Final Report

Ecological Characterization of Aquatic Refugia in the Arthur R. Marshall Loxahatchee National Wildlife Refuge

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Submitted to:

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U. S. National Park Service
Critical Ecosystems Studies Initiative
40001 State Road 9336
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February 2004

Executive Summary

Introduction

The American alligator is considered to be a keystone species in the Florida Everglades. Alligator holes are assumed to be critical component of the Everglades landscape, due to their potential role as a dry season refugia for aquatic animals. While previous studies have examined the spatial distribution and ecological characteristics of alligator holes in Water Conservation Area 3 (WCA3) (Mazzotti et al. 1999), further studies in other areas in the Everglades are necessary if we are to gain a comprehensive understanding of the role of alligator holes in supporting ecological processes within the Everglades.

Objectives

Objectives of this study were to obtain data on location, structure, and function of alligator holes in the A.R.M. Loxahatchee National Wildlife Refuge. We addressed structural aspects of alligator holes by asking the following questions:

1. What is the variation in size of alligator holes in the Refuge?
2. Are alligator holes round or irregular in shape?
3. Do different types of holes exist on the Refuge?
4. What is the variation in peat and water depths of alligator holes?
   a. Are there differences in water and peat depths between the surrounding ecotone?
   b. Are there differences in water and peat depths between the marsh surrounding an alligator hole, and at randomly selected marsh sites?
   c. Do water depths and peat depths vary between different types and sizes of alligator holes?

We characterized the biological aspects of alligator holes by asking:

1. What plants commonly establish on alligator holes?
2. Does plant diversity vary between different parts of an alligator hole, and/or between different types and sizes of holes?
3. Does plant diversity vary between alligator holes and randomly selected marsh sites?

Results

A total of 2,855 potential and known alligator holes were identified from 1 m resolution Digital Orthographic Quarter Quads (DOQQs) obtained from the Labins website (http://www.labins.org/imap/). The DOQQs were developed to be comparable to photos of 1:12,000 scale. Seventy-four of the holes were observed in the field before they were mapped, and 10 were confirmed in the field after mapping them. Of the remaining holes, 697 were considered highly likely to be refugia/holes, and the remaining 2,074 considered less likely to be refugia or holes. Small holes (<5-6m) are often difficult to pinpoint on the photos, even with Global Positioning System (GPS) coordinates as a guide.

The accuracy assessment (for commission) conducted on 150 of the possible holes identified from the DOQQs showed that holes mapped with high confidence had an accuracy rate of 49%. Holes mapped with low confidence had 33% accuracy, and the overall accuracy (commission) of the mapping effort was 37%. In addition, 47 holes were encountered driving to the holes selected for ground-truthing. Only five of these had been identified in the original mapping effort indicating that many true holes were probably not mapped. Reasons for the low accuracy of this effort include the complexity of the habitat in the Refuge, poor quality of some of the photos, and relatively high water levels at the time of photo acquisition. The mapping effort could be greatly improved by photos taken in the dry season. An attempt to acquire such photos has been in the works since 2001; unfortunately, the company contracted to do the work has been unable to fly due to unfavorable weather conditions. The results of that contract are still pending.

Thirty of the known holes were chosen for ecological characterization. For comparison, we also randomly selected 15 marsh reference sites. Due to logistic constraints, we were only able to sample 26 holes and 14 marsh sites.

Alligator holes sampled in this study averaged 125.1 m^2 in surface area. Pond water depths were significantly deeper than those for the surrounding marsh. Average water relief for alligator holes was 55.65 cm below the surrounding marsh, while the ecotones at the edges of holes were significantly shallower than the surrounding marsh. Peat depths ranged from 151 to greater than 365 cm. The majority of alligator holes had median peat depths between 251 and 300 cm.

The five most abundant plant species at alligator holes were 1) white water lily (*Nymphaea odorata*), 2) sawgrass (*Cladium jamaicense*), 3) floating heart (*Nymphoides aquatica*), 4) eastern purple bladderwort (*Utricularia purpurea*), and 5) annual spikerush (*Eleocharis geniculata*). At marsh reference sites, the five most abundant plant species were 1) white water lily (*Nymphaea odorata*), 2) eastern purple bladderwort (*Utricularia purpuria*), 3) annual spikerush (*Eleocharis geniculata*), 4) leafy bladderwort (*Utricularia foliosa*), and 5) floating heart (*Nymphoides aquatica*).

We found that alligator holes had higher species richness and diversity than marsh reference sites, and that species richness was significantly higher in the ecotone and surrounding marsh than it was in the pond. We conclude that alligator holes are associated with localized increases in plant diversity in the A.R.M. Loxahatchee National Wildlife Refuge.

I. Background and Purpose

The American alligator (*Alligator mississippiensis*) is considered a keystone species in the Florida Everglades (Craighead 1968, Kushlan 1974, Mazzotti and Brandt 1994). Alligators are top predators in the Everglades ecosystem and influence many populations of prey items as they grow from 50 g hatchlings to 75,000 g adults. Furthermore, activities of alligators may be important in structuring plant and animal communities and in creating environmental heterogeneity in the Everglades.

Alligators have a strong effect on plant communities through excavation and maintenance of ponds (commonly referred to as “alligator holes”) and trails. The disturbance to the environment associated with these activities has been found to result in significant topographic and hydrologic variation in otherwise flat and shallow wetlands (Mazzotti et al. 1999). The relatively higher areas around the perimeter of many alligator holes may provide suitable substrate for colonization by plants less tolerant of flooding than typical marsh species, and may also be important nesting, resting or foraging sites for a variety of wildlife populations. Deeper water areas of the ponds themselves may also be of critical importance to wildlife, acting as dry-season refugia for many species of aquatic animals (Kushlan 1972).

Due to their potential role as dry season refugia for aquatic animals, alligator holes are considered a critical component of the Everglades landscape. Aquatic fauna, such as forage fish and macro-invertebrates, move into the deeper water associated with ponds and sloughs as the surrounding marsh dries down (Kushlan 1972). As these aquatic organisms become concentrated, they become prey for a wide variety of wetland dependent species, especially nesting wading birds. Alligator holes may also serve as sources of organisms that can re-colonize surrounding areas as water levels in the surrounding marsh increase at the end of the dry season. If alligator holes do fulfill these important roles in the Everglades, then decline of this keystone species could result in a loss of ecological processes that would not be restored through hydrological restoration alone.

Potential importance of alligator holes to ecological communities in the Everglades makes their study imperative. Efforts are underway to answer questions about structure and function of alligator holes such as: Are there different types of ponds? Do they function differently? Are they distributed randomly throughout the Everglades? Do they differ in different areas of the Everglades? Do alligator holes act as dry season refugia for aquatic organisms? Do other alligator holes function as sinks for aquatic organisms, concentrating them in areas with high vulnerability to predators or with decreasing water quality as the dry season progresses? If both situations occur, what aspects of a hole’s physical structure, hydrology, or location determine whether it will act as a source or a sink? What are the impacts of changes in long-term patterns of marsh hydrology on alligator hole distribution and abundance?

Dry season refugia for aquatic animals are assumed to be a critical component of the Everglades landscape and are an important attribute in the conceptual models being used to develop the monitoring and assessment plan for the Comprehensive Everglades Restoration Plan (CERP). Relationships among dry season refugia, aquatic fauna, wading birds and alligators are recognized as a key uncertainty in the CERP monitoring and assessment plan, and distribution and occupancy of alligator holes has been identified as a performance measure for the freshwater marsh conceptual model. However, ecology of these aquatic refugia has remained almost completely unstudied. This project integrates GIS/GPS technology, field biology and photo-interpretation to provide some of the missing information that has become critical for making ecosystem restoration decisions. These data constitute an important step in defining the role of aquatic refugia in the freshwater Everglades. Because of the interdependence of wading birds, aquatic fauna and aquatic refugia, this project is critical to evaluation of all CERP projects and science objectives that deal with the potential effects of changes in hydropattern. Thus, it is essential to collect these data prior to major hydrological changes, so that influences of CERP projects can be evaluated.

A previous study has examined spatial distribution and ecological characteristics of alligator holes in Water Conservation Area 3 (WCA3) (Mazzotti et al. 1999). Further studies in other areas in the Everglades are necessary, however, to gain a comprehensive understanding of the role of alligator holes in supporting ecological processes within the Everglades.These studies are also needed for understanding the effect of long-term changes in hydrology on alligator hole distribution and abundance.

In this study we follow up on results from WCA3 by examining location, distribution, types, and structure of alligator holes in the A.R.M. Loxahatchee National Wildlife Refuge. Section II of this report describes methods developed for mapping alligator holes using color-infrared aerial photography and DOQQs. Section III reports on the ecological characterization of alligator holes on the Refuge.

II. Mapping Everglades alligator holes in the A.R.M. Loxahatchee National Wildlife Refuge using Digital Ortho Quarter Quads

Introduction

The American alligator (*Alligator mississippiensis*) of the Florida Everglades has the ability to alter structure of the landscape (Craighead 1968, Kushlan 1974). Large size and weight of the alligator, in combination with soft organic sediments (peat) of the Everglades, results in creation and maintenance of small ponds (alligator holes) caused by wallowing activities of the alligator. Furthermore, displaced sediments and vegetation are often mounded around the perimeter of ponds, creating an elevated substrate that may be colonized by plants. Overall, activities of alligators can significantly increase topographic and hydrologic variation of otherwise flat and shallow wetland landscape, resulting in increased vegetation and wildlife diversity (Craighead 1971, Mazzotti et al. 1999).

