shoreline that supports emergent or floating-leaved vegetation only; not including the deeper-water, submersed aquatics. These areas are primary zones of productivity, driving nutrient and oxygen cycles; preventing erosion; trapping sediment; and providing cover, substrate, and forage for a suite of aquatic organisms ranging from microscopic zooplankton to large vertebrate predators.

Unfortunately, these systems are vulnerable to changes in watersheds and shoreline activities, as surrounding human populations increase. Many of Florida’s lakes are facing problems such as degraded water qualities from urban and agricultural runoff, seawall construction, flood control and water-use demands disrupting historical hydroperiods and stage fluctuations, substrate alterations as a result of sedimentation or organic material accumulation, and the introduction of hundreds of exotic species of flora and fauna competing with and displacing natives.

The most recognized and prevalent of these issues is eutrophication, the degradation of habitat and water quality as a result of artificially increased nutrient levels (by means of fertilizers, stormwater, sewage effluent, etc.). The term eutrophication became more widely used in the 1940s as scientists realized that nutrients entering and accumulating in lakes as a result of industrial activities were causing changes in a matter of decades that would otherwise occur naturally over centuries or longer (Harper 1992). A general theory of succession supports the idea of lakes gradually accumulating nutrients and increasing productivity over time. This theory suggests that in early stages,
lakes have few nutrients and low productivity (oligotrophic); and gradually accumulate nutrients through sedimentation and their own biological turnover, leading to a highly productive state, eventually eliminating macrophytes and becoming dominated by phytoplankton (hypereutrophic) (Lindeman 1942). This trend is considered a natural process of lakes evolving from a clear-water state with vegetation adapted to low nutrient levels; to an eventual muck-filled, algae-laden lake unable to support vegetation and having turbid, high-energy water columns. Theoretically, agricultural and urban runoff dramatically accelerates the speed and magnitude of nutrient increases, causing noticeable changes within decades (rather than centuries).

However, some argue that increasing the level of nutrients in a lake does not necessarily guarantee a turbid algal state, especially in shallow, warm-water lakes (Scheffer 1998). In Florida, where growing seasons are basically year-round, and submersed aquatics can occupy 100% of shallow-lake areas, high levels of nutrients can be tied up in extremely productive macrophytic and epiphytic communities, reducing wind/wave actions and limiting nutrient levels in the water column. These conditions are unfavorable for the development of phytoplankton for several reasons (Moss et al. 1996): calm waters within dense vegetation are not turbulent enough to keep phytoplankton suspended, which is necessary for substantial development; the structure of the vegetation provides cover and substrate for micro-invertebrates that graze on phytoplankton; and through macrophytic and epiphytic uptake, the amount of nutrients in the water column is reduced. However, large-scale vegetation removal by natural or artificial disturbances may be enough to switch the lake to a turbid, algal state. This phenomenon of highly eutrophic lakes existing as either algae- or macrophyte-dominated lakes is a theory
known as alternative stable states. Indeed, shallow eutrophic lakes have been shown to switch from one state to another without any change in nutrient inputs (Blindow et al. 1993, Scheffer et al. 1993, and Moss et al. 1996). One example of such a switch is Lake Apopka, located in central Florida.

Once renowned for its largemouth-bass fishery, Lake Apopka was almost completely covered with submersed vegetation in the 1940s (Clugston 1963) though sewage effluent and agricultural runoff had been increasing since the 1920s. In 1947, a category four hurricane moved across Florida, uprooting substantial amounts of vegetation and stirring sediments throughout the lake, resulting in large fish kills and unvegetated areas in the lake. By 1950, all of the submersed vegetation had disappeared and high wind events in 1951 resulted in additional fish kills, presumably due to oxygen depletion from highly organic sediments. Since then, Lake Apopka has been in a turbid, algal state; and all attempts at restoration, beginning as early as 1952 (US Environmental Protection Agency 1978) have failed to reestablish vegetation.

This is a serious issue facing most water bodies in Florida, and its effects are compounded by the disruption of historical sheet flows and hydroperiods of these systems. Watershed development increases nutrient inputs and also increases demand for flood control and water supply; turning naturally dynamic lakes and wetlands into reservoirs, and meandering rivers into streamlined channels. Many of the major hydrological changes in Florida were a result of devastating hurricanes in the 1920s and 1940s that caused large-scale losses of life and property. In the 1930s the Army Corps of Engineers responded with aggressive plans to improve flood control and navigation, creating a vast system of levees and canals throughout central and southern Florida.
Ultimately, results of this program were compartmentalization of the Everglades, impoundment and isolation of Lake Okeechobee, and channelization of the Kissimmee River (a major inflow to Okeechobee).

Lake Okeechobee was completely encircled by levees in the 1960s, isolating it from much of its historical littoral zone (although levee construction early in the 20th century gradually lowered water levels, and allowed the current littoral zone to develop over the past 100 years) (Davis 1943). Upon impoundment in the 1960s, water levels were regulated to minimize flooding during the wet season (May–October) and to maximize water storage for the dry season (November–April), raising the average lake level from 4.3–5.0 m (14.3–16.4 ft) above sea level (Ager and Kerce 1970). Vegetation studies in 1969 (Ager and Kerce 1970) documented a doubling of cattail (Typha spp.) populations in deeper water and a tripling of torpedo grass (Panicum repens) populations in shallower water since the late 1950s (Sincock 1957). In 1978, the water-regulation schedule was raised by 0.5 m and substantial decreases in the diversity of community types and willow (Salix caroliniana) were noted, with further increases in cattail and torpedo grass; the latter displacing diverse, native communities of rushes (Eleocharis spp. and Rhynchospora spp.) (Pesnell and Brown 1977, Milleson 1987). By the early 1990s, more than 60 km² of shallow, native marsh had been displaced by torpedo grass (Schardt 1994).

A general decrease in specific diversity or structural complexity of communities after water-level stabilization (Keddy 1983, Wilson and Keddy 1988, Wilcox and Meeker 1991) or eutrophication (Seddon 1972, Lachavanne 1985, Harper 1992) has been well documented. Additionally, the degree of spatial or structural heterogeneity of plant
communities affects the diversities of other organisms that are more or less vegetation dependent (Juge and Lachavanne 1997), including associated microflora (Wetzel 1975), invertebrates (Anderson and Day 1986, Giudicelli and Bournard 1996), and fish (Tonn and Magnuson 1982). Declines in fisheries were noticed after habitat degradation (Wegener and Williams 1974) and consequently, habitat restoration became a priority for agencies in charge of Florida lake management. In addition to implementing pollution controls to limit nutrient inputs, the need to more closely mimic natural hydrological patterns was also recognized. Although watershed development eliminated the possibility of reaching historical flood levels, mimicking historical droughts was possible. Artificial dry downs were performed to counteract the effects of prolonged impoundment, by exposing organic substrates to oxidation and sparking seed germination and vegetative propagation of stressed plant populations. While successful in expanding the lakeward extent of the littoral zone, reestablishing native flora, and consolidating organic substrates (Wegener and Williams 1974), the benefits of these projects seemed to diminish as the systems became further removed from their pre-impoundment state. Over time, more aggressive, competitive species became established under stable-water conditions; and extremely infrequent dry downs became ineffective at reducing the abundance of these competitive species. As the benefits of dry downs became more short-lived, efforts to prolong and increase their impacts were developed.

To expedite the natural removal processes of organic substrates and to assist the establishment of desirable species, managers began using bulldozers and other heavy equipment to mechanically remove muck and unwanted vegetation from shorelines during artificial dry downs. This process was first performed in 1987 on a large lake in
central Florida, called Lake Tohopekaliga. Though many lakes have undergone such treatment since (Lake Kissimmee, Lake Istokpoga, Alligator Chain of Lakes, Lake Jackson, Orange Lake, etc.), effects of this type of disturbance are still not fully understood even in terms of the fisheries they are supposed to benefit (Allen et al. 2003). In spite of the uncertainty, this practice is commonly used, and another larger scale muck removal project was scheduled for Lake Tohopekaliga in 2004. The remainder of this paper will detail the history of the lake, the specifics of this project and the studies designed to monitor its effects.

**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 at an average depth of 2.1 m at maximum pool (16.75 m NGVD) (HDR Engineering 1989, Remetrix LLC 2003). The immediate watershed is 340 km², though an additional 686 km² of East Lake Toho watershed ultimately drains into Lake Toho through canal C-31 (HDR Engineering 1989). Nearly half of these 1334 km² 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).

Considered a eutrophic lake, the water is slightly stained from upland tannins and relatively free of algal blooms, with visibility ranging from 0.5–1.5 m. The mixed emergent littoral vegetation covers roughly 25% of the lake’s area (Remetrix LLC 2003), supporting highly productive fisheries, large populations of wintering migratory birds, significant nesting of endangered and threatened species (Snail Kite, *Rostrhamus sociabilis*, and Sandhill Crane, *Grus canadensis*) and dozens of species of reptiles and...
amphibians. Like most water bodies in Florida, however, constant vigil and intervention is required to maintain productivity or natural habitats in the face of watershed development and exotic species introductions. Below is a brief summary of the history of Lake Toho and the challenges of balancing flood control and water storage capacities, recreational and economical benefits, and quality habitat for native faunal communities.

**History of Lake Tohopekaliga**

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 water bodies 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 reduction in the
range of stage levels 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 of the lake 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 March 2004. The vertical black line represents the approximate time of impoundment in 1964 while the blue lines indicate artificial dry downs. The natural drought in 1962 was the lowest 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, discharges were not completely eliminated until 1988. By this point nutrient loading and water level stabilization had noticeably affected the littoral habitats, water qualities, and fish populations, sparking a new era in lake restoration by management agencies.


**Restoration Efforts and Previous Studies**

In 1969, the Florida Fish and Wildlife Conservation Commission recommended that all effluent discharges into Lake Toho be stopped and that an artificial dry down 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. 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. 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 dry down was performed. Contrary to the others, which were performed 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. This process occurs as stable, high water levels cause a buildup of gases in the root mats of senescing vegetation and as organic debris are deposited by wind and wave actions; eventually causing the mat to become buoyant enough to release from the substrate and create a floating mat of organic matter and root material. Over time, wind and wave actions act to push back, break apart, or fold over the deep water edge of these mats (Kahl 1993), creating progressively thicker mats that can eventually support woody vegetation (Mallison et al. 2001) (Figure 1-3).

The goal of the 1987 dry down was to reestablish native grasses in place of the 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 the southeastern 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.
Figure 1-3. The formation of floating mats and subsequent organic barrier, blocking the access of sport fish to important, shallow water spawning areas. The process occurs as follows: A) Stabilized water levels begin to drown emergent vegetation at the deeper end of its depth tolerance, causing senescence and a buildup of gases in the root mat B) Gas buildup reaches a point that causes floatation, pulling the root mat from the organic layer beneath it C) Wave actions fold over the thinner, leading edges of the floating root mat D) Prolonged folding and the presence of the floating edge act to build organic material under and within the root mat, forming a thicker, drier mat E) Eventually the mat supports woodier and shorter hydric period vegetation, forming an organic barrier that limits access of sport fish to shallow water spawning areas. All line drawings of plants used in these figures were copied with permission from Aquatic Plants in Pen and Ink (IFAS Pub. No. SP233).
In 2004, the largest and most comprehensive muck removal project to date was implemented on Lake Toho. Upon dropping lake levels roughly 2 m below high pool stage, nearly 7,000,000 m³ of muck and vegetation were removed from over 80% of the shoreline. The remainder of this paper will focus on the studies designed to monitor the effects of this project.

**Study Objectives**

Sampling methods implemented in earlier studies have focused on the frequency of species occurrence along water depth gradients, comparing pre- and post-restoration data. These methods reveal inundation tolerances of individual species and are effective in
monitoring shifts in their locations along the measured gradient. However, they are primarily exploratory methods, not generally used to test hypotheses or to make inference to any area other than that occupied by the line transect. In this respect, previous studies have not quantitatively measured the response of vegetation to restoration efforts, nor have they attempted to monitor the response of the littoral communities as a whole (rather than on an individual species basis). Kershaw and Looney (1985) stated that to understand vegetative dynamics of a system, species composition, distribution, and the relative degree of abundance of each must be described. Differences in structural and specific diversities can have profound effects on organisms relying on that habitat for food, cover, or substrate (Wetzel 1975, Giudicelli and Bournaud 1996), on rate of nutrient uptake or immobilization (Mitsch and Gosselink 1993, Sorrell et al. 1997, Van der Nat and Middelburg 1998), on quality and quantity of detritus, rate of organic accumulation in the soil (Wilson and Keddy 1988), erosion control, wave energies, and so on. To fully comprehend treatment effects applied to the littoral communities of Lake Toho, quantitative measurements of successional responses are critical. Densities and biomasses are more stringent measures of the spatial and architectural complexity of the habitats targeted for restoration than frequency of occurrence, as recorded in previous studies. Defining the pre-existing communities and monitoring their response at a multi-species level will provide insight to the effects and efficacy of these restoration efforts.

The ultimate goal of this project is therefore to establish long-term monitoring sites and protocols to address the following questions:

- At a community level, what are the effects of different habitat restoration techniques in terms of vegetation succession? Essentially, are both muck removal
and herbicide application necessary to establish historical, grassy habitats or are either of them effective by themselves?

- On a lake-wide scale, how will the littoral vegetative communities respond to this restoration project?

These questions were addressed with the designation of two separate study areas; the first hereafter referred to as the Treatment-Selection study and the second called the Whole-Lake Monitoring study. Long-term effects of these treatments will not be known until years of post-treatment data have been collected and analyzed. Chapters 3 and 4 will detail the design, establishment and monitoring protocols of these study areas, respectively, that are essential to estimating those effects. However, as no restoration efforts had yet been performed during the period of this study, the bulk of these chapters and the majority of this paper will focus on the description of the lake’s littoral communities before the treatment was applied. These questions are addressed for each study area:

- What vegetative communities were present before the project and how were they distributed?

- What were the underlying gradients associated with those compositions and distributions?

- Based on this pre-treatment information, what inferences can be made about the littoral communities within the lake?

Brief discussions of the findings in each study area are included at the end of Chapters 3 and 4 with comparisons to several previous studies, and Chapter 5 includes a summated, cumulative discussion of the communities identified in these chapters. Before presenting these results, basic descriptions of several of the important species encountered on Lake Toho are provided in Chapter 2. Most of these species will be
continually referred to in the following chapters and an understanding of their growth forms, life histories and physical characteristics will aid interpretation.
CHAPTER 2
SPECIES OF INTEREST

Introduction

Habitat management of any type, aquatic or terrestrial, ultimately leads to the classification of frequently encountered species as native, natural, desirable or invasive, exotic, nuisance, aggressive, and so on. Typically, managers have a target habitat consisting of a suite of desirable native species, usually an approximation of the historic or natural habitat, and are faced with the elimination or constant invasion of species that are considered disruptive to that habitat. In Florida, non-native or exotic species are assigned labels according to their potential to spread, invade, or otherwise dominate, alter, and disrupt natural habitats. A list of these aggressive, invasive exotics is posted by the Florida Exotic Pest Plant Council (www.fleppc.org).

The most well known exotics in Florida include water hyacinth (*Eichhornia crassipes*) and hydriina (*Hydrilla verticillata*). Both of these plants have the remarkable ability to completely dominate water bodies, displacing practically every other species if left unmanaged. Hundreds of millions of dollars have been spent in attempts to control the spread and abundance of these two species alone since their introductions. At present there are at least 35 exotic species in Florida’s aquatic systems and over $70 million a year is spent in fighting their spread or abundance.

In attempting to restore a system to some historical state, eliminating exotic species is only a small part of the process. The biggest challenge usually lies with identifying the causal mechanisms that altered the system to begin with. Changes in water qualities,
nutrient levels, depth and duration of flooding, etc. have major impacts on species compositions and distributions, resulting in undesirable changes in native vegetation as well. One of the best cases of such habitat alterations and vegetation response is the expansion of cattail (*Typha* spp.) into the Everglades Water Conservation Areas as a result of high phosphorous levels in receiving waters (SFWMD 1992, Davis 1994). The historically oligotrophic Everglades and the vegetation adapted to those conditions are unable to compete with species like cattail at higher nutrient levels, and alterations to natural hydroperiods, sheet flow, and fire frequencies compound these effects. The problems facing many of Florida’s lakes are quite similar.

As a result of decreased flood stages, water level stabilization, and increased nutrient inputs, exotics and several native species have become problematic to lake managers in the restoration of historical habitat. Listed below is a brief description of important species on Lake Toho, including invasive exotics, nuisance natives, and the desired species that comprise the target habitat of the lake restoration project.

### Exotic Species

- **Hydrilla (*Hydrilla verticillata*)**: experts argue whether hydrilla or water hyacinth is the most invasive and disruptive exotic plant in Florida. Hydrilla is a submersed aquatic brought to the US from Asia through Florida as an aquarium plant, most likely in the 1950s, through Miami or Tampa Bay ports. It was first discovered in the 1960s in Miami and Crystal River (Blackburn et al. 1969) and by the 1970s occurred in all major water bodies in all drainage basins. It out competes most native submersed species with rapid growth of up to 2.5 cm per day (Langeland 1996) and extensive branching at the water surface, up to one half of its standing crop occurring in the top 0.5 m of water (Haller and Sutton 1975). An exceptional tolerance to low light conditions allows its establishment in depths beyond most other submersed species, and as such can be found in up to 15 m in depth in spring-fed Crystal River and regularly occurring at 3 m in most lakes (Langeland 1996). Vegetative and asexual reproduction are most common, forming new plants from any whorl of leaves broken off or from turions produced on tubers and in leaf axils. Subterranean turions can remain viable after several days out of water and for up to 4 years in undisturbed sediments (Van and Steward 1990), surviving herbicide applications and ingestion by waterfowl. This makes the plant easy to spread.
between water bodies on boats and boat trailers, fishing lures and bird legs. After 30 years of herbicide applications, more resistant strains of *Hydrilla* are much more common. Non-target, native species that used to be unaffected by the low levels of herbicides used to kill Hydrilla, are now being affected by the need for higher concentrations. Without constant herbicide application and mechanical removal by management agencies statewide, Hydrilla would quickly fill most water bodies in Florida from substrate to water surface. Thus far, no methods have been effective at killing the roots of the plant, with rapid regrowth occurring from tubers immediately following decreased herbicide concentrations in the water column. A leaf-mining fly (*Hydrellia pakistanae*) has been established in Florida as a biological control, but its efficacy is as of yet unknown (Buckingham et al. 1989).

- **Water hyacinth (*Eichhornia crassipes*):** arguably the most invasive and disruptive exotic plant in Florida. A free floating plant, it is attached to mother and daughter plants by floating stolons, creating dense mats of vegetation capable of completely covering most water bodies. It was introduced to the United States in 1884 at an exposition in New Orleans and reached Florida in 1890 (Gopal and Sharma 1981). By the late 1950s it occupied about 51,000 ha of Florida’s waterways (Schmitz et al. 1993). Its growth rates exceed any other tested vascular plant (Wolverton and McDonald 1979), doubling its populations in as little as 6-18 days (Mitchell 1976). Large mats degrade water quality by depleting oxygen levels, shading out submersed species, rapidly producing organic matter, crowding out and crushing emergent species and blocking access to the air-water interface essential to many aquatic organisms (Gowanloch 1944, Penfound and Earle 1948). After 100 years of effort, populations are finally under control through constant maintenance and herbicide applications.

- **Torpedo grass (*Panicum repens*):** A very competitive grass with stems to 1 m tall, growing from sharp-tipped (torpedo like) floating or creeping rhizomes. It was first collected in the US in Alabama in 1876 (Beal 1896) and introduced to Florida for cattle forage in 1926 (Tarver 1979). By 1992 it was established in over 70% of Florida’s public waters, displacing 6000 ha of native marsh in Lake Okeechobee (Schardt 1994). It will grow in upland areas but thrives in wet, sandy soils, stimulated by tilling and fertilization (Hodges and Jones 1950), rapidly colonizing disturbed shorelines by rhizome extension and fragmentation (Holm et al. 1977).

- **Para grass (*Brachiaria mutica* also *Urochloa mutica*):** A rapidly growing grass with stems from 1–4 m long, with floating stems up to 6 m long (Handley and Eckern 1981). The lengthy and extremely dense stems fall over and lay on top of one another, creating horizontal mats up to 1 m thick (Holm et al. 1977). It aggressively competes with other plants by high productivity and allelopathic qualities that enable the formation of dense monocultural stands (Chang-Hung 1977, Handley et al. 1989). It was most likely introduced to Florida as early as the late 1870s (Austin 1978) and was recommended for pasturage here in 1919 (Thompson 1919). This grass occurred in up to 52% of Florida’s public water bodies in 1986 but decreased to 46% by 1994 (Schardt 1997). Grazing remains a highly effective method of control.
• **Water lettuce (Pistia stratiotes):** Experts argue whether this plant is native or exotic but is included in this list due to its potentially invasive and highly competitive nature. Like water hyacinth, it is a free floating plant connected by short stolons to mother and daughter plants. William Bartram first reported it in 1756, describing it as blocking waterways and preventing boat access. While the effects of dense floating mats are the same as hyacinth, including shading submersed species, decreasing oxygen levels and crowding out emergents, its slower growth rate has kept it from becoming as big a problem. Through regular removal and herbicide applications, and with several biological insect controls successfully established, water lettuce populations remain under control.

• **Alligator weed (Alternanthera philoxeroides):** – An emergent perennial with hollow stems able to form large, dense mats, occasionally floating. This species was problematic when its populations reached a high in the 1960s before the first biological insect control (Agasicles hygrophila) for an exotic plant was released. With unprecedented success, by the 1980s its populations were severely limited and no longer posed a threat. Though still very frequent in Florida lakes and water bodies, insect damage can easily be seen on most plants, constantly keeping its populations in check.

**Nuisance Natives**

While each of the species listed below may be desirable in many situations and certainly have high value to wildlife under many circumstances, their potential to form dense, monocultural stands or floating mats and to produce massive amounts of organic litter often leads to their classification as a nuisance. Typically, dense vegetation and high amounts of organic matter are considered to impede sport-fish reproduction, block recreational access and eventually create the same problems in terms of diversity and habitat as the aforementioned invasive exotics. For these reasons the native species listed below are frequently sprayed with herbicides to keep their abundance and distribution under control.

• **Pickerel weed (Pontederia cordata):** A stout, broadleaf, emergent plant with stems up to 1 m in height. Large, highly aerenchymous rhizomes form dense mats, capable of lifting off the substrate and becoming buoyant with rising water levels. Provides good habitat for macroinvertebrates, reptiles, amphibians and small fish when not floating, and nesting substrate for several birds (common moorhen, Gallinula chloropus; purple gallinule, Porphyryla martinica; sandhill crane, Grus canadensis) when floating. Pickerelweed is highly productive, out-competes many
species in stable environments and contributes large amounts of organic material to the substrate, capable of forming nearly monocultural stands around shorelines of lakes.

- **Smartweed (Polygonum spp.):** Another broadleaf emergent plant, with stems up to 1.5 m in length. In deeper water, *P. densiflorum* forms floating mats with long horizontal stems. It is highly competitive, especially in shallow, disturbed shorelines and is usually among the first to colonize such areas. Capable of forming dense, monocultural stands, producing large amounts of litter.

- **Cattails (Typha spp.):** A tall, robust, emergent species, growing to over 3 m in height and covering large areas of wetlands, lakes and rivers. One of the most common aquatic and wetland plants anywhere in the world, capable of forming monocultural stands of only one or two individuals due to prolific rhizomous reproduction. Occasionally, floating mats may form in large colonies if high water levels persist. Each seed head contains tens of thousands of wind and water dispersed seeds, rapidly colonizing recently disturbed or early successional wetlands. While providing excellent cover and nesting substrate for many animals and birds, their tremendous amounts of litter production and dense growth habit occasionally makes them problematic to lake managers.

**Desired Aquatics**

Though not specifically more useful to wildlife than many of the nuisance native vegetation, the relatively sparse growth patterns of the species listed below lends to higher diversities, lower litter production, increased oxygen levels, and better access for anglers. These plants are also more typical of oligotrophic systems where a lack of productivity contributes to sandier substrates and clearer water. The association of these species to oligotrophic conditions leads to their preference over species more typical of eutrophic, highly productive systems that accumulate organic material and have turbid water. The following are a few species generally thought to be representative of a more natural, historic system before higher nutrient levels and water level stabilization affected their ability to compete.

- **Egyptian paspalidium (commonly called Knot Grass) (Paspalidium geminatum):** A tall species of grass with stems reaching heights of 3 m. It typically grows on sandy substrates and is generally thought to be good sport fish habitat. Though capable of forming monocultural stands, it often coincides with
submersed species in deeper water. Grows to depths of at least 2 m but generally is
out competed in shallow waters without significant efforts to establish it there.

- **Maidencane (Panicum hemitomon):** Another deep water grass species that forms
  thin stands among submersed species. Relies solely on vegetative reproduction
  through rhizomes unless seeds are exposed during drought conditions. Grows to
depths of 3 m in clear water and on sandy substrates. Also thought to be good sport
fish habitat.

- **Southern watergrass (Luziola fluitans Synonymy: Hydrachloro carolinnensis
  Beauv.):** A perennial grass that forms dense colonies in many water bodies in
Florida, occurring in shallow water or on normally flooded shorelines. Its leaves
can be underwater (to 1 m), floating, or emergent to 20 cm in height and on stems
to 1 m long. When occurring on moist soils, stems act as runners and leaves are
attached to the soil, creating a dense carpet of small, fragile leaves (7.4 mm wide to
7 cm long). Upon flooding, the stems become erect and the leaf blades densely
cover the surface of the water, giving the appearance of a firm substrate. This grass
tends to be more common in disturbed areas, especially on grazed shorelines where
herbivory limits the height of competing vegetation.

- **Giant bulrush (Scirpus californicus):** A large species of rush, stems reaching
  heights over 3 m. Typically grows on sandy substrates with vegetative rhizome
reproduction. Dense stands provide nesting substrates for some bird species,
though generally occurs in higher energy environments and deeper water (2 m).
Lack of any leaf cover permits growth of submersed aquatics within dense stands.
Also thought to be good sport fish habitat.

The aforementioned species are a select few of interest to those managing aquatic
habitats within the state of Florida. All of these species occur on Lake Toho, some
constantly managed against and others physically planted for establishment. The
manipulation of species and habitats requires monitoring programs to assess the
responses and effectiveness of the treatments and strategies applied. The scale and
intensity of the habitat management project on Lake Toho provides an excellent
opportunity for discerning both the immediate and long-term effects of the commonly
applied treatments, as well as experimental combinations of treatments. The following
chapters detail the distributions and abundances of the species and communities found on
Lake Toho prior to the treatments, including the species listed above.
CHAPTER 3  
TREATMENT-SELECTION STUDY

Introduction

To counteract the effects of impoundment, eutrophication, and invasion of exotic species on aquatic habitats, lake restoration efforts have become higher priority and increasingly disruptive in nature. In 1971, for example, the artificial dry down of Lake Toho was considered a ‘drastic’ move and the removal of 172,000 m$^3$ of muck in 1987, unprecedented (HDR Engineering 1989). These projects pale in comparison to the 2004 dry down and removal of 7,000,000 m$^3$ of muck. With the exception of three study sites on the lake, virtually every significant stretch of shoreline is scheduled to be scraped, leaving sandy beaches from roughly 30–120 cm in depth at high water. These depth zones targeted for removal are generally occupied by dense, monocultural stands of species like *Pontederia cordata* or *Typha* spp., and often create floating mats either within or on the deep-water edge of these communities. As described in Chapter 1, these mats can become progressively thicker as wind and wave actions fold the leading edge over and onto itself and deposit drifting organic materials.