Alligator holes are approximately one meter deeper than surrounding marsh. They may range from two to 20 m in diameter and are found in a variety of wetland habitats including sawgrass (*Cladium jamaicense*) marsh, wet prairie (emergent rush marsh including *Eleocharis spp*. and *Rhynchospora spp*.), and slough [deeper water with floating aquatic plants such as spatter-dock (*Nuphar luteum*), white water lily (*Nymphae odorata*), floating heart (*Nymphoides aquatica*), and bladderwort (*Utricularia spp*.)]. Alligator holes may be surrounded by shrubs and trees (often wax myrtle, *Myrica cerifera*) that have taken root on the raised banks or may simply be small open water depressions found within a marsh matrix. Once established, alligator holes are kept clear of encroaching vegetation by maintenance activities of resident alligators.

Alligator holes have long been hypothesized to provide critical dry season refugia for Everglades wildlife (Davis 1943). As surrounding marsh dries down, fish and other aquatic organisms concentrate at an alligator hole, becoming an important food source for nesting wading birds, resident alligators, and other wildlife. With return of favorable water conditions, remaining organisms may reproduce and radiate out into surrounding wetlands.

Although importance of alligator holes in the Everglades is widely postulated, only one systematic study of alligator holes has been conducted (Mazzotti et al. 1999). That study of abundance, distribution, and ecological characteristics of alligator holes in WCA3 explored usefulness of color infrared (CIR) aerial photography in mapping alligator holes in the Everglades and supported the contention that alligator holes are important determinants of marsh plant and animal diversity. This study follows up on the previous one by pursuing similar questions in the A.R.M. Loxahatchee National Wildlife Refuge. Specifically, we used DOQQs photographic maps, available through the Land Boundary Information System (LABINS), to ask the following questions:

- Are DOQQs useful for mapping alligator holes?
- How accurate was the identification and location of alligator holes from DOQQs?

Materials and methods

Study Area

The study focused on the interior portion of the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Refuge), a 57,324 ha area of northern Everglades wetland. Located in Palm

Beach County, Florida, south and east of Lake Okeechobee, it was once a connected part of the historic Everglades system. Construction of canals and levees of Water Conservation Area 1 (WCA 1) has effectively isolated the interior of the Refuge from its original watershed. Water levels within the interior of the Refuge are regulated by the Corps of Engineers and South Florida Water Management District by using pump stations and spillways. Water regulation is carried out according to a schedule that takes several factors into consideration, including wildlife requirements. These hydrological modifications have changed the system from a dynamic, sheet-flow driven system to an impounded marsh with the majority of overland flow inputs being shunted around the marsh via exterior canals (Brandt et al. 2000).

The Refuge is peat-based wetland system consisting of a mosaic of sloughs, wet prairie, sawgrass, patches of brush, and tree islands. The deep organic soils range from 1.25 m to greater than 4.5 m. Sloughs are the deepest marsh communities and dominant vegetation includes *Utricularia spp.*, *Nymphaea odorata*, *Nymphoides aquatica* and *Nuphar luteum* (Lodge 1994). Emergent plants such as *Eleocharis spp*., *Rhyncospora tracyi, Panicum hemitomon, Sagittaria lancifolia* and *Pontedaria lancelota* are common in wet prairies (Gunderson 1994). Sawgrass strands are areas dominated by *Cladium jamaicense* with little other vegetation present (Lodge 1994). Tree islands within the Refuge are dominated by *Persea palustris, Myrica cerifera* and *Ilex cassine* (Arrington 2003).

Mapping

Potential alligator holes were identified from DOQQs downloaded as .tif files from the Labins website (http://www.labins.org/imap/). Photos were flown at the end of December 1999 when water levels in the center of the Refuge were approximately 16.7 NGVD, or about 50cm above the marsh surface. Photos were georeferenced to Universal Transverse Mercator (UTM) using the North American Datum of 1983 (NAD 83) with a resolution of 1m and were developed to be comparable to photos of 1:12,000 scale. These were the most recent and best quality photos available. The Refuge currently has a contract out to acquire 1:10,000 color-infrared photos; however, the contractor has not been able to complete the contract because of unfavorable weather conditions.

All areas thought to be alligator holes were mapped on the digital photographs using Geographic Information Systems (GIS). These were generally small, dark gray through dark blue to black marks, sometimes round but more often amorphous, potentially representing water areas free of vegetation. Holes were assigned a high or low confidence code based on the interpreter's confidence in the mapping, and a hole type was assigned based on the holes' appearance. Types were as follows:

Type 1: circular (or nearly so) dark mark in marsh
Type 1a: dark mark in marsh, amorphous
Type 2: dark 'slash' through or along edge of tree island or dense sawgrass, generally in direction other than northeast – southwest (which is very likely a shadow, but could be masking a alligator hole)
Type 3: dark mark nestled into a corner or along side of tree island or other dense vegetation
Type 4: dark mark, often roundish, surrounded by dense vegetation, but not a slash

Printouts of mapped holes with UTM coordinates were used for ground-truthing. Seven ground-truthing visits to the Refuge were made between August 16 and November 19, 2002. Earlier visits were devoted to navigating to known alligator holes (those previously identified by investigators), to begin to understand how field appearance relates to a signature on photos. Later visits attempted to refine the search image of signatures. In the field, an open water area was considered to be an alligator hole if it met two conditions:

1) it was free of emergent and surface vegetation (e.g. *Eleocharis*, lily pads), and
2) water depth in the cleared area was deeper than its surroundings. Depth of all possible holes was not measured. However, the majority of alligator hole water depths were taken and these were deeper than surrounding waters, indicating a depression.

Coordinates of all alligator holes seen were recorded, either in UTM using North American Datum of 1927 (NAD27) or NAD83. Those recorded using NAD27 were later projected using the NAD83 system. Most ground-truthing occurred in the central portion of the Refuge. Ground-truthing was used iteratively to improve mapping.

Accuracy Assessment

One hundred and fifty mapped alligator holes were randomly selected from high and low confidence groups using a random number generation function. A total of 109 low confidence holes and 41 high confidence holes were field checked using GPS to determine if they were actual holes. If a hole did not exist at the exact coordinates, all areas within a 30 m radius were searched for potential holes. Accuracy of GPS coordinates was assumed to be within ± 30 m. A hole was determined by size and difference in depth from surrounding marsh depth. If an area appeared clear of vegetation, 4-5 depth measurements were taken in the hole and in surrounding marsh using a PVC pole, marked in tenths of meters. If hole depths were 50 cm or greater than the average marsh depth then the area was classified as a hole or refugia. If an area appeared like a hole but was only 25 to 50 cm deeper than the surrounding marsh, then size was the determining factor. Average water depths and dimensions of the hole or refugia were estimated by sight and recorded. A general description of the hole and surrounding area were also described. If a hole did not exist at the coordinates ± 30 m, average water depth and a description of the area were still recorded. If a hole was seen while traveling to predetermined locations, its coordinates in UTM (NAD 83) were taken and the same procedures were followed as described above.

Results and Discussion

A total of 2,855 potential and known alligator holes were identified on the aerial photos (Figure 1). Of these, 74 were observed prior to mapping, 10 were confirmed in the field after mapping, 697 were considered highly likely to be refugia, and the remaining 2,074 were considered less likely. Small holes (<5-6m) were often difficult to pinpoint on photos, even with coordinates as a guide. Tables 1 and 2 present the breakdown of holes mapped with high confidence and those mapped with low confidence.

The majority of holes observed in the Refuge were at least partially surrounded by water with emergent vegetation of insufficient density to present an unambiguously defined alligator-maintained area. Most alligator holes identified before this study, as well as alligator holes for which coordinates were recorded in the field during this study, provided little help in identifying holes on photographs. Image quality also affected which marks were mapped. Flown on four separate days during 1999, they vary considerably in color balance, contrast, and general clarity. A dark mark that appears to be a potential hole on one image may be totally absent on its overlapping neighbor image; overlapping images differed in darkness and/or shape. Nearly all circular very dark marks were mapped. Those holes mapped with a fairly high level of confidence. Image quality also influenced this part of the mapping effort, as water and vegetation configuration may appear very different from one image to the next.

Many of these marks are easily confusable with wet areas, that upon inspection, show no sign of alligator activity. Potential holes in very wet sloughs – on the photos these appear as fairly extensive areas of dark blue to blue to black - or open water areas, were rarely mapped. In addition to image quality, water depths at the time the photos were flown affected our ability to map holes. Flights occurred in December when water levels in the Refuge were just beginning to recede and were generally still above the marsh surface throughout the Refuge. Photos at the end of the dry season when water levels are down would provide better imagery for alligator hole mapping.

A total of 150 mapped holes were ground-truthed (approximately 5%) as part of the accuracy assessment (Figure 2). Of the 150 randomly selected holes, 19 were inaccessible by airboat due to dense vegetation. Another 19 holes were randomly selected of the same type to replace the inaccessible holes. Of the 150 mapped holes, 46 were determined to be holes and 10 were identified as refugia. Holes mapped with high confidence of all types had 49% accuracy. Holes mapped with low confidence had 33% accuracy. Accuracy includes the actual number of refugia and holes assessed by ground truthing that were mapped from the satellite imagery. Holes and refugia were not identified separately in the mapping process. Forty-seven new holes were identified. Five of these new holes had been mapped in the original effort.

Within each type (1, 1a, 2, 3, & 4), the high confidence holes had better accuracy except for type 2 (Tables 1 and 2). Type 2 were seen as dark ‘slash’ through or along the edge of tree islands or dense sawgrass, generally in a direction other than northeast-southwest (which is very likely a shadow, but could be masking a gator hole). When both high and low confidence holes were grouped together, type 1 were the most accurate (47%). The accuracy of type 1a, 2, 3, and 4 were 37%, 23%, 43%, and 37% respectively.