The purpose of the 1987 muck removal project was to remove the mats and dense vegetation that were blocking fish spawning and nursery utilization of the shallower reaches of the littoral zone, as well as impeding navigation of anglers. Habitat diversity was also believed to be much lower in dense stands of *Pontederia* than native grassy communities that once occupied the shorelines, before impoundment and eutrophication. Since *Pontederia* had become extremely dominant in the shallower zones and was
thought to be at least partially responsible for the creation of organic barriers, mechanical scraping for the 2004 project was scripted to remove this entire community. Literally, the shoreward and lakeward extent of the *Pontederia* community was marked with PVC poles, and bulldozers removed everything in between.

The 1987 project revealed that muck removal had only temporary effects, as *Pontederia* and *Polygonum* species quickly reestablished and out competed most others upon reflooding. The solution was thought to lie in monitoring and managing littoral succession with cocktails of herbicides to control which species rebound and flourish. Unfortunately, several broad applications must be made in order to impede the growth of unwanted vegetation and to establish more desirable species, leaving the scraped areas relatively barren during this period. These practices, combined with muck removal at such a large scale, greatly increase the uncertainty of desired outcomes since both the intensity and temporal extent of the disturbance are increased. With only small percentages of the shoreline left unscraped, and the regrowth process slowed and limited, monitoring the effects of this disturbance is imperative to making decisions about future, similar projects.

The ultimate goal of this study was to establish and test a robust sampling design to compare the differential vegetation responses to three separate shoreline-restoration practices performed during an artificial dry down. These treatments will be tested in another study at a later date and include

- Mechanical removal of muck and vegetation with unrestricted succession (i.e., no herbicide management) during dry down.
- Mechanical removal during dry down, followed by herbicide application to aid establishment of desirable species.
• Aggressive herbicide application during and following dry down, with the goal of eliminating unwanted species without any mechanical removal of substrates or vegetation.

• No treatment (control), other than artificial dry down.

These treatments were not applied during the term of this study, with the dry down and muck removal process beginning several months after sampling concluded.

The primary objective of this study was to collect baseline data for the experiment prior to dry down and treatment application. This included 1) defining pre-existing littoral communities and their compositions, 2) identifying the underlying environmental gradients associated with littoral distributions, and 3) using these baseline data to construct a predictive vegetation model as an example of a future management tool in lake restoration.

Methods

Study Sites

The littoral zone of Lake Toho is highly variable in terms of slope, communities, wave actions, shoreline use, and so on. To minimize inter- and intra-site variation that would confound treatment comparisons, yet provide robust spatial inference, we chose three replicate areas (study sites) with similar slopes, an absence of physical anomalies such as coves, stream outflows or abrupt changes in topography, and areas with similar grazing pressures, all bordered by cattle ranches (Figure 3-1). Cattle ranches are the predominant land use practice for the southern two-thirds of the lake, with most ungrazed or substantially developed shorelines occurring on the northern end.

The sites all contained fairly dense stands of Pontederia and occupied a depth zone of roughly 0–135 cm (0–53 in) in water depth at a maximum pool stage of 16.75 m
Figure 3-1. Locations of three replicate study sites receiving various treatments. Site one is located just south of Brown’s Point on the south western shoreline of the lake, site two is located on South Steer Beach on the southeastern stretch of shoreline and site three is located in Goblet’s Cove on the east shore. Each study site stretched 1600 m (approx. 1 mi) of shoreline, composed of the four previously described treatment blocks of 400 m each (Figure 3-2). Maximum water depth of the plots, or their lakeward extent from the shoreline, was delimited by the approximate maximum water depth to be mechanically scraped during a dry down and extended just beyond the deep water extent of the *Pontederia* community. The total area of each treatment block varied slightly then, as each was 400 m in shoreline length but the lakeward extent determined by slope and community type. A 25 m spray buffer was established around each 1600 m study site to minimize the effects of routine herbicide applications in other areas of the lake. Due to the extremely invasive nature of water
hyacinth (*Eichhornia crassipes*) and water lettuce (*Pistia stratiotes*) and given the problems they have caused on Lake Toho historically, occasional spraying of small groups of these species was allowed when and if they appeared. Additionally, study sites were unable to be isolated from lake-wide applications of floridone treatments, which were applied systemically in the constant management of the nuisance submersed aquatic, *Hydrilla*. All other applications, however, including the periodic spraying of cattails or floating mats was eliminated.

Digital Orthographic Quarter Quads (DOQQ’s) taken in 1999 at 1-m$^2$ resolution were layered with a bathymetric map (Remetrix LLC 2003) of the lake using Arcview GIS 3.2 software. Eight random sample points were selected in each treatment block, stratified by four depth classes. The locations of these points were restricted to areas with a maximum slope of 0.3 m over 30 m. This was accomplished by overlaying a 30x30 m grid onto the bathymetric GIS (Geographical Information Systems) layer and restricting point selection to the contour lines that were at least one grid cell apart. Two of the grid cells were randomly selected from each depth class and the coordinates of their centroids were located in the field with a Global Positioning System. This procedure resulted in 32 random sample locations per study site, eight per treatment block and two per depth class, all located a minimum of 30-m apart and on similar slope gradients.

Sampling was initiated in June of 2002, providing two years of pretreatment habitat descriptions. All three study areas were sampled in their entirety twice a year, in June and December of 2002 and May and December of 2003. These sampling times coincided with low pool (summer) and high pool (winter) water stages as well as growing and
Figure 3-2. Individual study sites and their assigned treatments. A) Site 1. B) Site 2. C) Site 3. White is designated as a control plot, Orange is an aggressive herbicide treatment, Green is muck removal without herbicide follow-up and Blue is muck removal followed by repeated herbicide application.
Figure 3-2. Continued

non-growing seasons. For temporal analyses, one site was randomly selected for sampling each month, resulting in 11 months of 32 samples in the period of our study.

Environmental Variables

Vegetation samples were collected using a 0.25-m² quadrat, cutting all standing vegetation at the substrate level and placing it in plastic bags where it was transported to the University of Florida for sorting. The numbers of stems were counted for each species in each quadrat and the species were then oven dried to a constant weight to determine dry biomass. Importance values were calculated for each species in each quadrat with the formula:

\[(\text{Relative Biomass} + \text{Relative Density})/2 \times 100\]

This value gives a good estimate of species importance within a given quadrat and is not biased towards large, few-stemmed (e.g., *Typha* spp.) or small, numerous-stemmed
species (e.g., Eleocharis spp.) (McCune and Grace 2002). This calculation also relativizes 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.

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

Hydrological variables were all collected based on the lake stage as recorded by water control structure S-61 H on the south end of the lake. The average of at least four water depths taken at each sampling location was referenced to the lake stage on that day, giving a rough estimate of elevation for each sample. All depths were computed based on high pool stage (16.75 m NGVD). Hydroperiods were then calculated for each location based on the number of days flooded over the two year period of October 2001 to October 2003.

Data Analysis

The four sampling periods during the winter and summer of 2002–2003 yielded four repeated measures of the 96 sampling locations. Plant species densities and biomasses in each quadrat were summed from those sampling periods and then relativized and their Importance Values (IV) computed. This gave an estimate of the relative importance of each species in each quadrat over the four sample periods. For
example, the stem counts and biomasses of species one (Sp₁) in quadrat one (Q₁) were
added together for the four sampling periods. Assuming the species occurred in all four
samples, the formula would look like

\[(Sp₁Q₁T₁ + Sp₁Q₁T₂ + Sp₁Q₁T₃ + Sp₁Q₁T₄) = \text{Importance Value}\]

The IV’s of all species were added together and a percentage of the total
cumulative IV was calculated for each species. To reduce noise from rare species, only
those with cumulative IV’s composing 95% of the total were retained for analysis.
Typically, species that occur in <5% of the samples are deleted (McCune and Grace
2002) but we used 5% of the total IV. This method is 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.

The resultant matrix consisted of 96 samples by 24 species, reduced from the 66
species encountered throughout the study. All analyses of this matrix, unless otherwise
specified, were performed using PCORD software (McCune and Mefford 1999).

Outlier samples were tested for using an Outlier Analysis, which creates a
frequency distribution of average Sorenson distances of each sample from every other
sample in species space. At a cutoff level of 2.0 standard deviations from the grand mean
(McCune and Grace 2002), no outliers were detected.

A hierarchical, agglomerative Cluster Analysis was performed to find groups (or
communities) of similar species compositions. 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
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 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 results are expressed as a percentage, or Indicator Value, which is a measure of how representative a species is of a particular group. A value of 100 would indicate a perfect representative, a species that was always present in that group and never occurred in any other group. The statistical significance of that value is then evaluated with a Monte Carlo test (1000 permutations), with the null hypothesis being that the value is no larger than expected by chance (McCune and Grace 2002). The corresponding p-values of each species were the basis for the decision on how many clusters to choose (i.e., the level of clustering that produced the most species with p-values <0.05) (McCune and Grace 2002). The species with low p-values and high indicator values were used as the community descriptors (cluster labels) in future analyses.

The mean IV’s of the indicator species at several depths were tallied for each cluster and plotted against water depth. This was done as a simple, direct gradient analysis to show a preliminary distribution of communities as related to depth.

A Nonmetric Multidimensional Scaling (NMS) ordination was used to assess the dimensionality of our dataset (see following paragraph). This method of ordination works well with typical heterogeneous community datasets that are laden with zeros and
have non-normal distributions. Generally, in a species by sample unit matrix there may be a large proportion of zeros, or many species with few occurrences (high beta-diversity). The broader the range of environment covered by the study, the more sparse the matrix. This creates problems in many ordinations as zeros can be interpreted as shared values or positive relationships and are grouped together. This is referred to as the “zero-truncation problem” (Beals 1984 and McCune and Grace 2002). NMS is less affected by this problem because of its use of ranked distances. Additionally, NMS avoids assumptions of linear relationships among variables unlike other, more common ordination methods like PCA and CCA.

The purpose of the ordination was exploratory in nature to assess the dimensionality of the dataset (i.e., to see how well the data were structured). Too many dimensions are difficult to interpret and would be representative of a very complex dataset. The goal of the ordination is to examine the data in as few dimensions as possible, without losing the structure inherent in the data. Each dimension, or axis, is synthetic and represents measured or unmeasured environmental variables along which samples are distributed. The amount of variance explained by the ordination and how it is distributed along the primary axes is reported as a coefficient of determination \( (r^2) \) between distances in the ordination space and the original space. Pearson and Kendall correlations of the measured environmental variables are also calculated to show which, if any variables are related to the synthetic axes. The overall structure, or how well the dataset was able to be grouped, is reported as a stress value and instability measure. McCune and Grace (2002) state that stress values for community data typically lie
between 10 and 20 and instabilities around 0.0001. Clarke (1993) and McCune and Grace (2002) give more information on NMS.

Ordination results are shown in a graph of sample units plotted in species space in the number of dimensions (axes) suggested, grouping samples with similar species compositions and separating those with differences. This plot shows the relationship of each sample to one another; the larger the distance between samples, the more dissimilar their compositions. To show the distribution of samples along the measured environmental gradients, joint plots of correlated variables ($r^2 > 0.30$) were overlayed onto the ordination diagram, with length and direction representative of their correlation to the axes. The sample units were color coded according to the groups formed by the Cluster Analysis to show community distribution along the gradients.

A Classification And Regression Tree (CART) model (S-Plus Tree Library, De’ath 2002) was then used to predict the communities identified by the cluster analysis using the measured environmental variables alone. These models have been applied most often to classify habitats or vegetation communities based on environmental characteristics, resulting in an overall description of how different the groups are, which variables distinguish the groups and a predictive model that can classify new samples into those groups (Urban 2002). This procedure works by recursively partitioning the multidimensional dataset into subsets that are more homogeneous in terms of the response variable, in this case, cluster or community membership (Vayssieres et al. 2000). The heterogeneity of each subset is measured as an impurity, calculated in our model using the Gini index (Breiman et al. 1984, Crawley 2002, Venables and Ripley 2002). The goal of each split is to maximize the reduction in impurity. The model
identifies a single variable (and its threshold value) as the indicator for each branch of the
tree, as opposed to groups being distinguished along multivariate axes as in discriminant
analysis or logistic regression. This approach allows the inclusion of non-linear species
responses and is unaffected by interactions among variables (Vayssieres et al. 2000,
McCune and Grace 2002).

Once the largest possible tree has been grown, a process of eliminating superfluous
branches begins, called “pruning back to an honest tree” (Breiman et al. 1984). This is
done by testing each subtree for its error rate based on data that were not used to grow the
largest tree. Using cross validation, which acts as a test sample while extracting
information for all the cases of a data set, the final tree is constructed from all of the data,
using the best tree size (Vaysieres et al. 2000). The performance of the model is
measured by a misclassification rate, while the amount of variation explained by the tree
is reported as 1-Relative Error, or more strictly, 1-Cross Validated Error.

The final output is a pruned tree with barplots under each leaf showing the
composition of the final groups, as well as the number of samples in that leaf. Threshold
values of the variables determining the splits are shown at each node and the length of the
branches between nodes indicates the strength of the split. Several combinations of the
variables water depth, hydroperiod, percent organic and bulk density were used as
continuous predictors, while site and whether or not the sample occurred on a floating
mat were used as categorical variables. The final tree incorporated water depth, bulk
density, study site, and floating mat variables.

A Multivariate Regression Tree (MRT) analysis was conducted to identify
communities based on species IV’s and where they occurred along environmental
gradients, and to compare the resultant communities (leaves of the tree) with those formed in the cluster analysis and CART model. This was done with the same Tree Library in S-Plus as our CART analysis, which is somewhat limited in terms of distance measure options. This software only allows for Euclidian distance measures with MRT analyses, which is not typically used with non-normal data. De’ath (2002) and Urban (2002) suggested ideally using a distance-based MRT (db-MRT) for data of this type, but since we were primarily interested in MRT as an independent comparison to the other analyses, we opted for a practical rather than ideal solution and employed the Euclidian distance measure provided in the software. 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 this 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. Species variances are tabulated to show the contributions of individual species at each split and how well the tree explains their variations, as well as the percent of variation explained by each split. 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 but where they occurred on the environmental gradients as well, providing a more detailed, inclusive description than those defined by the Cluster Analysis.
Results

Of the 66 species recorded over the four sampling periods, 24 comprised the top 95% of the cumulative importance values (Figure 3-3, Appendix A). The summed dataset resulted in 96 samples by 24 species, which was divided into five communities based on the cluster analysis. The number of clusters was chosen based on the ISA, where the group with the highest number of species with indicator values greater than expected by chance was selected. With five groups, 17 of the 24 species had p-values <0.05 (Table 3-1). The ISA identified the following species as strong indicators of community type (clusters):

- **Luziola fluitans**: (LUZFL) also known as *Hydrochloa caroliniensis*
- **Nuphar luteum and Nymphaea odorata**: (NUPLU_NYMOD) *Nuphar luteum* is currently being reclassified as *Nuphar advena*
- **Pontederia cordata and Alternanthera philoxeroides**: (PONCO_ALTPH)
- **Hydrilla verticillata, Lymnobium spongia, and Ceratophyllum spp.**: (HYDVE_LYMSP_CERSP)
- **Panicum repens and Eleocharis spp.**: (PANRE_ELESP)

These groups are hereafter referred to by species code, which consists of the first three letters of genus and the first two of specific epithet (e.g., *Luziola fluitans* = LUZFL) (Appendix A).

The approximate distributions of these clusters were preliminarily displayed by simply plotting the mean IV’s of each of the indicator species in each cluster against water depth (Figure 3-4). This plot showed the PANRE_ELESP community occurred in the shallowest depth zones, exhibiting a bimodal distribution with LUZFL occurring at intermediate depths. The PONCO_ALTPH community completely dominated depths
ranging from roughly 0.6–1.2 m in depth, while the HYDVE_LYMSP_CERESP and NYMOD_NUPLU communities occurred at deeper water depths.

The NMS ordination resulted in three dimensions, cumulatively explaining 78% of the information in the dataset. Axis 1 explained the majority (41%) and bulk density and percent organic were most correlated (Pearson and Kendall) to this axis ($r^2 = 0.54$ and 0.27, respectively). Water depth and hydroperiod were most correlated to Axis 2 ($r^2 = 0.55$ and 0.48, respectively), but this axis explained the least amount of variation (17%). Axis 3 was the second most important axis, explaining 21%, suggesting some of the structure in species composition remains unexplained by our measured variables.
Figure 3-5 is a plot of sample units in species space, showing the two dimensions most correlated to our measured environmental variables. By overlaying cluster membership onto the ordination, we see the distribution of the communities along these axes and their relation to one another.

Shallow water communities are located at the top of the graph and deeper water communities at the bottom. Those associated with highly organic soils are on the left and those with high bulk densities (mineral, low organic) are on the right. This figure also shows the obvious interactions between hydroperiod and water depth as well as between bulk density and percent organic, and their orthogonality to each other. Figure 3-6 is the

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Species with high indicator values are highlighted accordingly and are used as community descriptors for each group.
same diagram but with the plots labeled, showing a clear grouping of Site 1 in the deepest water zone. Nearly the entire HYDVE_LYMSP_CERSP community comprised Site 1 samples, while the deeper samples of Site 2 and 3 lie within the PONCO_ALTPH community. The labels assigned to each sample indicate the site first (1-2-3), the treatment plot second (A-B-C-D), the depth class third (1-2-3-4) and which of two samples it represents from that depth class last (A-B).

Figure 3-4. Plot of mean IV’s of the indicator species in each cluster over several depth classes

Plotting the weighted average species scores onto the ordination diagram shows the average position of each species along each ordination axis (McCune and Meoff 1999). Figure 3-7 shows all 24 species and their relative positions to the measured gradients, with the indicator species from each cluster highlighted accordingly. The species occupying the upper right corner of the graph, in the shallow water and with high bulk
densities are mostly grassy species, including *Eleocharis* spp., *Axonopus furcatus*, *Panicum repens*, *Luziola fluitans*, *Eleocharis quadrangulata*, and a small, succulent

Figure 3-5. NMS ordination plot of sample units in species space, color coded by community. Distances between samples is representative of the dissimilarities in species compositions. Joint plots of correlated environmental variables are displayed as red vectors, based on Pearson and Kendall correlation coefficients. The direction and length of the vector is representative of the direction and strength of the variable’s relationship to the corresponding axis.
Figure 3-6. The same NMS plot shown in Figure 3-5 but with sample units labeled for interpretative purposes.
Figure 3-7. Weighted average species scores overlayed onto NMS ordination plot. Indicator species are highlighted and color coded according to cluster (community) membership. Locations are representative of each species’ average location along the measured environmental gradients.

*Ludwigia repens*. As the samples increased in depth, the bulk densities generally decreased. The species with the lowest bulk densities and organic matter were

*Pontederia, Sagittaria lancifolia* and *Typha* spp. The deepest water samples had higher bulk densities and consisted of mostly submersed or free floating species, including

*Hydrilla, Utricularia* spp., *Ceratophyllum* spp., and *Lymnobium spongia*. 
We can also show the distribution of our indicator species in relation to these gradients by scaling the symbols of the sample units they occurred in according to their IV’s; the larger the symbol, the higher the IV in that sample. There was considerable overlap between samples with high values of Panicum repens and Eleocharis spp., justifying the grouping of these species into a single community (Figures 3-8 and 3-9). Luziola fluitans was also important in several of the PANRE_ELESP samples, though highest values occurred in slightly deeper water (Figure 3-10).

Dominance of Pontederia is evident in Figure 3-11, though some overlap occurs with the LUZFL community at shallower depths and higher bulk densities, representing the transitional area between dense Pontederia and shallower, grassy communities. The high values of percent organic matter associated with this community is easily displayed by scaling the sample symbols according to their soil percentages, instead of their species IV’s. Clearly, there is a strong relationship between samples with high IV’s of Pontederia and those with highly organic soils (Figure 3-12). Figure 3-13 shows the distribution of Hydrilla along the gradients.

The CART model produced a tree pruned to six leaves, with four of the five communities represented (Figure 3-14). The NYMOD_NUPLU community was not delineated at this level of branching, while the LUZFL and the PANRE_ELESP communities were found at varying levels of dominance depending on soil characteristics and water depth. Essentially, the PANRE_ELESP community was completely dominant at less than 18 cm (7 in) in water depth but overlapped with LUZFL from 28–57 cm (11–22 in). LUZFL, meanwhile, was dominant between 18–28 cm (7–11 in) and was the most dominant community at less than 57 cm (22 in) when bulk densities were low.
Figure 3-8. Importance values of *Panicum repens* in the sample units plotted in the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 3-9. Importance values of *Eleocharis* spp. in the sample units plotted in the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 3-10. Importance values of *Luziola fluitans* in the sample units plotted in the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 3-11. Importance values of *Pontederia cordata* in the sample units plotted in the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 3-12. Percentage of organic matter in each of the sample units plotted in the NMS ordination. Larger symbols represent percentages of organic material within that sample.
Figure 3-13. Importance values of *Hydrilla verticillata* in the sample units plotted in the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 3-14. CART model of community distribution along the measured environmental gradients. This model was pruned from a maximum tree size of 12 branches to six, based on a cost complexity pruning curve, selecting the smallest tree within one standard error of the best. The numbers of samples in each leaf are shown in parentheses below each bargraph, which shows the compositions of communities within each leaf (e.g. nearly all of 53 samples in the right-most leaf are the PONCO_ALTPH community).

On the deeper water side of the tree, two leaves were formed based on bulk densities. The PONCO_ALTPH community had lower bulk densities (<0.93g/cm³) while more mineral soils had HYDVE_LYMSP_CERSP communities. The number in parentheses below the PONCO_ALTPH community shows the complete dominance of this group over all others in the tree, with 53 of the 96 total samples occurring in this group. Bulk density was slightly more important in determining community distribution in the model than water depth, while site and floating mat categorical variables were the
least important. The misclassification rate of the model was 35% and the amount of variation explained was 64% (1-Relative Error). These values are well within range considering the dynamic and complex system this dataset represents.

The confirmatory MRT was pruned to eight leaves with very similar groups as the CART model (Figure 3-15). Water depth was only slightly more important than bulk density in leaf formation, while site differences did account for one split in the tree. The first split was at 48 cm (19 in) in water depth, with Panicum repens, Luziola fluitans, and Eleocharis spp. comprising the shallower groups, very similar to the CART model. Below 18 cm (7 in) in water depth, Eleocharis was common, while between 18 and 28 cm (7 and 11 in) Luziola was extremely dominant. From 28–48 cm (11–19 in), however, there was a considerable mix of all three species, Panicum repens, Luziola fluitans and Eleocharis spp. This overlap between communities was also evident in the NMS diagram.

On the deeper water side of the tree, between 48 and 61 cm (19 and 24 in), a mix of Luziola and Pontederia is found representing the border between the shallower grassy communities and the dominant zone of Pontederia. The dense, monocultural zone of Pontederia occurred between 61 and 108 cm (24 and 42.5 in) with 36 of the 96 total samples representing this group. At water depths greater than 108 cm (42.5 in), however, there were three groups depending on site and soil characteristics. Site 1 had very dominant Hydrilla and Lymnobium spp., while Sites 2 and 3 had Nymphaea odorata at higher bulk densities and a Pontederia/Hydrocotyle spp. community at low bulk densities. The occurrence of Hydrocotyle spp. with Pontederia at that water depth and
Figure 3-15. MRT analysis, with terminal groups of species based on IV’s and their associated environmental variables. This confirmatory analysis shows species groupings and distributions along environmental gradients, independent of the cluster analysis. The numbers of samples in each leaf are shown in parentheses below each bargraph, which shows the compositions of species within each leaf.

low bulk densities is indicative of a floating mat community. This difference between sites in the deep water was also evident in the NMS diagram (Figure 3-6).

Table 3-2 details the nodes of the tree, showing the contributions of each species at each split and the variance explained for each species. For example, PONCO comprises 27.8% of the total species variance, of which 19.8% is explained by the tree, 8.7% by the first split. LUZFL, also responsible for the first split, comprises 19.9% of the total species variance, 10.7% of which is explained by the tree, with 5.6% in the first split.
The second split of 18cm is determined by LUZFL (1.2%) and ELESP (1.2%), and the third by LUZFL (2.8%) and PANRE (1.1%). The fifth split in the tree, separating Sites 2 and 3 from Site 1 is determined by HYDVE (5.5%). These five species, PONCO, LUZFL, PANRE, ELESP, and HYDVE comprise 75.3% of the total species variance, with 47.6% of it explained by the tree. Cumulatively, then, these species comprise 87.5% of the variance explained by the tree (47.6% of 54.4%). This confirms their importance as species representative of structure in our dataset, as suggested by the Indicator Species Analysis.

The importance of the environmental variables is also displayed by Table 3-2, with the summed total of each column representing the tree variation explained by that threshold value of the variable in the split. The first split of 48 cm in water depth was by far the most important, accounting for 36.4% of the variation explained by the tree (19.81% of 54.43%). This suggests the largest differences in communities and the most obvious structural variations occurred at roughly 48 cm in water depth. The second most important split was at 108 cm in water depth, accounting for 21.4% (11.65% of 54.43%) of the variation. These two splits represent the shallow and deep water extent of the PONCO community, respectively, and outline the two primary community transitional zones in terms of species compositions and distributions along the water depth gradient.

**Discussion**

In vegetation science, the concept of the plant community is absolutely fundamental. It is at the community level that populations and individuals of a plant species can be identified and grouped together to characterize the vegetation of an area of a few square meters to several square kilometers. It is also at this level that the effects of
Table 3-2. Species variance in the MRT analysis of the Treatment-Selection study.

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Column totals represent the contribution of each split to the amount of variation explained by the tree. Row totals represent the amount of species variance explained by the tree (tree total) and the contribution of each species to total species variance, respectively.

Allogenic factors are more easily examined and quantified, as interactions between species affect the responses of individual species (Kent and Coker 1992). No studies on Lake Toho in the past have approached vegetation description from a community level, nor have any documented quantitative measures of individuals. This study provides the first detailed description of the littoral communities targeted by restoration efforts, explains their distributions along environmental gradients, and implements a sampling design for the development of predictive management tools in lake restoration.
Community Descriptions

The Cluster Analysis, the NMS ordination, the CART and the confirmatory MRT analyses all described the dominance of the PONCO_ALTPH community. NMS ordination diagrams clearly showed the differences in soil characteristics for this group, having the lowest average bulk density (0.27 g/cm$^3$) and highest average percent organic matter (51.6%) of any community. The CART model showed that regardless of site differences, 53 of 63 samples taken in over 57 cm (22 in) of water were dominated by PONCO_ALTPH. The confirmatory MRT produced very similar results, with 55 of 69 samples in over 48 cm (19 in) of water composed primarily of Pontederia, only substantially occurring with other individuals at the shallower (48–61 cm) and deeper (>108 cm) ends of its range.

The three groups identified by the MRT at depths greater than 108 cm (42.5 in) consisted of Nymphaea odorata, Pontederia and Hydrocotyle spp., or Hydrilla and Lymnobium. The presence of Hydrocotyle spp. with Pontederia suggests that the community is floating at that depth, indicative of the deep-water extent of the Pontederia community, transitioning to either floating leaved or submersed species, depending on the site. At this transitional zone, habitats ranged from dense, organic floating mats to sparsely vegetated, sandy soils over the distance of as little as one meter. The factors determining community composition in this area were probably more related to storm events and wave energies than actual water depths. With calm, stable water levels the floating edge of the PONCO_ALTPH community would most likely march lakeward, while periods of high wave energies would work to push back, break apart and even fold over the floating mat edge (Figure 1-3, Chapter 1). Some of the most diverse samples in this study occurred on thick floating mats, with as many as 18 species in one quadrat.
The small groups identified in this study containing *Nymphaea* and *Hydrilla* (14 of 96) were not representative of their overall presence in the littoral zone, but rather a result of their more frequent occurrence in deeper water beyond the study sites. The Whole-Lake Monitoring study detailed information regarding compositions and distributions of communities beyond 130 cm in depth (Chapter 4).