Holes in the south-central area of the Refuge were easily distinguished from the surrounding marsh. These holes were mostly within white water-lily areas and were obviously free of vegetation, usually lined on one side by emergents. Holes in the north end were harder to identify. In areas of *Eleocharis spp*. wet prairie, open areas of white water-lily appeared as holes until closer inspection.

Depth was not always the best indicator of the presence or absence of an alligator hole. In areas near the canal, water depths were higher naturally, usually close to 1 meter. Several mapped holes appeared like real holes when seen in the field, i.e. clear of vegetation and/or signs of alligator presence. However, the hole depth was within 10-20 cm of the surrounding marsh depth. Though not true holes, areas like this probably act as refugia early in the dry season.

Summary

In this study, alligator holes were mapped with a much lower accuracy than those reported for WCA 3A (Campbell and Mazzotti 2001). Campbell and Mazzotti (2001) were able

to successfully locate and map an extensive area of the Everglades using color infrared photography (1:24,000), with an overall accuracy rate of 86%. By comparison, the overall accuracy rate for mapping of alligator holes from DOQQs for the Refuge was only 37%. While a higher error rate was expected on the Refuge due to the lack of clarity of signatures on the DOQQ photos, an overall accuracy rate of 75% was hoped for when mapping holes coded with a 'high' level of confidence. The 49% accuracy rate we observed was therefore disappointing. When high and low confidence holes were taken together, Type 1 holes (dark mark, circular or amorphous, in the marsh) had an accuracy rate of 47%. Other hole types had even lower accuracy rates.

Several factors influenced our ability to map holes in the Refuge as successfully as Campbell and Mazzotti (2001) did in WCA 3A. The photos were flown when most of the Refuge was wet (December), making it more difficult to identify areas that might hold water when the rest of the marsh is dry. These were the best photos available at the time. Hopefully, a set of 1:10,000 color-infrared photos will be available by summer 2004. The Refuge has a more complex mosaic of wet prairie, slough, and tree islands than WCA 3A, which makes it harder to identify holes and refugia. Photos of a smaller scale and additional ground truthing will help to deal with this issue.

These results lead us to conclude that despite their 1 m resolution, the DOQQs were not adequate for mapping alligator holes in the Refuge. Instead, the use of CIR aerial photography, flown at a scale of no greater than 1:24,000 is the preferred method at this time. Another option for future evaluation is the use of hyperspectral satellite imaging.

Despite the low accuracy on the alligator hole/refugia map, this effort provided the coordinates of over 160 known holes (from the initial ground truthing and accuracy assessment). Identification of these areas allowed us to initiate field sampling to describe ecological characteristics of alligator holes in the Refuge.

III. Ecological characterization of alligator holes in the A.R.M. Loxahatchee National Wildlife Refuge

Introduction

Animals interact with their environment in a variety of ways. In the process of obtaining food, acquiring shelter, and finding mates, animals induce changes in physical, chemical, and biological attributes of their environment. While their effects on population and community dynamics are well recognized, only recently have studies begun to investigate roles of animals in ecosystem processes, including their impacts on landscapes, nutrient cycling, and successional dynamics (Naiman 1988, Pastor et al. 1993, Jones et al. 1997). Roles of organisms in an ecosystem stem far beyond trophic interactions mentioned above, for they also include direct physical manipulation of the environment. These manipulations are important because they have the capacity to modify community, landscape, and ecosystem level structure and functioning.

Animal disturbances impact community and ecosystem level processes by directly and indirectly altering surrounding habitat, which ultimately contributes to an increase in environmental heterogeneity - a process referred to as "ecosystem engineering" (Pickett and White 1985, Naiman 1988, Lawton 1994, Jones et al. 1997). Means by which animals alter their environment are varied. Digging by ground-dwelling animals such as pocket gophers (Hobbs and Hobbs 1987, Huntly and Inouye 1988), prairie dogs (Bonham and Larwick 1976, Whicker and Detling 1988), badgers (Platt 1975), termites (Woods and Sands 1978), and soil invertebrates such as ants (Rogers and Lavigne 1974, Hobbs 1985), are well-recognized for inducing changes in soil properties and altering plant community structure and composition (Naiman 1988). Beavers are also characterized as "ecosystem engineers," as construction of dams creates disturbance patches that alter the original stream and forest habitat.

The American alligator (*Alligator mississippiensis*) is another important ecosystem engineer. Alligators, through the creation and maintenance of alligator holes, influence the structure of plant and animal communities in the Everglades ecosystem (Craighead 1968, Mazzotti and Brandt 1994). These alligator holes, characterized by a depression in the bottom of the marsh (peat or limestone bedrock) with freshwater filling the resulting basin (Craighead 1968), provide a reliable source of water during the dry season when the surrounding marsh is subject to dry-downs (Kushlan 1972, DeAngelis 1994). Availability of water during the dry season is important to alligators for a variety of reasons: it provides foraging and nesting habitat for many female alligators and juveniles (Mazzotti 1989, Kushlan and Jacobsen 1990) and provides a necessary open water area for mating (Garrick and Lang 1975). Importance of the hole reaches far beyond utility to the alligator itself, however, as these ponds also provide important dry season refugia for many aquatic animals. As water in the surrounding marsh declines, aquatic organisms such as fish (Kushlan 1974, Loftus and Ecklund 1994), aquatic invertebrates, reptiles, and amphibians (Kushlan and Kushlan 1980) become concentrated in alligator holes, and wading birds (Hoffman et al. 1994) and mammals (as well as alligators) utilize the holes as foraging sites.

In addition to impacts on animal communities mentioned above, vegetation also is affected by alligator holes. While creating and maintaining holes, alligators remove vegetation and soil from within and around a pond and place them upon the pond's banks (McIlhenny 1935, Craighead 1968). Removal of vegetation and altering of soil properties through movement of substrate can cause changes in plant community composition and structure that may be physically, chemically, and biotically distinct from surrounding undisturbed marsh. This type of disturbance creates gap dynamics in plant succession, as disturbance provides new habitat for vegetation establishment (Pickett and White 1985, Gunderson 1994). By providing a source of spatial and temporal heterogeneity, alligator holes may alter plant community attributes such as species composition, richness, and diversity (Craighead 1968, Denslow 1985). Alligator holes may play a key role in structuring plant and animal communities in the Everglades through provision of a continuous water source and elevated, disturbed soil.

Although researchers consider alligator holes to be an essential component of the Everglades ecosystem (Davis 1943, Mazzotti and Brandt 1994), mechanisms through which they structure plant and animal communities have received limited study. We now have qualitative and quantitative information describing the effects of alligator holes on plant and animal diversity at alligator holes in Big Cypress National Preserve (BCNP) and Water Conservation Area 3 (Kushlan 1974, Campbell 1999, Palmer 2000). BCNP and WCA3 differ dramatically from the Refuge in peat depths, however; BCNP and WCA3 have approximately 1 m of peat, while the Refuge has at least 1.25 m to greater than 4.5 m of peat on top of bedrock (Silveira 1996). These differences in peat depth could create significant differences in structure and function of alligator holes on the Refuge when compared to those in WCA 3. Furthermore, structure and function of alligator holes may depend on temporal and spatial variation in the landscape, such as surrounding vegetation matrix and local hydrology. Thus function of an alligator hole in one location at a certain time may be completely different than that of another alligator hole at another location and time. To understand these differences, it is necessary to conduct an ecological characterization of alligator holes across the Everglades landscape.

The first component of the ecological characterization of an alligator hole is examination of the morphological attributes (size, shape, and peat and water depths) of the hole. In our examination of alligator holes at the A.R.M. Loxahatchee National Wildlife Refuge, we asked the following questions:

1. What is the variation in size of alligator holes in the Refuge?
2. Are alligator holes round or irregular in shape?
3. Do different types of holes exist on the Refuge?
4. What is the variation in peat and water depths of alligator holes?
    a. Are there differences in water and peat depths between the surrounding ecotone?
    b. Are there differences in water and peat depths between the marsh surrounding an alligator hole, and at randomly selected marsh sites?
    c. Do water depths and peat depths vary between different types and sizes of alligator holes?

The second component of ecological characterization addresses biological attributes of a alligator hole. In fulfilling this component, we asked:

1. What plants commonly establish on alligator holes?
2. Does plant diversity vary between different parts of an alligator hole, and between different types and sizes of holes?
3. Does plant diversity vary between alligator holes and randomly selected marsh sites?

Materials and methods

Of 92 known holes identified during accuracy assessment (as described in the previous chapter on mapping), 26 were selected for sampling (Figure 3). Selected holes occurred primarily in the central portion of the Refuge. Holes were selected using a multi-stage random selection procedure. From known holes, we randomly selected 9 holes. Using GIS, we plotted selected holes, along with other known holes, on the South Florida Water Management District's 2 x 2 mile grid representing the Refuge. We then sampled all known holes in each 2 x 2 mi. grid cell containing one randomly selected hole, for a total of 21 holes. To obtain 26 alligator holes to sample, we then went to the first cell to the immediate right of the originally selected cell and selected all known holes occurring in that cell. To select 14 marsh reference sites, we added random distances from –2000 to +2000 m to X and Y coordinates of the first 15 alligator holes chosen by the random selection process outlined above.