The transition from dominant *Pontederia* to shallower, grassy species was represented by the *Luziola fluitans* and *Pontederia* mixed group formed between 48 and 61 cm (19 and 24 in) in depth by the MRT. From there, groups were formed with varying levels of *Panicum repens*, *Eleocharis* spp., and *Luziola* as depths decreased. The same patterns were evident in the CART model, the NMS ordination, and the plot of IV’s vs. depth, showing a general, dominant mixture of these species in shallow water. The highest average species richness was in the PANRE_ELESP and the LUZFL communities, averaging 12.4 and 7.7 species per sample, respectively. As water depths increased, richness decreased, going from 6.0 species per sample in the PONCO_ALTPH community to 5.9 and 5.3 in the NYMOD_NUPLU and HYDVE_LYMSP_CERSP communities, respectively. However, if the floating mat samples were excluded from the PONCO_ALTPH community, two of which had 14 and 18 species in a single quadrat, the average richness fell to 5.1 species per sample, the lowest average of any community.

These results show the highly competitive nature of *Pontederia* and its associated community in shallow water habitats and its ability to accumulate organic material with its high productivity and densities. However, our data do not provide any information as to the extent of organic accumulation in this community as we only collected the top 10 cm of substrate for our soils analyses. Based on several deeper cores taken for
photograph purposes, however, it is our belief that Site 3 had the deepest organic soils but still rarely in excess of 20 cm. This would be logical since Site 3 occurs in a narrow, isolated cove on the east side of the lake with presumably much lower energies than Sites 1 and 2. Additionally, this cove is the receiving point for canal C-31, which directly drains East Lake Toho and is most likely a source of elevated nutrient levels. In retrospect, peat depths in addition to our measured properties would have been useful for comparative reasons, but our focus was on the soil characteristics in the zone of highest root/rhizome activity.

Regardless of the actual depths of organic material on the lake, there is good evidence that the majority of the littoral zone has very sandy substrates both shoreward and lakeward of the *Pontederia* community. With the exception of the NYMOD_NUPLU community (21.3%), no other group had an average organic soil content of more than 11%, as compared to 51.6% in PONCO_ALTPH. In fact, the sandiest soils occurred in the HYDVE_LYMSP_CERSP community, with an average of only 3.6% organic material. These data highlight the concerns of the lake managers, showing that much of the shallow reaches of littoral zone on Lake Toho are densely vegetated and dominated by *Pontederia* communities, having low diversities, highly organic soils and occasionally forming floating mats. These communities are located primarily between 57 and 108 cm (22 and 42.5 in) in water depth at maximum pool, beyond which lie sandy substrates and several communities of floating leaved and submersed aquatics.

The formation of such distinct zones of vegetation is no doubt aided by the stable water levels maintained since the lake was impounded in 1964. For example, lake stage
data for the 10 years prior to the dry down initiated in November of 2003, show that the present dense zone of *Pontederia* was flooded 82-100% of the time. The highest water levels over this period covered the shallow edge of this community with up to 0.88 m of water, while the lowest water levels never exposed the deep edge, remaining flooded at a minimum depth of 60 cm. However, if we look at the stage data for a 10-year period prior to the impoundment (1950-1960), this same zone had a hydroperiod of 66%–90%, drying out much more frequently than at present. In fact, the lowest water levels dropped below even the deepest edge of this community by nearly 0.5 m. The biggest contrast, however, between historic and present day water levels, were the flood stages. The highest water levels over the historical 10-year period would have flooded even the shallowest edge of this community by almost 2 m. Such an astatic environment would surely limit the ability of species like *Pontederia* to dominate large sections of shoreline, with droughts encouraging germination of grass species and flood waters ripping loose floating mats. It is clear from the results of this study that the *Pontederia* community has benefited from the stabilized lake levels and has increased its shoreward and possibly lakeward extent since impoundment.

**Previous Studies**

Vegetation studies in the early 1970s (Holcomb and Wegener 1971) and late 1950s (Sincock et al. 1957) recorded species frequencies along transects that ran perpendicular to shore and spanned the entire extent of the littoral zone, providing inundation tolerances or distributional ranges of each species. The only previous study that compared pre and post muck-removal habitats in 1986 (Moyer et al. 1989) also looked at individual species responses by recording their frequency of occurrence along four transects. These data were presented as the frequency of several common species and
gave no reports of how they were distributed along depth gradients. No quantitative measures were recorded and evidence of increased/decreased densities or changes in structural habitat characteristics could not be identified.

Though these three studies were conducted in different areas of the lake and used different techniques, a general trend in habitat change is still evident. The earliest study, prior to the impoundment of the lake in 1964, showed a higher diversity of grassy species in the zones now targeted for restoration, most of which no longer occur. However, Panicum repens and Luziola fluitans were among the most frequent in shallow areas even then. In the early 1970’s, Pontederia cordata and Polygonum spp. had appeared at low frequencies and were described as occurring in narrow bands just below the low pool line. It was reported that Luziola and Panicum were the dominant plants in the zones of periodic inundation and together with Pontederia served as good spawning habitat for sport fish, including largemouth bass. By the 1986 study, however, Pontederia, Polygonum and Alternanthera philoxeroides were among the most frequently encountered species, along with Luziola, Panicum repens and Bracharia mutica. These findings were more similar to the results of this study, though no quantitative comparisons can be made. While Panicum repens and Luziola still dominate the shallower areas, it appears that Pontederia has moved shoreward from the mean low pool level into the zone of periodic inundation. One reason for this may have been the dry down in 1987 that coincided with the muck removal. Wegener et al. (1973) suggested there were substantial increases in both the densities and expansion of Pontederia following the 1971 dry down, and similar results probably occurred after the 1979 and 1987 dry downs. Even the transects located in scraped areas showed an almost complete
rebound of *Pontederia* in just two years after the 1987 muck removal project (Moyer et al. 1989) and an even quicker response probably occurred in the unscraped areas.

**Management Implications**

The results of this study will help to more accurately determine *Pontederia* community responses to dry down and several other treatments. By measuring structural characteristics of the habitat targeted for restoration and defining the communities in terms of specific densities and biomasses, the effects of the various treatments will be quantified and much less cryptic than in previous studies. The CART model used in this study on the pretreatment data was able to predict which communities occurred in the targeted areas, given several environmental conditions. The MRT analysis was extremely supportive of those predictions and community definitions, as well as their distributions among water depths, soil types and site locations. Using the same CART and MRT analyses on data collected in the future, predictive models can be used to determine community types and responses to given treatments. For example, Figure 3-16 shows a hypothetical CART model that predicts communities based on several factors (type of treatment applied, water depth, time since application, etc.) that would provide managers with a valuable tool in lake restoration. These models will be applicable to future restoration efforts on Lake Toho as well as other similar lakes in the region. With the framework implemented in this study, the long-term monitoring programs necessary to determine the effects of these large-scale restoration efforts are now in place.
Figure 3-16. A hypothetical CART model to be created following years of post-treatment data collection. With reasonable probabilities, for example, one could predict community compositions based on the treatment applied and the location along the environmental gradients.
CHAPTER 4
WHOLE LAKE MONITORING

Introduction

The previous chapter dealt primarily with the pre-restoration communities lying within the targeted areas of muck removal. The sampling techniques of that project were designed specifically to monitor the differential successions of littoral communities following various treatments. Therefore, inter- and intra-site variations were minimized and the sampling efforts were restricted to depth zones receiving specific treatments. Beyond the treatment plots, however, similar restoration efforts are planned for most of the remaining shoreline, including muck removal and aggressive herbicide application to control successions. These treatments will undoubtedly have an enormous impact on the littoral communities of the lake, including those not specifically targeted by mechanical removal or even herbicide efforts. This emphasizes the need to monitor and document the spatial and temporal responses of the littoral zone as a whole, in addition to determining the efficacy of specific treatments, as discussed in Chapter 3.

Previous studies of natural or artificial dry downs on Lake Toho (Wegener et al. 1973, Moyer et al. 1989) and Lake Okeechobee (Smith and Smart 2004) have documented a rapid growth and lakeward expansion of several grass and sedge species (Eleocharis spp., Panicum hemitomon, Panicum repens, Paspalidium geminatum, Luziola fluitans, etc.) in response to sediment exposure. However, these studies generally only reported increases in frequencies and gave no estimates of changes in the structures of communities. Without such information, there is little known about the spatial and
temporal effects of such activities. For example, was the increase in grassy species
temporary or still evident years after flooding? Were the effects similar throughout the
lake and along the same depth gradients? How long, if ever, did it take for the littoral
communities to rebound to pre dry down conditions and for that matter, what were the
pre and post dry-down communities?

More questions arise as the intensity of restoration efforts increase and now include
mechanical removal and aggressive herbicide applications in addition to dry downs. The
ultimate goal of this study was to establish a long-term sampling protocol to determine
quantitatively, the spatial and temporal responses of littoral communities throughout
Lake Toho. Upon establishment, the objectives were to 1) define preexisting
communities and their compositions and 2) identify the underlying environmental
gradients associated with their distributions.

Methods

Study Sites

Lake Toho has a highly variable littoral zone in terms of slopes, wave energies,
shoreline activities, and so on, and the resultant communities differ as well. To capture
this variability, five monitoring sites were selected from the less-developed, southern
two-thirds of the lake (Figure 4-1). Sites 1, 3, and 4 were located in broad, gently sloping
areas of shoreline, presumably more sedimentary in nature and subject to lower wave
energies, while Sites 2 and 5 were located on much steeper, higher energy areas of
shoreline. Additionally, all sites were subjected to grazing pressures with the exception
of Sites 4 and 5.

The boundaries of each site were determined by placing a 60-ha rectangle on
DOQQ’s with 1-m² resolution (1999) and bathymetric (Remetrix) layers in ArcView GIS
3.2 software. The area of the rectangle stayed 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).

![Figure 4-1. Five study site locations, each encompassing the 0–2 m depth zone. Sites 4 and 5 were located on ungrazed shorelines and Sites 2 and 4 were located on steep slopes. Each site contained 18 sample locations, stratified by six depth classes, with two samples occurring in each.](image)

**Vegetation Sampling**

Sampling locations were stratified by six depth classes and were located on maximum slopes of 30 cm change over 30 m in distance. This was accomplished by placing 30x30 m grids onto the same GIS bathymetry layer and randomly selecting three grid numbers from each depth class (Chapter 3). Coordinates of the centroids were
recorded and the sample was located in the field with a GPS (Global Positioning System) on each sampling occasion. A total of three samples per depth zone were selected, resulting in 18 per site and 90 on the lake (Figure 4-1). These locations were sampled twice a year during high (winter) and low (summer) water periods, in June and December of 2003, and May and December of 2004.

Vegetation was clipped at the substrate from 0.25-m² circular plots and sorted by species. Stem counts and biomass were recorded on sight. Before weighing, each sample was squeezed and shaken until residual water was removed. While giving less accurate measures of biomass than dry weight methods, this was an efficient way to account for the overall size of an individual and combined with its stem count, the relative importance of a species in a particular quadrat. Importance values were calculated using the formula:

\[(\text{Relative Biomass} + \text{Relative Density})/2 \times 100\]

This value is not overly biased by large, few-stemmed species (e.g., *Typha* spp.) or small, numerous-stemmed species (e.g., *Eleocharis* spp.). This measure had an additional advantage since wet weights were used and undoubtedly, different species had differential amounts of water retention, even after squeezing. The Importance Values (IV’s) were relativized to each sample, eliminating potential bias of heavier weight, submersed species in one sample versus drier, shallow-emergent species in other samples.

**Data Analysis**

The four sampling periods during the winter and summer of 2002–2003 yielded four repeated measures of our 90 sampling locations. The densities and biomasses of the species in each quadrat were added together from those sampling periods and then
relativized and IV’s computed. This gave an estimate of the relative importance of each species in each quadrat over the four sample occasions. For example, the stem counts and biomasses of species one in quadrat one were added together over the four sample times; assuming the species occurred each period, the formula would be

\[(Sp_{1Q1T1} + Sp_{1Q1T2} + Sp_{1Q1T3} + Sp_{1Q1T4}) = \text{Importance Value}\]

The IV’s of all species were added together and a percentage of the total cumulative IV was calculated for each species. To reduce noise from rare species, only those with cumulative IV’s composing 95% of the total were retained for analyses.

Samples were grouped based on species compositions using an agglomerative, hierarchical cluster analysis. The number of groups and the representative species of those groups were identified using an Indicator Species Analysis (ISA). A Nonmetric Multidimensional Scaling (NMS) ordination was used to illustrate the relationships between groups and to show their distribution along the water depth gradient. Detailed descriptions of these analyses are provided in the Methods section of Chapter 3.

A Classification And Regression Tree (CART) analysis was performed to see how accurately the communities defined by the cluster analysis could be predicted using water depth, study site, grazing influence and whether or not a sample occurred on a floating mat as environmental variables. A Multivariate Regression Tree (MRT) was then created to compare the communities defined by the cluster analysis to those defined by species IV’s and their positions along environmental gradients. Detailed descriptions of these methods are provided in Chapter 3.

**Results**

Of the 52 species recorded over the four sampling periods, 20 comprised the top 95% of the cumulative importance values (Figure 4-2, Appendix B). Our summed
dataset resulted in 90 samples by 20 species, which was divided into six communities based on the Cluster Analysis. The number of clusters was chosen based on the ISA, where the group with the highest number of species with indicator values greater than expected by chance was selected. With six groups, 14 of the 20 species had p-values <0.05 (Table 4-1). The ISA identified the following species as strong indicators of those groups:

- **Luziola fluitans and Panicum repens**: (LUZFL_PANRE)
- **Typha spp.**: (TYPSP)
- **Pontederia cordata**: (PONCO)
- **Hydrilla verticillata and Ceratophyllum spp.**: (HYDVE_CERESP)
- **Nuphar luteum**: (NUPLU)
- **Paspalidium geminatum**: (PASGE)

The NMS ordination resulted in a three dimensional solution, cumulatively explaining 0.739 percent of the variation in our dataset. Axis 1 explained the majority, 0.392, with Axes 2 and 3 explaining 0.195 and 0.152, respectively. For illustrative purposes, only the two most important dimensions were displayed. Pearson and Kendall correlation coefficients showed a fairly strong correlation of water depth to Axis 1 ($r^2 = 0.576$) and a slight correlation to Axis 2 ($r^2 = 0.307$). Figure 4-3 shows a joint plot of sample units in species space with the water depth correlation vector. The distance between sample units is representative of the dissimilarities in their species compositions, with like samples grouped and unlike samples separated. The correlation of water depth to Axis 1 and the direction of the vector suggest that the samples located on the right side of the graph occur in deeper water than those on the left. The numbers of species that occurred in each sample before rare species were deleted was also plotted as a diversity, or richness measure. Richness was found to be slightly correlated to Axis 2, simply
Figure 4-2. Percent of cumulative Importance Value (IV) for each species, with 20 comprising 95% of the total. See Appendix B for a list of these 20 and the 32 less common species.

showing that the samples near the bottom of the graph generally had more species than those near the top.

Additionally, the weighted average species scores were plotted along these axes, showing the average location of each species along the measured gradient (Figure 4-4). Keeping in mind that water depth increases from left to right along Axis 2 and diversity increases from top to bottom along Axis 1, we can suggest that generally, the species to the right occur in deeper water, while the species on the top of the graph occur in fairly uniform, or even monotypic communities. This indicates that when those species occurred, diversity tended to be lower, or they tended to dominate each quadrat they were found in.
Table 4-1. Indicator values of species in the Lake-Monitoring study, with values ranging from 0-100.

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

The indicators species’ distributions in relation to these gradients can be shown by scaling the symbols of the sample units they occurred in according to their IV’s; the larger the symbol, the higher the IV in that sample. Figures 4-5 and 4-6, respectively, show how Panicum repens and Luziola occur frequently and with high values in the shallower depth zones as well as with higher diversities. Pontederia cordata, however, shows significant occurrence in other communities as well, specifically with the LUZFL_PANRE community at the deeper end of their range (Figure 4-7). Many of the samples in the deeper water had large amounts of Hydrilla (Figure 4-8) and a few were dominated by Paspalidium geminatum (Figure 4-9). The grouping of the HYDVE_CERSP and PASGE clusters and the occurrence of both species in either group shows the similarity and spatial proximity of these two communities.
Figure 4-3. Lake-Monitoring Study ordination plot of sample units in species space, color coded by community. Distances between samples is representative of the dissimilarities in species compositions. Joint plots of correlated environmental variables are displayed as red vectors, based on Pearson and Kendall correlation coefficients. The direction and length of the vector is representative of the direction and strength of the variable’s relationship to the corresponding axis.
Figure 4-4. Weighted average species scores overlayed onto the Lake-Monitoring study NMS ordination. Indicator species are highlighted and color coded according to cluster (community) membership. Locations are representative of each species’ average location along the measured environmental gradients.
Figure 4-5. Importance values of *Panicum repens* in the Lake-Monitoring samples, as plotted by the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 4-6. Importance values of *Luziola fluitans* in the Lake-Monitoring samples, as plotted by the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 4-7. Importance values of *Pontederia cordata* in the Lake-Monitoring samples, as plotted by the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 4-8. Importance values of *Hydrilla verticillata* in the Lake-Monitoring samples, as plotted by the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 4-9. Importance values of *Paspalidium geminatum* in the Lake-Monitoring samples, as plotted by the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.
Figure 4-10. Importance values of *Nuphar luteum* in the Lake-Monitoring samples, as plotted by the NMS ordination. Larger symbols represent large IV’s within that sample. Samples are colored according to community.

*Nuphar luteum* also overlaps with the HYDVE_CERSP community and occurs in the TYPSP community as well (Figure 4-10). The large spread of samples in the TYPSP community suggests *Typha* occurs over a broad range of water depths and occasionally overlaps with either the PONCO or NUPLU communities. The PONCO, TYPSP and NUPLU communities occur near the top of axis one, indicating lower diversities where these species dominate.
The CART model produced a rather complex tree, pruned to 11 groups. At this level, 68.8% of the variation was explained by the model, with a 40% misclassification rate. There were essentially three large groups formed; LUZFL_PANRE community occurring in <63 cm (25 in) of water, a mix of PONCO communities and transitional groups between 63 and 127 cm (25 and 50 in) of water, and a predominantly HYDVE_CERESP community occurring at depths greater than 127 cm (50 in) (Figure 4-11). There were several site differences delineated in the tree, most separating Sites 2 and 4 from the others. This separation occurred at both above and below 127 cm in water depth, indicating significant site variation at several depths. Sites 2 and 4 were split from the others at depths <127 cm due to a less robust PONCO community. The terminal groups of these sites showed a mixture of either LUZFL_PANRE or HYDVE_CERESP with the PONCO communities, while Sites 1, 3, and 5 displayed the more typical, monocultural PONCO group.

At depths >127 cm, Sites 2 and 4 were split from the others due to a more dominant PASGE community, with mixes of TYPSP and HYDVE_CERESP communities occurring at various depths. Sites 1, 3, and 5 however, all had robust HYDVE_CERESP communities at >127 cm in water depth.

The MRT was pruned to eight leaves and produced similar results to the CART (Figure 4-12). The four most abundant communities were *Luziola fluitans* at <63 cm (25 in) in water depth, a robust *Pontederia* community between 63 and 117 cm (25 and 46 in), dominant *Hydrilla* between 117 and 158 cm (46 and 62 in), and a codominant community of *Hydrilla* and *Paspalidium geminatum* at depths >158 cm (62 in). These
results were confirmatory of the CART model, with the same dominant species occurring at similar depth locations.

Figure 4-11. CART model of Lake-Monitoring community distributions along the measured environmental gradients. This model was pruned to 11 leaves based on a cost complexity pruning curve, selecting the smallest tree within one standard error of the best. The numbers of samples in each leaf are shown in parentheses below each bargraph, which shows the compositions of communities within each leaf (e.g., all 22 samples in the left-most leaf are the LUZFL_PANRE community).

One interesting difference between the MRT and CART model was the separation of grazed and un-grazed sites at <63 cm in water depth in the MRT. Sites 4 and 5 had no grazing pressures and the communities were much more diverse, with the terminal node represented by a suite of species rather than one individual, including *Eleocharis* spp., *Bacopa caroliniana*, *Bracharia mutica*, *Panicum repens*, *Paspalum notatum* and
**Pontederia.** The other substantial site differences occurred between 117 and 158 cm (46 and 62 in) in depth, with Sites 3 and 4 having significant *Nymphaea odorata* and *Typha* communities while Sites 1, 2, and 5 were dominated by *Hydrilla*.

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Figure 4-12. Communities identified in the Lake-Monitoring study by IV’s and their associated environmental variables, using the MRT analysis. This confirmatory analysis shows species groupings and distributions along environmental gradients, independent of the cluster analysis. The numbers of samples in each leaf are shown in parentheses below each bargraph, which shows the compositions of species within each leaf.

Table 4-2 details the species variance, amount explained by the tree, and the species responsible for each split of the MRT. *Hydrilla* comprised 22.5% of the total species variance, of which 13.03% was explained by the tree, 5.96% in the first split. Also responsible for the first split was *Pontederia*, with 3.97% of its variance explained. This simply means that the abundances of *Hydrilla* and *Pontederia* were both highly
variable among samples, and largely determined community structure as well.

*Pontederia* (4.14%) and *Luziola* (3.35%) determined the second split, while *Luziola* (2.62%), *Hydrilla* (1.74%), *Paspalidium* (3.26%), *Hydrilla* (5.13%) and *Typha* (1.71%) determined the remaining splits, consecutively. Summarily, these five species comprised 73.4% of the total species variance, 40.1% of which was explained by the tree.

Cumulatively, these species comprised 87% of the variance explained by the tree (40.1 of 46.3). This supports the results of the cluster and indicator species analysis which identified these species as indicative of the inherent community structure in our study areas.

Table 4-2. Tabulation of species variance for the MRT analysis of Lake-Monitoring sites.

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<thead>
<tr>
<th>Species</th>
<th>&lt;117cm</th>
<th>&lt;63cm</th>
<th>Site:4,5</th>
<th>Site:2</th>
<th>&lt;158cm</th>
<th>Site:1,2,5</th>
<th>&lt;145cm</th>
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</table>

Column totals represent the contribution of each split to the amount of variation explained by the tree. Row totals represent the amount of species variance explained by the tree (tree total) and the contribution of each species to total species variance, respectively.

The most important split in the tree occurred at 117 cm in water depth, accounting for 35% (16.25% of 46.32%) of the variation explained by the tree. The second most
important split occurred at 63 cm in water depth, accounting for 20.3% (9.42% of 46.32%) of the variation. These two splits represent the most abrupt changes in communities in terms of species compositions and their distribution along the depth gradient.

Discussion

Community Descriptions

There were six distinct communities identified within the littoral zone of Lake Toho during our study. Based on the NMS and CART analyses and confirmed by the MRT, most of these communities were distinctly distributed along the depth gradient, with the LUZFL_PANRE community dominating between the high and low pool water lines, dense PONCO communities occurring just above and below the low pool line, and the deeper water generally having either HYDVE_CERSP or PASGE communities. TYPSP and NUPLU communities were also present but were less common and more patchily distributed in the deeper water zones.

Average species richness for each community ranged from 9.5 species per sample in the LUZFL_PANRE community to 3.5 in the HYDVE_CERSP community, following a general decreasing trend with increasing water depths. The exception to the rule was the NUPLU community that had the deepest average depth of any community (159 cm) and the second highest richness, with an average of 6.0 species per sample. However, other deep water communities (HYDVE_CERSP and PASGE) had lower average depths than NUPLU due to their broader range of distribution, not necessarily because they never occurred in deeper water. However, the relatively high number of species in the few NUPLU samples is of interest and may help to explain the frequent visitation of these habitats by anglers.
The dominant PONCO community had higher average richness than the HYDVE_CERSP (3.5), TYPSP (3.8) and PASGE (3.8) communities, with an average of 4.8 species per sample. However, if the floating mat samples were excluded, having an average of 7.0 species per sample, the PONCO community richness fell to 3.6, the second lowest of all communities. The CART model found that between 63 and 127 cm (25 and 50 in) in water depth, the PONCO community was extremely dominant in 13 of 25 samples and had a significant presence in all 25, occurring with HYDVE_CERSP, LUZFL_PANRE, and TYPSP communities at these depths. The MRT confirmed these results, showing Pontederia as the single dominant species between 63 and 117 cm (25 and 46 in) in 19 of 23 samples and was still abundant in the remaining four samples, occurring with Hydrilla. These two species do not actually occur in the same area, spatially, but do occupy the same depths on occasion. Their grouping in both the CART and MRT analyses is representative of the transitional zone between the dense, leading edge of the PONCO floating communities and the open water, submersed communities, where sharp, distinct boundaries separate the two. The fact they do not overlap spatially is evident in the NMS diagrams of species IV’s or weighted species averages. Notice that the samples with high IV’s of either species do not overlap and that the two are very distant from each other in the ordination, showing distinctly different compositions between samples containing either species.

Variations in communities by site were delineated in CART and confirmed in the MRT, with each defining similar patterns. The CART model found that Sites 2 and 4 had more dominant PASGE communities in deeper water (>127 cm) than Sites 1, 3, and 5, which were dominated by HYDVE_CERSP communities. The MRT produced slightly
different terminal groups, showing a mixed community of *Paspalidium* and *Hydrilla* in all 23 samples (100%) in depths >158 cm, regardless of site, and that site differences occurred between 117 and 158 cm (46 and 62 in), with *Hydrilla* dominating those depths at Sites 1, 2 and 5. Sites 3 and 4 were found to have *Nymphaea* communities between 117 and 145 cm and *Typha* communities between 145 and 158 cm. The NMS diagram of species IV’s shows the regular occurrence of *Hydrilla* and *Paspalidium* at the same depths and even in the same samples (Figures 4-8 and 4-9). Additionally, the very close proximity of the two communities in the ordination, HYDVE_CERSP and PASGE, shows the similarities in their species compositions. It is probable that these two species occur together more often than the CART model suggests.

Most of the deeper water site differences were a result of the clumped distributions of the communities at those depths. While *Paspalidium* and *Hydrilla* tended to occur throughout the deep water, the floating leaved and cattail communities were much sparser and patchily distributed. *Panicum hemitomon* and *Scirpus californicus* were also patchy, and did not occur frequently enough in our samples to be classified as their own communities. While the shoreline slope dramatically affected the width of the communities between sites, their compositions or distributions by depth did not seem to differ consistently.

Another interesting site difference delineated by the MRT was between grazed and ungrazed sites at depths <63 cm. While there was no substantial difference in average species richness between the sites (9.5 and 11.7, respectively) there were no singly dominant species throughout the shallow depths of the ungrazed areas. The bar graphs under the terminal groups of the MRT show this difference well, as the eight samples
from the ungrazed sites had several frequently dominant species, while the 14 samples from the grazed sites were completely dominated by *Luziola* (Figure 4-12). The visual difference between the grazed and ungrazed shorelines was quite striking, with species like *Bracharia mutica, Hibiscus grandiflorus* and *Ludwigia* spp. much more prevalent in the ungrazed areas. Apparently, the low stature and carpet forming growth habit of *Luziola* allows it to escape herbivory while benefiting from the absence of canopy grasses eliminated by grazing. Without it, other species most likely tower above and shade out *Luziola*, resulting in several taller, dominant species in the ungrazed communities.