Sites were located in the field using a handheld GPS receiver. Upon arriving at the hole, we sketched the hole and its surroundings, and noted presence of alligators, alligator trails, and surrounding vegetation matrix. Two transects, perpendicular to each other, were set up using Polyvinyl Chloride (PVC) poles and tape measures. For elliptical or irregularly shaped alligator hole sites, one transect was run across the longest axis of the site and the other along the shorter axis. Using a compass, direction of each transect was recorded. Each transect ran through the main pond, any ecotone present, and 10 meters into surrounding marsh. For marsh sites, two 30-meter transects were erected running from north-to-south and east-to-west. If original coordinates would have caused transects to intersect a tree island or alligator hole, the middle point was moved in 15 meter increments towards north, south, east, or west until transects were located in marsh. The direction of movement depended on feasibility of locating transects in that area without intersecting non-marsh habitat features (tree islands, alligator holes). If more than one direction would allow us to meet our criteria, we then chose at random between the feasible directions. Coordinates for the new point were then recorded in UTM (NAD 83).

Along each transect, water depth (defined as distance from surface of water to surface of substrate) was recorded at every half-meter interval using a marked PVC pole. Peat depth (defined as distance from surface of substrate to underlying bedrock) was measured at every two-meter interval using a marked PVC pole and rebar. To gauge depth, rebar was pushed into the substrate until it hit underlying bedrock. A marked PVC pole was placed next to the rebar where it protruded from the substrate and a measurement taken. Because rebar was of a known length this reading could then be subtracted from the length of the rebar to assess peat depth. If peat depths between two adjacent 2 m intervals varied 25 cm or more, measurements were taken at half-meter intervals between those two points until variation in peat depth was less than 25cm. Peat depth measurements were not taken on tree islands or floating vegetation mats.

Vegetation (including emergent aquatic plants, submerged vegetation near surface, vegetation in the boundary area, and extending 10 m into surrounding marsh) was measured using a line-transect method that assesses percentage cover and relative abundance of a species. (Barbour et al. 1987). Species abundance, richness, and diversity were derived from these measurements. Measurements were made along half-meter intervals across each transect, and every half-meter interval of each transect was identified as pond, ecotone, or marsh.

We calculated size and shape for each hole, using surface area of open water. Pond edge was determined by a sudden increase in water depth. Where ponds graded gradually into slough or marsh areas, edge was established by considering changes in vegetation and patterns of alligator trails, in addition to increases in water depth. Surface area was then calculated as an area of an ellipse ($\pi r_1 r_2$). Alligator hole shape was determined as a ratio of pond length to width, as calculated by $\pi r_1 r_2/\pi(r_1 + r_2)^2$. An alligator hole was considered circular if the ratio was close to one (> 0.9). If the ratio was less than 0.9, we classified the pond as irregular. Additionally, if a hole was calculated to be circular, we looked at drawings we had made of the hole to determine whether there were any serious anomalies in shape that were not reflected by transects.

Landscape variation in alligator hole water depths were assessed using water relief, as this variable negates any temporal effects associated with variability in hydrology. Pond depth was calculated as average pond water depth of an alligator hole minus average marsh water depth surrounding the hole. Elevation of ecotone was calculated by subtracting average ecotone water depth from average marsh water depth. We used standard t-tests to determine whether average water depths of ecotone and pond differed significantly from average water depth of surrounding marsh.

Species richness (S) for each site was the number of species encountered along each transect. We used the Shannon-Wiener diversity index (H') to calculate diversity scores, as results signify species equivalents. Vegetation species richness and diversity were calculated for each hole and for marsh reference sites. We also calculated species richness for each zone within a hole. We compared species richness between ecotone and marsh and ecotone and pond using standard 1-tailed t-tests with Bonferroni adjustments for multiple comparisons.

When comparing holes to marsh sites, we compared average water depth of marsh outside the hole to average water depth at our marsh reference sites. Because data were not normally distributed (Shapiro-Wilk: $W = 0.8803$, $p = 0.017$), but did approximate a lognormal distribution, we used nonparametric Wilcoxon rank sums two-sample test to compare average water depths.

We compared peat depths among alligator holes, and between holes and marsh sites, using median peat depths and depth classes to categorize peat depth. Classification was necessary because rebar used to measure peat depths was not always long enough to hit bedrock. Initially we used a 3.0 m length of rebar. After ten holes and marsh sites were completed, however, we switched to using a 3.65 m length of rebar. Despite changing to longer rebar, we did not always hit bedrock. Without hitting bedrock, it was impossible to measure peat depths accurately or to calculate average peat depths. We did place peat depths into depth classes and used median class for each site to graphically compare alligator holes to marsh sites. For sites for which median peat depth did not exceed the length of rebar (all but four holes and one marsh site), we also compared median peat depths using two-tailed t-tests.

We calculated species richness and diversity for marsh sites as outlined above, and compared them to values calculated for alligator holes. While diversity values were normally distributed for both hole and marsh sites, species richness had to be log-transformed to better meet assumptions of normality (Shapiro-Wilk goodness of fit test, $W = 0.87$, $p = 0.044$ vs. $W= 0.81$, $p = 0.001$ for normal distribution). Levene's test for homogeneity of variances showed that variances for species richness (lnS) were unequal between hole and marsh sites ($F = 6.13$; df 1, 38; $p = 0.018$), so we used a Welch's analysis of variance to test for differences in species richness between alligator and marsh sites. Because Welch's ANOVA is equivalent to an unequal variance t-test when only two levels are compared, we report results of ANOVA as a one-tailed t-test (probability > F = p/2), testing whether species richness is significantly higher at alligator holes. We used a standard one-tailed t-test to test whether species diversity (H') is higher at holes than at marsh sites, since variances of the two groups were not significantly different.

Plant species richness (S) and diversity (H') of marsh within 10 meters of the ecotone or pond edge of an alligator hole was calculated and compared to values already obtained for marsh sites. Using the Shapiro-Wilk goodness of fit test and Levene's test for homogeneity of variance, each group was shown to have a normal distribution and equal variance. An Independent Samples t-test was used to discover if there were any significant differences in species richness and diversity between two groups.

As detailed above, median peat depths were calculated. Peat values were placed into depth classes at marsh sites and compared to peat depth classes obtained from marsh surrounding alligator holes. Average relative water depth for marsh at each alligator hole site (within 10 meters of ecotone or pond edge) was compared to average depths of marsh sites using nonparametric Wilcoxon rank sums two-sample test.

Results and Discussion

Alligator holes sampled in this study averaged 125.1 m^2 +/- 160.8 (SE 35.5) in surface area (N = 26, Table 3). Median hole size was 86.3 m^2. The smallest hole had a surface area of 3.5 m^2, and the largest had a surface area of 633.2 m^2 (Figure 4). Size is considered to be a defining measure of an alligator hole (Mazzotti et al. 1999) because larger holes cover more area and may be associated with larger and more diverse ecotones. They also provide a larger area that can function as an aquatic refuge.

All but one alligator hole reported on in this study appeared to be active, based on actual presence of an alligator or presence of well-defined trails. Holes were highly variable in both size and shape, with 11 of 26 holes approximating circularity and remaining 15 showing irregularity in shape. Both size and shape of alligator holes can only be considered an approximation, however, since alligators generally extended for an unknown distance beneath adjacent vegetation mats or tree islands.

Pond water depths were significantly deeper than those for surrounding marsh ($t = 9.04$, df 50, $p < 0.0001$) (Figure 5). Average water depth for ponds was 105.11 cm+/- 32.35 (SE 0.97). Average water depths for surrounding marsh and ecotones, respectively, were 54.18 cm +/-22.06 (SE 0.49) and 32.75 cm +/- 32.63 (SE 1.43). Average water relief for alligator holes was 55.65 cm +/- 21.57 cm (SE 4.23) below surrounding marsh. Ecotones were significantly more shallow than surrounding marsh ($t = 3.36$, df = 46, $p < 0.0016$) (Figure 5), with an average water relief of 16.95 cm +/- 18.81 (SE 4.01) above surrounding marsh. Four alligator holes lacked an ecotone completely. Average water depth at marsh reference sites was 50.39 cm +/- 18.57 (SE 0.45), which did not differ significantly from average water depth at marshes surrounding alligator holes.

Median peat values for alligator holes showed a fairly even distribution among size classes, while marsh sites fell predominately into the 251-300 cm range (Figure 6). When comparing marsh adjacent to an alligator hole to reference marsh sites, we found that the same trend existed (Figure 7).

The 10 most abundant plant species recorded at alligator holes, listed in order of importance, were as follows: 1) white water lily (*Nymphaea odorata*), 2) sawgrass (*Cladium jamaicense*), 3) floating heart (*Nymphoides aquatica*), 4) eastern purple bladderwort (*Utricularia purpurea*), 5) annual spikerush (*Eleocharis geniculata*), 6) pickeral weed (*Pontedaria cordata*), 7) Tracy's beakrush (*Rhynchospora tracyii*), 8) arrow arum (*Peltandra virginica*), 9) swamp fern

(*Blechnum serrulatum*), and 10) leafy bladderwort (*Utricularia foliosa*). Sawgrass, swamp fern, and wax myrtle (*Myrica cerifera*) were the 3 most abundant plants in ecotone. White water lily, sawgrass, and eastern purple bladderwort were the most abundant plants in marsh surrounding holes, and in ponds themselves. White water lily, floating heart, and spatter-dock (*Nuphar luteum)* were the most abundant species in ponds themselves. Spatter-dock was observed in only two holes, however, and its presence as the third most abundant plant at holes was due to one very large hole that was virtually covered in spatter-dock. If spatter-dock is taken out of the list, eastern purple bladderwort is next most abundant plant in the characterized alligator holes.

Marsh, ecotone, and pond transects were all included to obtain one plant diversity value per gator hole. Species richness for alligator holes ranged from 9-34 species. Average species richness was 21.11 +/- 6.8 (SE 1.34). Diversity ranged from 0.49-2.75, with an average diversity of 1.89 +/- 0.51 (SE 0.10). Species richness and average diversity for all holes and marsh sites are presented in Table 4.

Species richness was significantly higher in ecotone and in surrounding marsh than it was the pond (Figure 8). Species richness in ecotone and in marsh was not significantly different from each other. Mean species richness was 16.5 +/- 6.6 (SE 1.40) for ecotone and 14.7 +/- 5.1 (SE 0.99) for surrounding marsh. Mean species richness for ponds was 6.8 +/- 3.0 (SE 0.59).

For marsh reference sites, the 10 most abundant plant species listed in order of importance were: 1) white water lily (*Nymphaea odorata*), 2) eastern purple bladderwort (*Utricularia purpuria*), 3) annual spikerush (*Eleocharis geniculata*), 4) leafy bladderwort (*Utricularia foliosa*), 5) floating heart (*Nymphoides aquatica*), 6) sawgrass (*Cladium jamaicense*), 7) Tracy's beakrush (*Rhynchospora tracyii*), 8) maidencane (*Panicum hemitomon*), 9) (*Utricularia gibba*), and 10) rush fuirena (*Fuirena scirpoidea*). Species richness for marsh sites ranged from 10-19 species, with an average diversity of 12.35 +/- 2.41 (SE 0.64). Diversity ranged from 0.87-2.20, with an average of 1.39 +/- 0.37 (SE 0.10).

Transformed species richness (lnS) was significantly higher at alligator holes than at marsh reference sites ($t = 35.2$, df 37.8, $p < 0.0001$). Diversity (H') was also significantly higher at alligator holes ($t = 3.26$, df 38, $p = 0.0001$). While no single area at a hole (pond, marsh, ecotone) was significantly higher in species richness or diversity from reference marsh sites, when alligators holes are viewed as a whole, they are significantly richer in species and diversity than marsh reference sites.

Summary

Results from this sampling effort show that alligator holes are associated with localized increases in plant diversity in the Refuge. Alligator holes act as small-scale disturbances and impact their surroundings by providing a variety of habitats. Variety in habitats is associated with topographic highs and lows of alligator holes, which support a variety of plant species. Still, it is only when viewed as a whole that alligator holes significantly impact their surroundings in the Refuge.

Future research should provide further insight into how alligator holes function in the landscape and whether there are different types of holes on the Refuge that function differently. Effects of hydrology and spatial arrangement on alligator hole structure and function should also be addressed.

Alligator holes are important in maintaining Everglades ecosystem processes. Our preliminary results indicate that one important mechanism in maintenance of diversity is presence of a mosaic of habitats at the alligator hole, but other mechanisms remain largely unstudied. We hope to be able to provide further insights into structural and functional differences between alligator holes on the Refuge, and among alligator holes across the Everglades, to incorporate relevant differences into Everglades restoration plans. Hydrologic restoration of the Everglades is only one part of the puzzle. Ecosystem restoration will also require maintaining or increasing habitat diversity. Alligator holes are a natural feature of the environment that contributes to this objective, and should therefore be incorporated into any restoration management plans for the Everglades ecosystem.

Acknowledgements

We especially thank Tanya Alvarez and Susanna Walters for there assistance with alligator hole characterization field work. We also thank numerous other "volunteers" including Camille Darby, Holly Fling, Jessica Walters, and Jocie Graham who helped with various parts of this study.

Literature Cited

Bonham, C.D. and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. Journal of Range Management. 29:221-225

Brandt, L.A., K.M. Portier, and W.M. Kitchens. 2000. Patterns of change in tree islands in Arthur R. Marshall Loxahatchee National Wildlife Refuge from 1950 to 1991. Wetlands 20:1-14.

Campbell, M.R. 1999. Everglades alligator holes: distribution and ecology. M.S. thesis, University of Florida, Gainesville, FL.

Campbell, M.R. and F.J. Mazzotti. 2001. Mapping Everglades alligator holes using color infrared aerial photographs. Florida Scientist 64(2):148-158.

Craighead, F.C., Sr. 1968. The role of the alligator in shaping plant communities and maintaining wildlife in the southern Everglades. Florida Naturalist 41:2-7, 68-74, 94.

Craighead, F.C., Sr. 1971 *The trees of south Florida, Vol. 1, The natural environments and their succession*. University of Miami Press, Coral Gable, FL.

Davis, J.H. 1943. The natural features of southern Florida, especially the vegetation of the Everglades. Geological Bulletin No. 25. Florida Geological Survey, Tallahassee.

DeAngelis, D.L. 1994. Pages 307-320 in S.M. Davis and J.C. Ogden, eds. *Everglades: the ecosystem and its restoration.* St. Lucie Press, Delray Beach, FL.

Denslow, J.S. 1985. Disturbance-mediated coexistence of species. Pages 307-324 in S.T.A. Pickett and P.S. White, eds. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL.

Garrick, L.D. and J.W. Lang. 1975. Alligator courtship. American Zoologist. 15:813.

Gunderson, L.H. 1994. Pages 323-340 in S.M. Davis and J.C. Ogden, eds. *Everglades: the ecosystem and its restoration.* St. Lucie Press, Delray Beach, FL.

Hobbs, R.J. 1985. Harvester ant foraging and plant species distribution in annual grassland. Oecologia. 67:519-523.

Hobbs, R.J. and V.J. Hobbs. 1987. Gophers and grasslands: a model of vegetation response to patchy soil disturbance. Vegetatio. 69:141-146.

Hoffman, W., G.T. Bancroft, and R.J. Sawicki. 1994. Foraging habitat of wading birds in the water conservation areas of the Everglades. Pages 586-614 in S.M. Davis and J.C. Ogden, eds. *Everglades: the ecosystem and its restoration.* St. Lucie Press, Delray Beach, FL.

Huntley, N., and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanism. Bioscience. 38:785-793.

Jones, C.G., J.H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946-1957.

Kushlan, J.A. 1972. An ecological study of an alligator pond in the Big Cypress swamp of Southern Florida. M.S. Thesis, University of Miami, Coral Gables, FL.

Kushlan, J.A. 1974. Observations on the role of the American alligator (*Alligator mississippiensis*) in the southern Florida wetlands. Copeia 1974:993-996.

Kushlan, J.A. and M.S. Kushlan. 1980. Everglades alligator nests: nesting sites for marsh reptiles. Copeia 1980:930-932.

Kushlan, J.A. and T. Jacobsen. 1990. Environmental variability and reproductive success of Everglades alligators. Journal of Herpetology 24:176-184.

Lawton, J.H. 1984. What do species do in ecosystems? Oikos 71:367-374.

Lodge, T.I. 1994. The Everglades Handbook. St. Lucie Press, Delray Beach, FL.

Loftus, W.F. and A.M. Ecklund. 1994. Long-term dynamics of an Everglades small-fish assemblage. Pages 461-483 in S.M. Davis and J.C. Ogden, eds. *Everglades: the ecosystem and its restoration.* St. Lucie Press, Delray Beach, FL.

Mazzotti, F.J. 1989. Structure and Function. Pages 42-57 in C.A. Ross and S. Garnett, eds. Crocodiles and Alligators. Weldon Owen PTY, Ltd., Australia.

Mazzotti, F.J. and L.A. Brandt. 1994. Ecology of the American alligator in a seasonally fluctuating environment. Pages 485-505 in S.M. Davis and J.C. Ogden, eds. *Everglades: the ecosystem and its restoration.* St. Lucie Press, Delray Beach, FL.

Mazzotti, F.J., L.A. Brandt, M.R. Campbell, and M. Palmer. 1999. An ecological characterization of Everglades alligator holes. Final Annual Report to the Everglades Agricultural Area Environmental Protection District. E.A.A. Environmental Protection District, Palm Beach, Fl.

McIlhenny, E.A. 1935. The alligators life history. Christopher Publishing House, Boston, MA.

Naiman, R.J. 1988. Animal influences on ecosystem dynamics. Bioscience 38:750-752.

Palmer, M.L. 2000. The structure and function of Everglades alligator holes. MS thesis, University of Florida, Gainesville, FL.

Pastor, J., B. Dewey, R.J. Naiman, P.J. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74:467-480.

Pickett, S.T.A. and P.S. White, eds. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL.

Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbance in tall-grass prairie. Ecological Monographs 45:285-305.

Rogers, L.E. and R.J. Lavigne. 1974. Environmental effects of western harvester ants on the shortgrass plains ecosystem. Environmental Entomology 3:994-997.

Silveira, J.A. 1996. Landscape pattern and disturbance in the Everglades: a spatial model of fire and vegetation succession in Water Conservation Area 1. Ph.D. Dissertation. University of Florida, Gainesville, FL. 177 pp.

Whicker, A.D. and J.K. Detling. 1988. Ecological consequences of prairie dog disturbances. Bioscience 38:778-785.

Table 1. Number and accuracy assessment for alligator holes/refugia mapped from Digital Orthographic Quarter Quads (DOQQs) in the A.R.M. Loxahatchee NWR with high confidence.

Type	# Holes Mapped	# Checked	# Holes Found	# Refugia	% Accuracy (Commission)
1	166	8	3	2	63
1a	227	8	4	1	63
2	73	9	1	0	11
3	120	8	5	0	63
4	111	8	4	0	50
Total	697	41	17	3	49

Table 2. Number and accuracy assessment for alligator holes/refugia mapped from DOQQs in the A.R.M. Loxahatchee NWR with low confidence.