**Previous Studies**

The studies conducted in the late 1950s (Sincock et al. 1957) and early 1970s (Holcomb and Wegener 1971) suggest the littoral zone of Lake Toho has changed substantially over the last 30 years. Though their techniques did not provide quantitative estimates or community descriptions, general differences can be detected. Prior to lake impoundment, for example, *Pontederia* did not occur in the vegetation studies and species like *Psilocarya, Stenophyllus, Echinocloa,* and *Fuirena* were fairly common in the seasonally inundated areas of shoreline. *Hydrilla* was not even documented until 1972, with species like *Valisneria* occurring in the deeper water. By 1970, however, *Alternanthera philoxeroides, Polygonum* spp., and *Pontederia* had become more common, though still described as occurring in narrow bands below the low pool line. *Scirpus californicus* was reported to exist in stands up to several acres in size in deeper water and *Paspalidium* was described as abundant. These descriptions do not provide comparable estimates of the littoral communities to our studies, but do depict major changes.
While *Panicum repens* and *Luziola* have long been recorded in the shallow communities, they may be more dominant today than historically. Both the 1971 and 1987 dry down studies seemed to substantially increase the frequencies of *Panicum repens* (Wegner et al. 1973 and Moyer et al. 1989), an effect also documented on Lake Okeechobee (Smith and Smart 2004). The biggest difference lies within the *Pontederia* community, which has seemingly pushed the *Panicum repens, Luziola*, and *Eleocharis* spp. communities shoreward with stabilized water levels. Whether the large-scale removal of this community is an effective means in reestablishing grassy species in its stead is not yet known. The implementation of long-term sampling protocols and the detailed descriptions of pre-treatment communities provided by this study will help to answer that question.
CHAPTER 5
SUMMARY

Communities

The vegetation samples we collected from June 2002 through December 2003 provided detailed information on the composition and distribution of plant communities that occurred during this period. Unlike previous studies, we sought to define, analyze, and monitor vegetation at a community level rather than by individual species and to collect quantitative measures of habitat quality rather than frequencies or percent cover estimates. The communities we defined were based on biomasses and densities of species, giving strong representation of the habitat and compositions as they occurred. The results of our two studies were very similar, showing distinct zones of vegetation distributed along depth and soils gradients. The communities defined by the Cluster Analyses and their predicted distributions with the CART models were well supported by the confirmatory MRT analyses performed in both studies. Had soils data been collected for the Lake-Monitoring study covered in Chapter 4, stronger predictions of community distributions would have been available for areas beyond those targeted for muck removal. These results are based on the latest multivariate community techniques, using far more descriptive measures of the vegetation characteristics than collected previously. Such descriptions are the first of their kind for Lake Tohopekaliga, and the resultant predictive models may eventually be applicable to other lakes undergoing restoration activities. The pre-treatment littoral communities defined by this study are described below.
**Shallow Grasses and Sedges**

These communities generally occurred in depths of less than 60 cm at high pool stage, having a 10-year hydroperiod of roughly 25%–85% (based on lake stage data from 1993–2003). The dominant species in this community varied over small changes in water depth, with considerable overlap between the three most important species. The shallowest group was mainly comprised of several species of *Eleocharis*, and then shifted to *Panicum repens* and *Luziola fluitans* as depths increased. *Luziola* was the single most important species of the three except along grazed shorelines, where it was virtually non-existent. The *Luziola* community occurred over a broader range of soil properties than the others, with values ranging from 4.8–13.5% organic material. This community had the highest average species richness, ranging from 2–23 species per 0.25-m² quadrat, with an average of nearly 10. High specific diversities are common in boundary communities lying within seasonally inundated areas.

The ungrazed sections of shoreline had high values of *Panicum repens* and *Eleocharis* spp. as well, but were not singly dominant as in the grazed areas, occurring more frequently with *Bacopa caroliniana*, *Hibiscus grandiflora* and *Bracharia mutica*. These ungrazed shorelines differed in that no one or two individuals completely dominated the communities.

**Dense Emergents**

Occurring just above the low pool line and extending well into the continuously flooded zone (60–120 cm, or 24–48 in) *Pontederia cordata* formed an extremely robust community. There were as many as 20 individual plants (not just stems) sampled in a single 0.25-m² quadrat, with wet biomasses as high as 3.1 kg and stems reaching over 1 m in height. All of the floating mats encountered during our studies occurred within
this community as well, lying at the deeper extent of its range. The average number of species occurring on these mats was 9.0, ranging from 5–18 per sample. Without the inclusion of the mats in the *Pontederia* community, average richness fell from 5.7 to 4.9 species per sample. This value is still higher than any other community occurring in deeper water, with the exception of floating-leaved communities.

The soils in the *Pontederia* group varied significantly, from 3.6–94.9% organic matter and from 0.03–0.82 g/cm³ bulk densities. This was a result of the large depth range this species occurred in, from the edge of the grassy communities in the sandier, shallow sections of shoreline to the submersed and floating-leaved communities in deeper water, where it formed organic mats in depths greater than 1 m. This community seems to have become more robust and expanded shoreward even since the late 1980s, and is far more abundant than recorded in the 1950s and 1970s. While water level stabilization is an obvious factor in its expansion, evidence from previous studies suggests artificial dry downs may have increased its lakeward extent as well.

**Cattails**

*Typha* spp. were patchily distributed along the deep water edge of the *Pontederia* community, forming extremely dense, monocultural communities, with the lowest average species richness (3.8) of any other group. This community was too infrequently encountered in our Treatment-Selections study, generally becoming dominant between 120 and 180 cm (48 and 71 in) in depth, and no soil cores were collected. Of the approximately 50 sample locations within this depth range, only eight were identified as predominantly *Typha* communities. This species is evidently extremely vulnerable to drought, which suggests it has probably expanded in the 13 years of flooded, stabilized
conditions on the lake since the 1987 dry down, though no comparisons to previous studies are available.

**Floating Leaved Communities**

This group occurred over a wide range of water depths (20–180 cm, or 9–70 in) occurring infrequently within dense *Pontederia* communities but was most dominant just beyond the deep water extent of this group (>110 cm). Two common species collectively formed this community, *Nymphaea odorata* and *Nuphar luteum*, though they rarely occurred in the same sample. While occupying the same depth zones, dense stands of either species occurred within a few meters of each other, but did not usually overlap. This is most likely due to light availability or underground competition, with either species capable of densely covering the surface of the water and dominating the substrate with large, creeping tubers.

Species richness was higher for this group than any other, with the exception of the shallow grassy communities, with an average of 5.9 species per sample. This was due to a large association with submersed aquatics, including *Hydrilla, Ceratophyllum* spp., *Utricularia* spp., and several grasses, including *Paspalidium geminatum* and *Panicum hemitomon*, as well as other floating-leaved species, *Nelumbo lutea* and *Nymphoides aquatica*. Two extremely infrequent species were located in this community, the submersed aquatic *Vallisneria americana* and a macroalgae, *Chara* spp.

**Deep Water Communities**

Several analyses distinguished between deep water communities of the submersed aquatics *Hydrilla* and *Ceratophyllum* spp. and the emergent grass *Paspalidium geminatum*. This distinction was primarily due to the occurrence of *Hydrilla* at virtually every water depth beyond the extent of the *Pontederia* community, at varying levels of
dominance. Occasionally, *Hydrilla* was the only species occupying heavily traveled, open water areas between *Typha, Nymphaea/Nuphar,* and *Paspalidium* communities, which led to a distinct community of submersed aquatics. However, the most abundant community identified by the Lake-Monitoring study in deeper water was a mix of *Paspalidium* and *Hydrilla.* All 23 samples located in depths >158 cm (62 in) in water were grouped with this community. The average number of species per sample was 4.0, the lowest of any group besides *Typha.* Given that this community represents the deepest extent of emergent species into the lake, low diversities were expected.

**Conclusion**

The vegetation communities identified in this study follow the classic zonation patterns typically occurring in the transitional zone between terrestrial and aquatic ecosystems (Clements 1916, Odum 1971, Segal 1971). This ecotone and its associated dynamic conditions support higher diversities and productivities of the species occupying those areas than in adjacent ecosystems (Odum 1971). As conditions stabilize along the water depth gradient, for example, hydrostatic pressures increase, light availability and oxygen levels decrease, and the environment becomes increasingly harsh with fewer species adapted to such conditions (Juge and Lachavanne 1997). This results in lower specific diversities and distinct zonation patterns, i.e. concentric belts running parallel to the shoreline (Segal 1971), as adapted species competitively exclude others in the harsh environment. These are the patterns shown on Lake Toho prior to dry down, with stabilized water levels having dramatically reduced the extent of shoreline subjected to past dynamics. With the high and low pool stages reduced by at least 2 m from historical ranges, the more diverse grassy communities occupying the highly astatic shorelines of the lake have been pushed back to less than 60 cm in depth, replaced by robust, dense
bands of vegetation well adapted to the stabilized conditions. The zone of dense *Pontederia* identified in this study would have historically been stranded nearly 0.5 m above the lake level during droughts and covered with up to 2 m of water during floods (based on the period of record from 1950–1960).

Such large, historical disturbance events continually reduced and expanded the range and abundance of species adapted to either dry or wet conditions, resulting in constant recession and succession, creating extremely diverse and dynamic environments (Mitsch and Gosselink 1993, Odum 1993). Consequently, when flood stages were dramatically reduced, so too was the perturbation that kept these communities from reaching equilibrium, and the “pulse-stabilized subclimax” vegetation (Odum 1971) was limited to the new low pool/high pool elevations. Lake managers are now creating their own large-scale disturbances in an effort to mimic the events that kept the shoreline in a state of ever changing conditions, with communities reflecting those dynamics. Whether the disturbances caused by bulldozers and herbicides can replace the effects of drought and floods is a question that will take years to answer. In hopes of reducing the uncertainties, we have implemented the long-term monitoring studies mentioned throughout this paper, and have provided a clear before picture of the littoral communities of Lake Tohopekaliga.

**2004 Habitat Enhancement Schedule**

In the spring of 2004 (data collection ceased in December 2003) the water levels in Lake Toho reached a target stage of 14.8 m (48.5 ft) NGVD and heavy equipment began removing muck from the shorelines. Two of the four treatment blocks at each of the sites were scraped with bulldozers and the material was deposited either upland or on the lakeshore well outside of the study areas. As stated previously, muck removal was
focused within the *Pontederia* community, scraping at least as far out as the deepest *Pontederia* plants. All vegetation, root mat and organic sediment were removed from these areas, leaving mostly sand from 30–120 cm in water depth at high pool. The plots designated for the herbicide treatment had not been completed as of August 2004, but broad-scale helicopter applications were scheduled to begin in October.
## APPENDIX A
### TREATMENT-STUDY SPECIES LIST

Table A-1. Most abundant species sampled in the Treatment-Selection study.

<table>
<thead>
<tr>
<th>Species Code</th>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALTPH</td>
<td><em>Alternanthera philoxeroides</em></td>
<td>Alligator weed</td>
</tr>
<tr>
<td>AXOFU</td>
<td><em>Axonopus furcatus</em></td>
<td>Big carpet grass</td>
</tr>
<tr>
<td>BACCA</td>
<td><em>Bacopa caroliniana</em></td>
<td>Lemon Bacopa</td>
</tr>
<tr>
<td>BRAMU</td>
<td><em>Bracharia mutica</em> (Forssk.) Stapf</td>
<td>Para grass</td>
</tr>
<tr>
<td>CERSP</td>
<td><em>Ceratophyllum</em> spp.</td>
<td>Coontail</td>
</tr>
<tr>
<td>EICCR</td>
<td><em>Eichhornia crassipes</em></td>
<td>Water hyacinth</td>
</tr>
<tr>
<td>ELEQU</td>
<td><em>Eleocharis quadrangulata</em></td>
<td>Square-stemmed Spikerush</td>
</tr>
<tr>
<td>ELESP</td>
<td><em>Eleocharis</em> spp. (Small)</td>
<td>Spikerushes</td>
</tr>
<tr>
<td>HYDSP</td>
<td><em>Hydrocotyle</em> spp.</td>
<td>Pennywort</td>
</tr>
<tr>
<td>HYDVE</td>
<td><em>Hydrilla verticillata</em></td>
<td>Hydrilla</td>
</tr>
<tr>
<td>LUDRE</td>
<td><em>Ludwigia repens</em></td>
<td>Red ludwigia</td>
</tr>
<tr>
<td>LUDSP</td>
<td><em>Ludwigia</em> spp. (leptocarpa and peruviana)</td>
<td>Ludwigia/Water Primrose</td>
</tr>
<tr>
<td>LUZFL</td>
<td><em>Luziola fluitans</em> (Michx.) Terrell &amp; H. Robbins</td>
<td>Watergrass (Syn. <em>Hydrochloa caroliniensis</em>)</td>
</tr>
<tr>
<td>LYMSP</td>
<td><em>Lymnobium spongia</em></td>
<td>Frog's bit</td>
</tr>
<tr>
<td>NUPLU</td>
<td><em>Nuphar luteum</em></td>
<td>Spatterdock (Syn. <em>Nuphar advena</em>)</td>
</tr>
<tr>
<td>NYMOD</td>
<td><em>Nymphaea odorata</em></td>
<td>Fragrant water lily</td>
</tr>
<tr>
<td>PANHE</td>
<td><em>Panicum hemitomon</em></td>
<td>Maidencane</td>
</tr>
<tr>
<td>PANRE</td>
<td><em>Panicum repens</em></td>
<td>Torpedo grass</td>
</tr>
<tr>
<td>POLHY</td>
<td><em>Polygonum hydropiperoides</em></td>
<td>Wild water-pepper</td>
</tr>
<tr>
<td>PONCO</td>
<td><em>Pontederia cordata</em></td>
<td>Pickerel weed</td>
</tr>
<tr>
<td>SAGLN</td>
<td><em>Sagittaria lancifolia</em></td>
<td>Duck potato</td>
</tr>
<tr>
<td>TYPSP</td>
<td><em>Typha</em> spp.</td>
<td>Cattails</td>
</tr>
<tr>
<td>PASSP</td>
<td><em>Paspalum</em> sp.</td>
<td>Unidentified species of Paspalum</td>
</tr>
<tr>
<td>UTRSP</td>
<td><em>Utricularia</em> spp.</td>
<td>Bladderworts</td>
</tr>
</tbody>
</table>

Nomenclature follows that of Tobe et al. 1998
Table A-2. Less abundant species sampled in the Treatment-Selection study.