Type	#Holes Mapped	# Checked	# Holes Found	# Refugia	% Accuracy (Comission)
1	104	22	8	1	41
1a	1,046	22	4	2	27
2	226	21	5	1	29
3	448	22	6	2	36
4	250	22	6	1	32
Total	2,074	109	29	7	33

Table 3. Summary of alligator hole attribute data. Measurements for Pond Length, Pond Width, Pond Area, and Transects 1 and 2 are in meters. Circularity determined as a ratio of pond length to width, with values ≥0.9 considered circular, and values <0.9 considered irregular in shape.

Site	Pond Length	Pond Width	Pond Area	Circularity	Circular?	Transect 1	Transect 2
20	17	6.5	86.8	0.800	N	37	40
858	11.5	9.5	85.8	0.991	Y	39.5	28.5
1098	2	7	11.0	0.691	N	34.5	27.5
1145	31	5	121.7	0.478	N	58	31
1206	19	7.5	111.9	0.812	N	44.5	27.5
1211	21.5	37.5	633.2	0.926	Y	44.5	62.5
1286	10	3	23.6	0.710	N	33	27
1301	21.5	17.5	295.5	0.989	Y	42	47
1319	10	2.5	19.6	0.640	N	37.5	27
1513	9	1.5	10.6	0.490	N	39	36
2227	13	10.5	107.2	0.989	Y	33	30.5
2292	13.5	12.5	132.5	0.999	Y	33.5	33
2369	4	6	18.8	0.960	Y	35	26
21	15.5	11.5	560.0	0.978	Y	35.5	35
22	11.5	8	289.0	0.968	Y	41.5	30
NH14	1	4.5	3.5	0.595	N	30	31.5
NH15	7	3	16.5	0.840	N	27	23.5
NH16	13	2.5	25.5	0.541	N	41	28.5
NH17	18	15	212.1	0.992	Y	38.5	35.5
NH19	7	5	27.5	0.972	Y	27.5	25.5
NH32	13	3.5	35.7	0.669	N	33	36
NH33	20	9	141.4	0.856	N	40.5	30.5
NH4	26.5	5	104.1	0.534	N	40.5	25.5
NH47	16	9	113.1	0.922	Y	48.5	41.5
NH7	12	6	56.5	0.889	N	35.5	27.5
NH9	5	2.5	9.8	0.889	N	25.5	23

Table 4. Species richness and diversity for alligator holes and marsh sites in A.R.M. Loxahatchee National Wildlife Refuge

Alligator Holes			Marsh Reference Sites		
Site ID	Richness (S)	Diversity (expH')	Site ID	Richness (S)	Diversity (expH')
1145	2.04	19	M3	1.13	11
NH7	2.25	25	M1	1.23	11
NH4	2.23	19	M15	1.15	13
NH19	0.98	9	M13	2.20	19
NH9	2.40	27	M10	1.80	13
NH17	2.16	29	M7	1.54	15
NH16	1.97	28	M14	1.02	10
NH47	2.75	33	M9	1.26	11
1098	1.77	26	M12	1.62	12
2369	1.82	18	M8	1.72	12
NH14	2.40	24	M6	1.66	14
858	1.27	17	M2	1.11	11
NH33	1.65	21	M11	0.87	10
1206	2.14	26	M5	1.13	11
NH32	2.39	30			
2227	0.49	11			
2292	1.70	10			
1513	1.79	21			
1211	2.01	21			
20	2.63	34			
1301	1.35	17			
1319	2.12	22			
1286	1.56	17			
NH15	1.95	16			
21	1.46	14			
22	1.91	15			

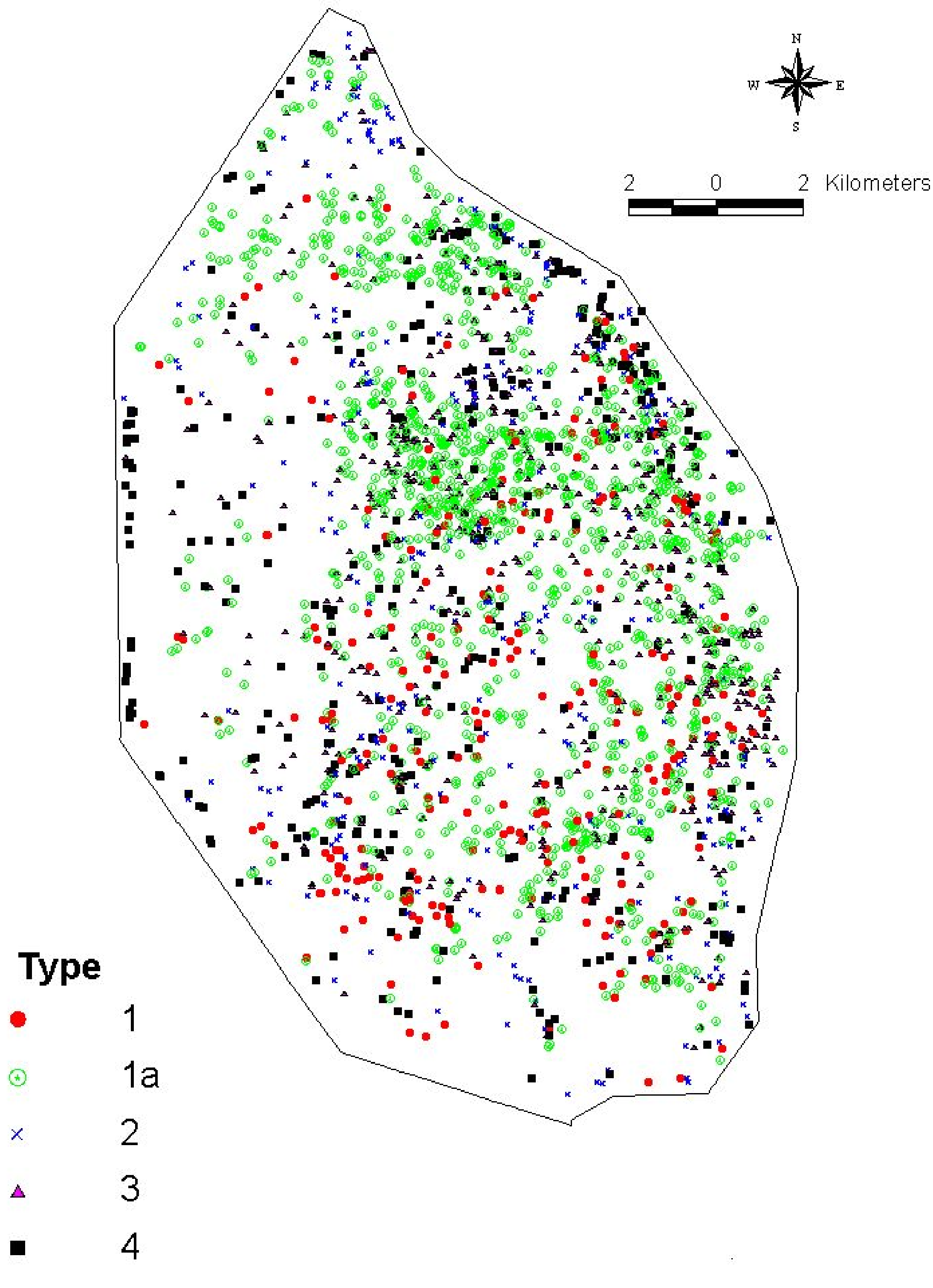

Figure 1. Potential alligator holes mapped from December 1999 Digital Ortho Quarter Quadrants (DOQQs) of the A.R.M. Loxahatchee National Wildlife Refuge. Coordinates are in Universal Transverse Mercator (UTM) and North American Datum of 1983 (NAD 83).