<table>
<thead>
<tr>
<th>Species code</th>
<th>Scientific name</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANDVI</td>
<td><em>Andropogon virginicus</em></td>
<td>Broom grass</td>
</tr>
<tr>
<td>BIDLA</td>
<td><em>Bidens laevis</em></td>
<td>Bur-marigold</td>
</tr>
<tr>
<td>CARSP</td>
<td><em>Carex</em> spp.</td>
<td>Sedge species</td>
</tr>
<tr>
<td>CENAS</td>
<td><em>Centella asiatica</em></td>
<td>Coinwort</td>
</tr>
<tr>
<td>CHASP</td>
<td><em>Chara</em> spp.</td>
<td>Musk grasses</td>
</tr>
<tr>
<td>CRAGR</td>
<td><em>Crab grass</em></td>
<td>Crab grass</td>
</tr>
<tr>
<td>CYPSP</td>
<td><em>Cyperus</em> spp.</td>
<td>Sedge species</td>
</tr>
<tr>
<td>DIOVI</td>
<td><em>Diodia virginiana</em></td>
<td>Buttonweed</td>
</tr>
<tr>
<td>ELELG</td>
<td><em>Eleocharis</em> spp. <em>Large</em></td>
<td>Large species of <em>Eleocharis</em></td>
</tr>
<tr>
<td>EUPSP</td>
<td><em>Eupatorium</em> spp.</td>
<td>Dogfennel</td>
</tr>
<tr>
<td>HABRE</td>
<td><em>Habenera repens</em></td>
<td>Water-spider orchid</td>
</tr>
<tr>
<td>JUNEF</td>
<td><em>Juncus effusus</em></td>
<td>Soft Rush</td>
</tr>
<tr>
<td>JUNMA</td>
<td><em>Juncus marginatus</em></td>
<td>Rush</td>
</tr>
<tr>
<td>LEEHE</td>
<td><em>Leersia hexandra</em></td>
<td>Southern cut grass</td>
</tr>
<tr>
<td>MICSP</td>
<td><em>Micranthemum</em> spp.</td>
<td>Baby tears</td>
</tr>
<tr>
<td>MYRCE</td>
<td><em>Myrica cerifera</em></td>
<td>Wax-myrtle</td>
</tr>
<tr>
<td>NELLU</td>
<td><em>Nelumbo lutea</em></td>
<td>Water lily</td>
</tr>
<tr>
<td>NYMAQ</td>
<td><em>Nymphoides aquatica</em></td>
<td>Banana lily</td>
</tr>
<tr>
<td>PANSP</td>
<td><em>Panicum</em> spp.</td>
<td><em>Panicum</em> spp. (not including <em>hemitomon</em>)</td>
</tr>
<tr>
<td>PASGE</td>
<td><em>Paspalidium geminatum</em></td>
<td>Egyptian paspalidum (commonly called knot grass)</td>
</tr>
<tr>
<td>PASNO</td>
<td><em>Paspalum notatum</em></td>
<td>Bahia grass</td>
</tr>
<tr>
<td>POLDE</td>
<td><em>Polygonum densiflorum</em></td>
<td>Smartweed</td>
</tr>
<tr>
<td>POLSP</td>
<td><em>Polygonum</em> sp.</td>
<td>Unidentified fuzzy species of <em>Polygonum</em></td>
</tr>
<tr>
<td>RHECU</td>
<td><em>Rhexia cubensis</em></td>
<td>Meadowbeauty</td>
</tr>
<tr>
<td>RHYNSP</td>
<td><em>Rhyncospora</em> spp.</td>
<td>Beakrushes</td>
</tr>
<tr>
<td>SACIN</td>
<td><em>Saciolepis indica</em></td>
<td>Indian cupscale</td>
</tr>
<tr>
<td>SAGLT</td>
<td><em>Sagittaria lattifolia</em></td>
<td>Arrowhead</td>
</tr>
<tr>
<td>SCICA</td>
<td><em>Scirpus californicus</em></td>
<td>Giant bulrush</td>
</tr>
<tr>
<td>SCICU</td>
<td><em>Scirpus cubensis</em></td>
<td>Bulrush</td>
</tr>
<tr>
<td>SESPU</td>
<td><em>Sesbania punicea</em></td>
<td>Purple sesban</td>
</tr>
<tr>
<td>WOOVI</td>
<td><em>Woodania virginica</em></td>
<td>Virginia chain fern</td>
</tr>
<tr>
<td>UNKNOWN</td>
<td>11 Unknowns</td>
<td>Infrequent ecotonal grasses and seasonal floating mat species.</td>
</tr>
</tbody>
</table>

Nomenclature follows that of Tobe et al. 1998
APPENDIX B
WHOLE-LAKE MONITORING STUDY SPECIES LIST

Table B-1. Most abundant species sampled in the Whole-Lake Monitoring study.

<table>
<thead>
<tr>
<th>Species code</th>
<th>Scientific name</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALTPH</td>
<td>Alternanthera philoxeroides</td>
<td>Alligator weed</td>
</tr>
<tr>
<td>BACCA</td>
<td>Bacopa caroliniana</td>
<td>Lemon Bacopa</td>
</tr>
<tr>
<td>BRAMU</td>
<td>Bracharia mutica (Forssk.) Stapf</td>
<td>Para grass</td>
</tr>
<tr>
<td>CERSP</td>
<td>Ceratophyllum spp.</td>
<td>Coontail</td>
</tr>
<tr>
<td>CHASP</td>
<td>Chara spp.</td>
<td>Musk grasses</td>
</tr>
<tr>
<td>ELESP</td>
<td>Andropogon virginicus</td>
<td>Broom grass</td>
</tr>
<tr>
<td>HYDSP</td>
<td>Hydrocotyle spp.</td>
<td>Pennywort</td>
</tr>
<tr>
<td>HYDVE</td>
<td>Hydrilla verticillata</td>
<td>Hydrilla</td>
</tr>
<tr>
<td>LUDSP</td>
<td>Ludwigia spp. (leptocarpa and</td>
<td>Ludwigia/Water Primrose</td>
</tr>
<tr>
<td></td>
<td>peruviana)</td>
<td></td>
</tr>
<tr>
<td>LUZFL</td>
<td>Luziola fluitans (Michx.) Terrell</td>
<td>Watergrass (Syn. Hydrochloa caroliniensis)</td>
</tr>
<tr>
<td></td>
<td>&amp; H. Robbins</td>
<td></td>
</tr>
<tr>
<td>NUPLU</td>
<td>Nuphar luteum</td>
<td>Spatterdock (Syn. Nuphar advena)</td>
</tr>
<tr>
<td>NYMAQ</td>
<td>Nymphoides aquatica</td>
<td>Banana lily</td>
</tr>
<tr>
<td>NYMOD</td>
<td>Nymphaea odorata</td>
<td>Fragrant water lily</td>
</tr>
<tr>
<td>PANHE</td>
<td>Panicum hemitomon</td>
<td>Maidencane</td>
</tr>
<tr>
<td>PANRE</td>
<td>Panicum repens</td>
<td>Torpedo grass</td>
</tr>
<tr>
<td>PASGE</td>
<td>Paspalidium geminatum</td>
<td>Egyptian paspalidium (commonly called knot grass)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PASNO</td>
<td>Paspalum notatum</td>
<td>Bahia grass</td>
</tr>
<tr>
<td>PONCO</td>
<td>Pontederia cordata</td>
<td>Pickerel weed</td>
</tr>
<tr>
<td>SCICA</td>
<td>Scirpus californicus</td>
<td>Giant bulrush</td>
</tr>
<tr>
<td>TYPSP</td>
<td>Typha spp.</td>
<td>Cattails</td>
</tr>
</tbody>
</table>

Nomenclature follows that of Tobe et al. 1998
Table B-2. Less abundant species sampled in the Whole-Lake Monitoring study.

<table>
<thead>
<tr>
<th>Species code</th>
<th>Scientific name</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANDVI</td>
<td><em>Axonopus furcatus</em></td>
<td>Big carpet grass</td>
</tr>
<tr>
<td>AXOFU</td>
<td><em>Bidens laevis</em></td>
<td>Bur-marigold</td>
</tr>
<tr>
<td>BIDLA</td>
<td><em>Centella asiatica</em></td>
<td>Coinwort</td>
</tr>
<tr>
<td>CENAS</td>
<td><em>Crab grass</em></td>
<td>Crab grass</td>
</tr>
<tr>
<td>CRAGR</td>
<td><em>Cyperus spp.</em></td>
<td>Sedges</td>
</tr>
<tr>
<td>CYPSP</td>
<td><em>Diodia virginiana</em></td>
<td>Buttonweed</td>
</tr>
<tr>
<td>DIOVI</td>
<td><em>Eichhornia crassipes</em></td>
<td>Water hyacinth</td>
</tr>
<tr>
<td>EICCR</td>
<td><em>Eleocharis spp. (Small)</em></td>
<td>Spikerushes</td>
</tr>
<tr>
<td>EUPSP</td>
<td><em>Eupatorium spp.</em></td>
<td>Dogfennel</td>
</tr>
<tr>
<td>HABRE</td>
<td><em>Habenera repens</em></td>
<td>Water-spider orchid</td>
</tr>
<tr>
<td>HIBGR</td>
<td><em>Hibiscus grandiflorus</em></td>
<td>Swamp Hibiscus</td>
</tr>
<tr>
<td>JUNMA</td>
<td><em>Juncus marginatus</em></td>
<td>Rush</td>
</tr>
<tr>
<td>LUDRE</td>
<td><em>Ludwigia repens</em></td>
<td>Red ludwigia</td>
</tr>
<tr>
<td>LYMSP</td>
<td><em>Lymnobium spongia</em></td>
<td>Frog's bit</td>
</tr>
<tr>
<td>MIKSC</td>
<td><em>Mikania scandens</em></td>
<td>Climbing hempweed</td>
</tr>
<tr>
<td>NELLU</td>
<td><em>Nelumbo lutea</em></td>
<td>Water lotus</td>
</tr>
<tr>
<td>POLDE</td>
<td><em>Polygonum densiflorum</em></td>
<td>Smartweed</td>
</tr>
<tr>
<td>POLHY</td>
<td><em>Polygonum hydropiperoides</em></td>
<td>Wild water-pepper</td>
</tr>
<tr>
<td>RHYNSP</td>
<td><em>Rhyncospora spp.</em></td>
<td>Beakrushes</td>
</tr>
<tr>
<td>SACIN</td>
<td><em>Saciolepis indica</em></td>
<td>Indian cupscale</td>
</tr>
<tr>
<td>SAGLN</td>
<td><em>Sagittaria lancelolia</em></td>
<td>Duck potato</td>
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<td>SAGLT</td>
<td><em>Sagittaria lattifolia</em></td>
<td>Arrowhead</td>
</tr>
<tr>
<td>SCICU</td>
<td><em>Scirpus cubensis</em></td>
<td>Bulrush</td>
</tr>
<tr>
<td>SESPU</td>
<td><em>Sesbania punicea</em></td>
<td>Purple sesban</td>
</tr>
<tr>
<td>UTRSP</td>
<td><em>Utricularia spp.</em></td>
<td>Bladderworts</td>
</tr>
<tr>
<td>VALSP</td>
<td><em>Vallisneria spp.</em></td>
<td>Eel grass</td>
</tr>
<tr>
<td>UNKNOWNS</td>
<td>Six Unknowns</td>
<td>Infrequent ecotonal grasses and seasonal floating mat species.</td>
</tr>
</tbody>
</table>

Nomenclature follows that of Tobe et al. 1998


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

Remetrix LLC. 2003. Aquatic vegetation survey of Lake Tohopekaliga. Remetrix LLC, Carmel, IN.


Thompson, J. B. 1919. Para grass. University of Florida Agricultural Experiment Station Press, Gainesville, FL.


BIOGRAPHICAL SKETCH

Zachariah C. Welch was born in Grand Rapids, Michigan, on March 30, 1976. Moving to Florida at the age of two, he spent most of his childhood trying to manipulate his younger siblings, and to beat his older brother at anything. It was evident at an early age that he had a propensity for getting dirty and an awkward shyness. As a toddler he gleefully emptied a can of oil-based wood stain onto his head and was often found romping through mud puddles if left unattended. When guests came to the house, he would hide in the corner or put his hands over his face, retreating like a turtle at the first sign of attention. He spent the majority of the first day of kindergarten underneath his desk, prompting home schooling from the first through the third grade. The combination of social awkwardness and a love for getting dirty drove him outdoors, and his older brother and he would spend hours every day running through and exploring the woods that surrounded their house, developing a great appreciation for nature over the years.

During high school he learned the importance of camaraderie and group morale playing football, while developing discipline and a strong work ethic carrying lumber and pounding nails for his father’s construction company. Following his older brother’s footsteps, he enrolled at the University of Florida where he struggled with the transition from a small-town school to the highly competitive college atmosphere. After two disappointing years of poor GPAs and a lack of direction, he decided to do what he loved and pursued a career in the outdoors, changing his major from engineering to wildlife ecology and conservation.
Thrilled with the fact that classes in his new major involved treks through the forest and identifying the same trees he ogled as a child, he excelled in upper division, graduating with honors and a Bachelor of Science degree in 1999. He also worked part-time for a doctoral student (while completing his undergraduate degree) who introduced him to the wonderful world of airboats and the beautiful swamps and marshes of Florida. Finally, he found his niche, working and studying in Mother Nature’s mud puddles.

Through several fortuitous meetings and situations, he was eventually offered a research assistantship for a Master of Science degree at the University of Florida, returning to his Alma Mater in 2000. Initially, he studied the colonial behaviors of the endangered Florida Snail Kite, driving airboats through virtually every major wetland system in south and central Florida. While collecting data in the summer, he stayed in temporary housing at a national wildlife refuge in south Florida, where he met another UF graduate student, Christa Zweig. After completing their respective field seasons and returning to Gainesville to take classes in the fall semester, they fell in love and married 2 years later.

Immediately after his return from south Florida, Zach had the opportunity to switch research projects and begin monitoring vegetation responses on a controversial habitat restoration project. Having been denied colonial nesting data by a drought year in the Everglades and having always had an interest in systems ecology, he was thrilled with the idea of establishing a habitat-monitoring program. For the rest of his graduate degree he enjoyed swimming in the weeds of Lake Tohopekaliga, forming lifelong friendships with revered colleagues. After presenting his thesis at local, statewide, and international
conferences he finally whipped his public-speaking fears, determined to never spend another day under his desk. Another day in the mud puddles, however, is inevitable.