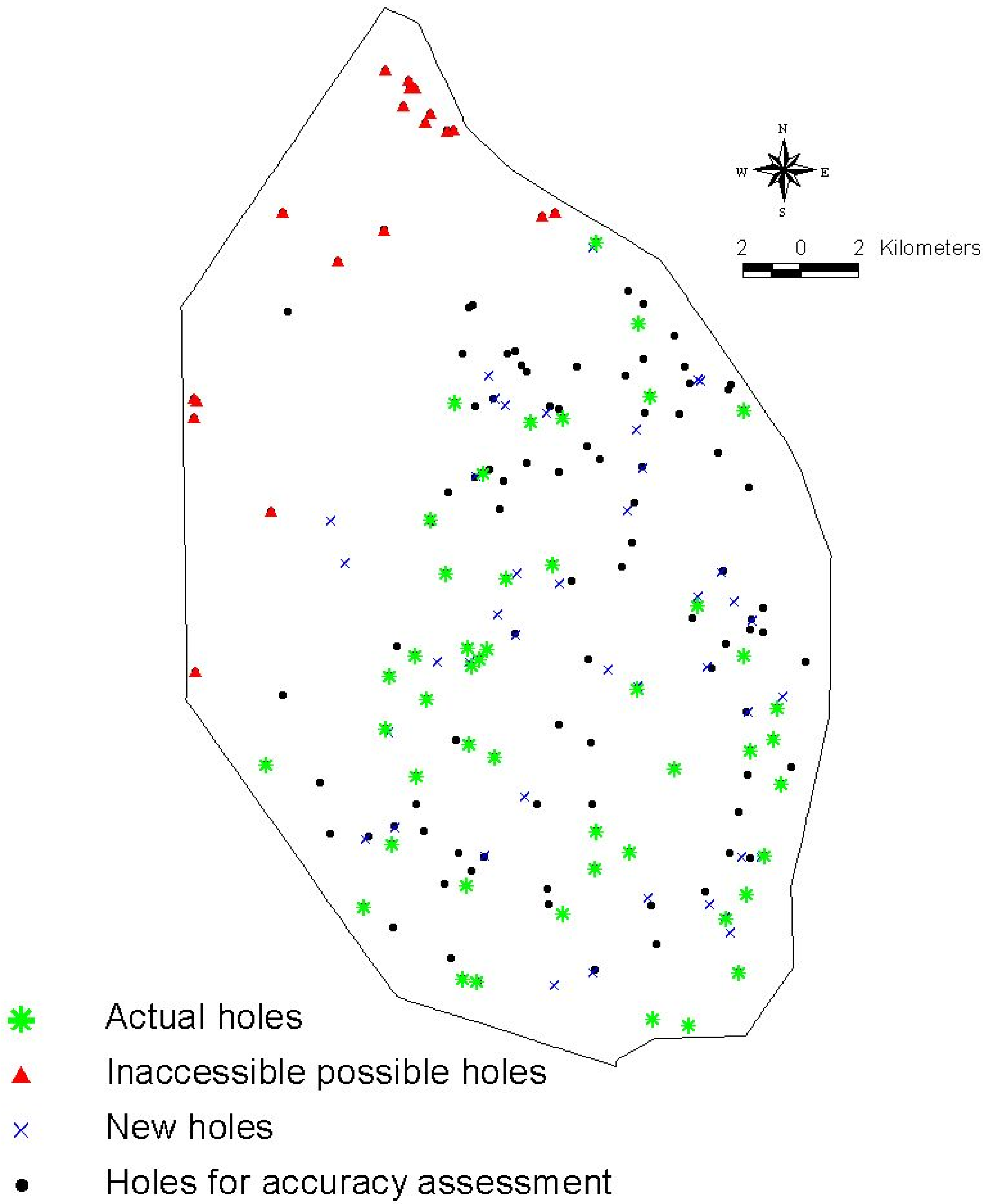

Figure 2. Sample of alligator holes selected for accuracy assessment at A.R.M. Loxahatchee National Wildlife Refuge. Coordinates are in Universal Transverse Mercator (UTM) and North American Datum of 1983 (NAD 83).

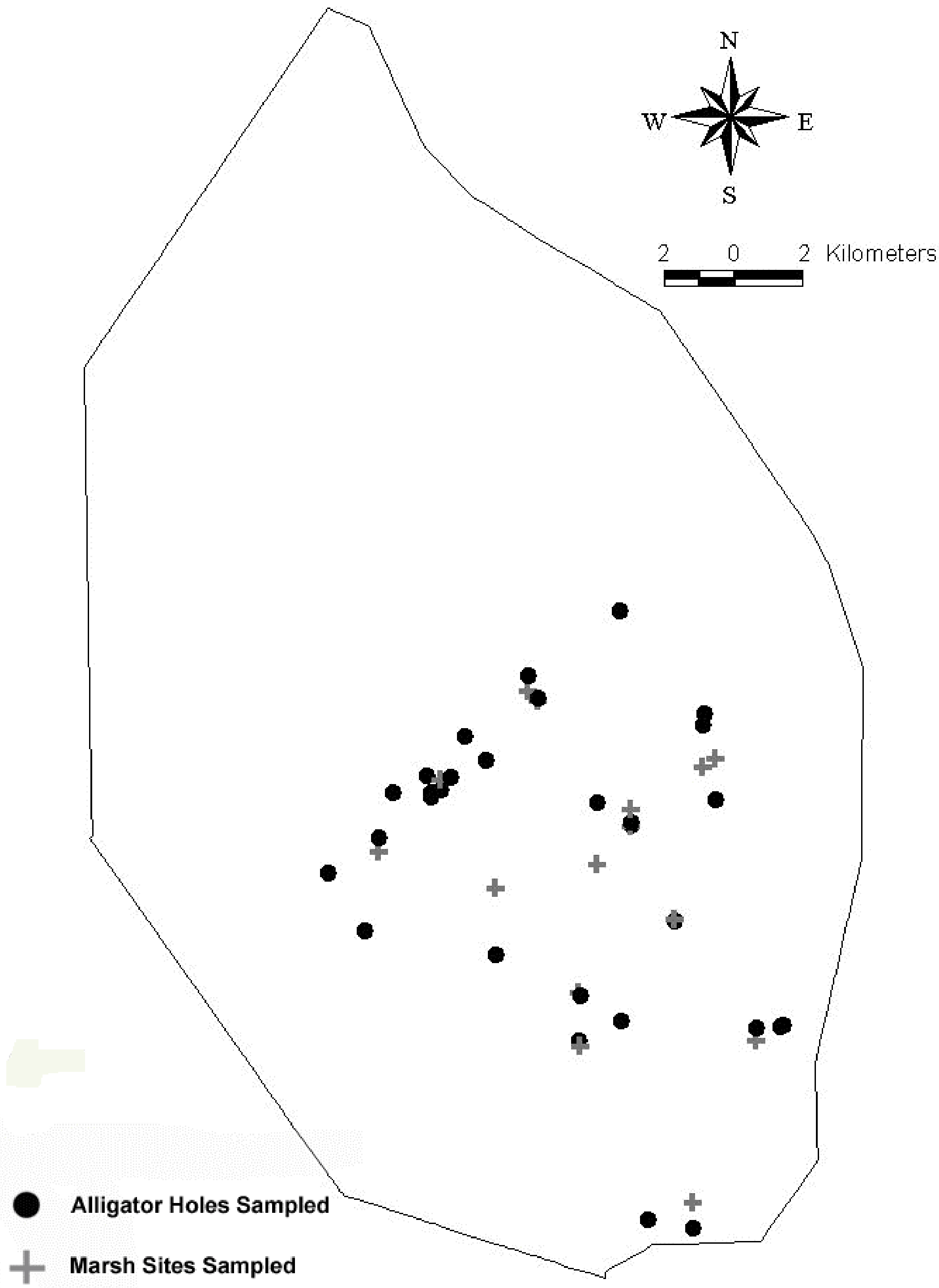

Figure 3. Location of alligator holes and marsh sites in the A.R.M. Loxahatchee National Wildlife Refuge used for ecological characterization study. Coordinates are in Universal Transverse Mercator (UTM) and North American Datum of 1983 (NAD 83).

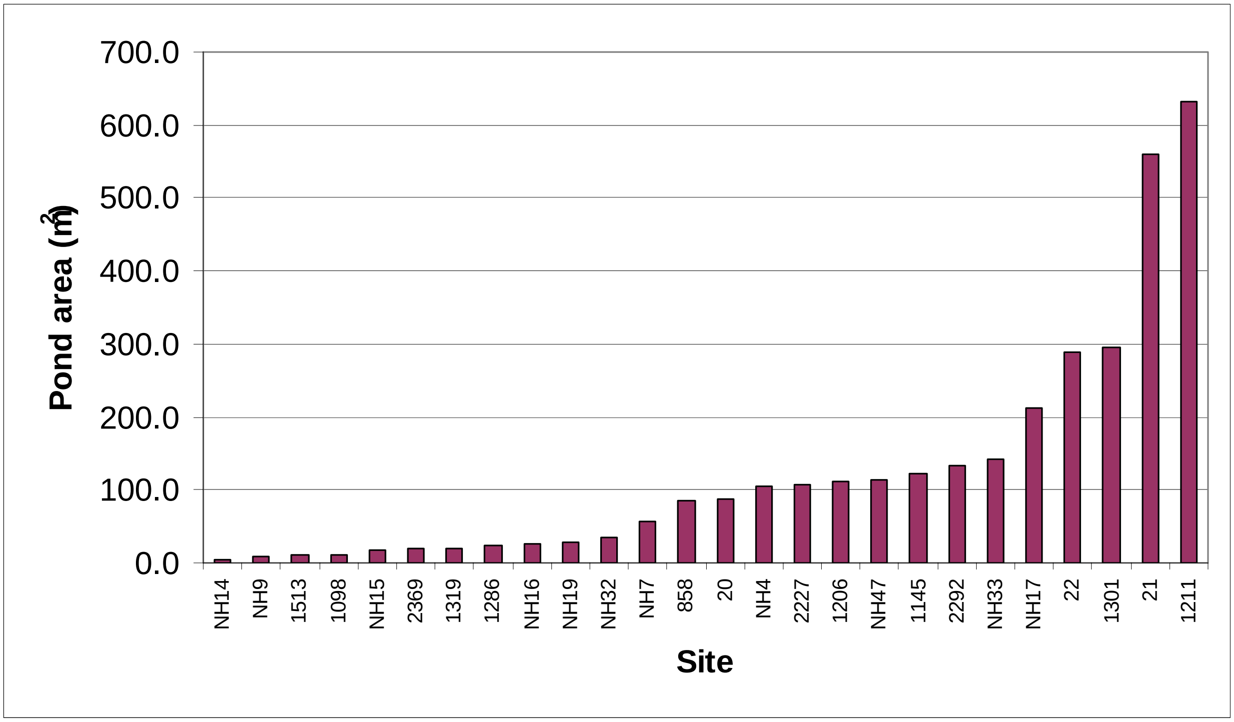

Figure 4. Size of alligator holes as determined by the surface area of the ponds.

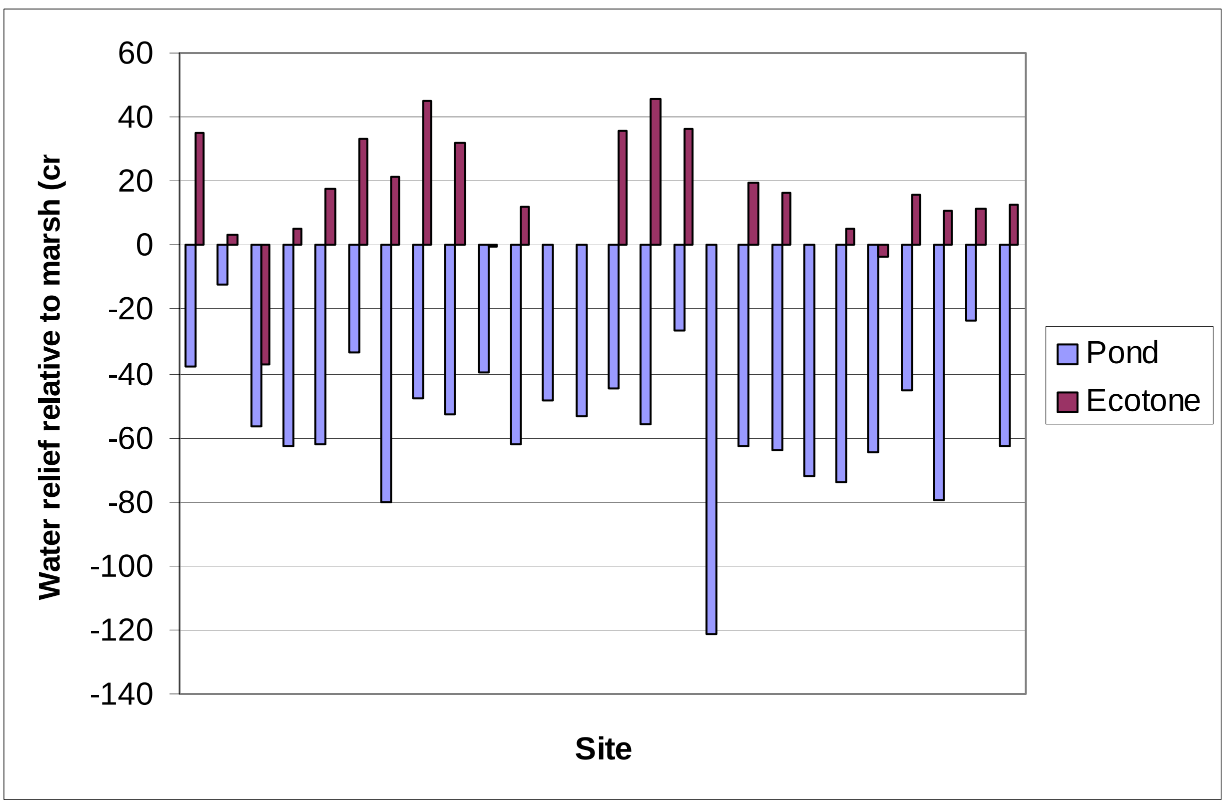

Figure 5. Average water relief of pond and ecotone relative to the average water depth of the surrounding marsh (here represented by 0).

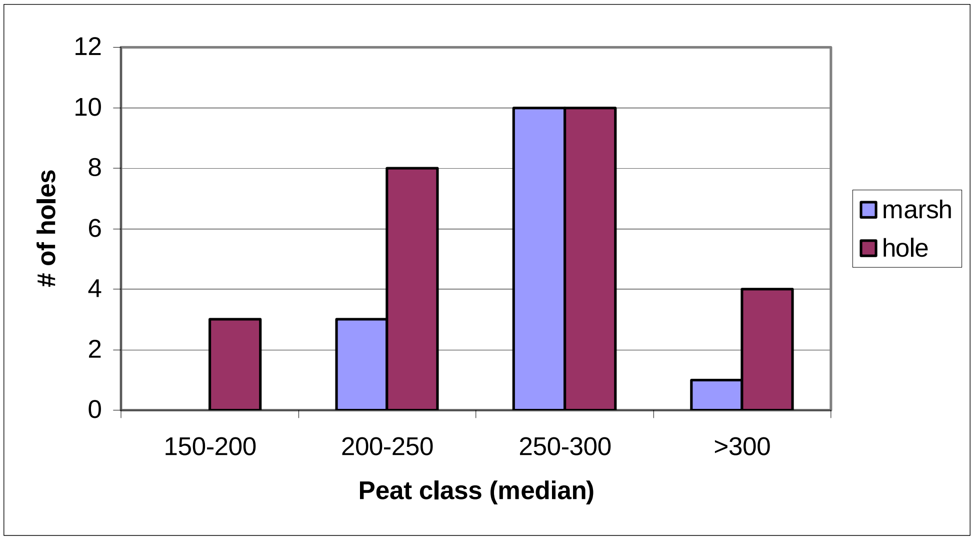

Figure 6. Distribution of median peat values for alligator holes and marsh sites. Peat classes measured in centimeters.

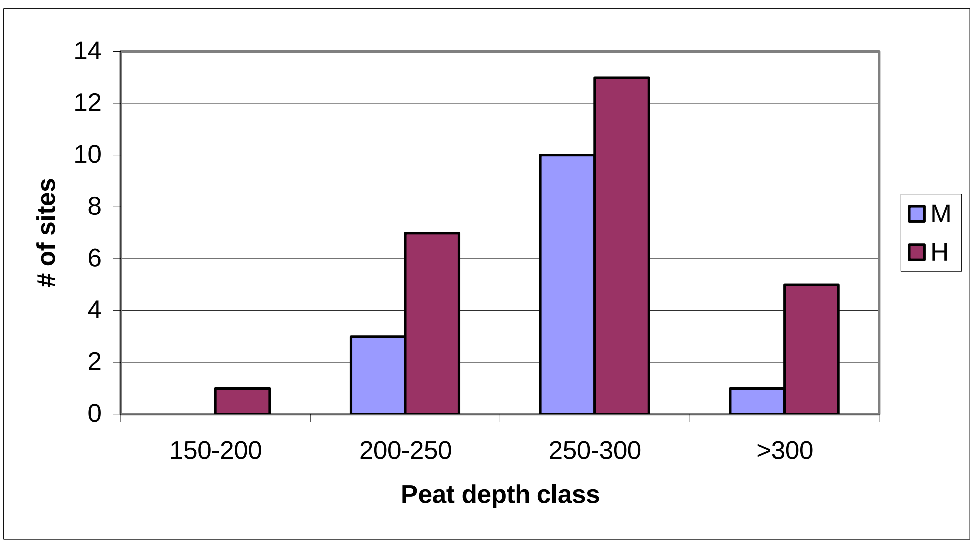

Figure 7. Distribution of median peat values for the marsh zones of alligator holes and for marsh reference sites. Peat classes measured in centimeters.

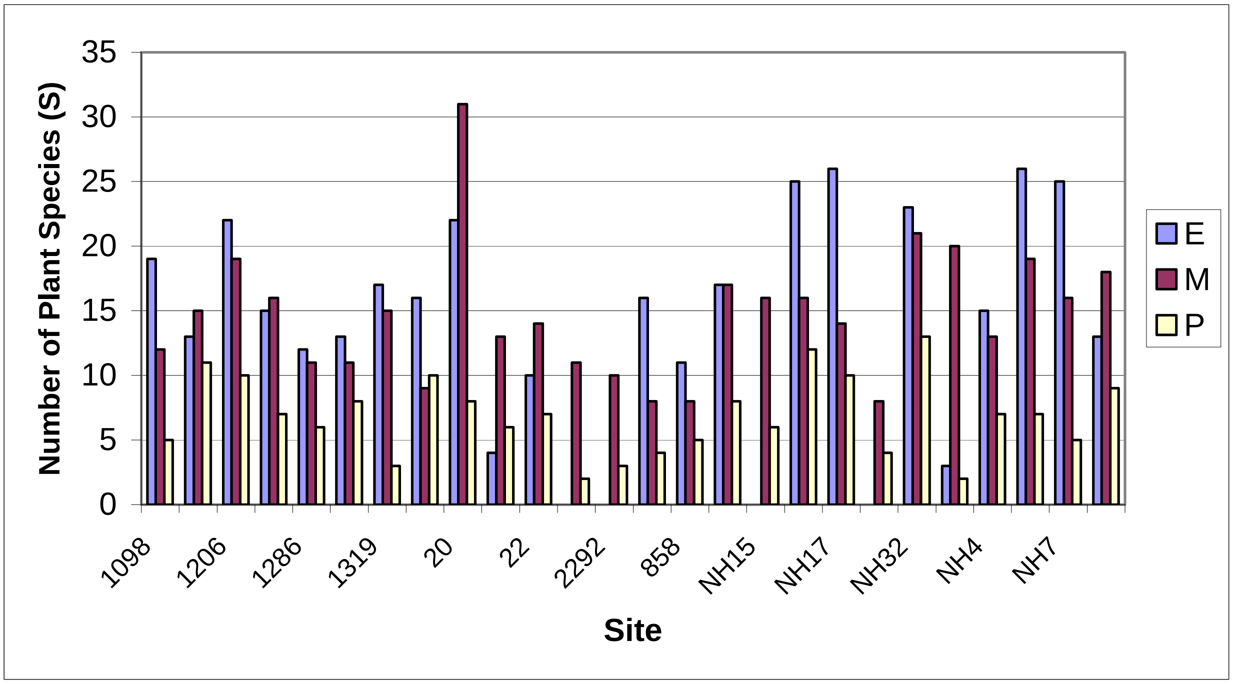

Figure 8. Total number of plant species encountered at alligator holes, separated by zone (E=Ecotone, M=Marsh, P=Pond)