

WADING BIRD FORAGING AND PREY CONCENTRATION IN THE RIDGE AND
SLOUGH LANDSCAPE OF THE EVERGLADES

By

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Nathan Dorn, Department of Environmental Sciences, and has been approved by all members of the supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

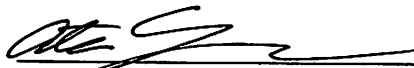
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ABSTRACT

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The hydrological and topographical variation of wetlands can affect the behavior, population growth, and local densities of aquatic species, which in turn can drive the behavior and density dynamics of gleaning predators. Prey availability, primarily determined by prey density and water depth in wetlands, is an important limiting factor for nesting wading bird populations, top predators in the south Florida Everglades. The Everglades is able to support large colonies of nesting wading birds because of the microtopographic variation in the landscape. Some types of prey concentrate in flat, shallow sloughs or become trapped in isolated pools as they move down from higher elevation ridges with receding water levels. Manipulations to the hydrology and landscape of the Everglades has negatively impacted nesting wading bird populations in the past, and may continue to be detrimental by allowing flat, shallow sloughs to be intersected by deep canals, a potential refuge for wading bird prey. In addition, the subtle elevation differences between the ridge and slough landscape may be an important

mechanism for increasing slough crayfish (*Procambarus fallax*) prey availability for the most abundant and seemingly depth-sensitive Everglades wading bird, the White Ibis (*Eudocimus albus*). I implemented a 2-year experimental study in four replicated man-made wetlands with controlled water recession rates in order to determine the effects of proximate deep water (akin to canals) on fish prey concentrations in the sloughs, as water levels receded similarly to a natural Everglades dry season. I also calculated average daily wading bird densities with game cameras (Reconyx PC800 Hyperfire) using time-lapse imagery over 60 days to determine when and where wading birds responded to changing prey concentrations. I completed an additional observational study on White Ibis and slough crayfish prey from the first year of data (2017). Crayfish make up the majority of the diet for nesting White Ibis, and literature has suggested crayfish are most abundant at slough depths much deeper than previously proposed foraging depth limitations for White Ibis. This study specifically compared recent determinations about crayfish movement dynamics in the ridge and slough system with White Ibis foraging behavior and depth limits. Results from the first experimental study suggest that canals might be an attractive refuge for relatively large prey fishes (> 3 cm SL) in sloughs, but it is uncertain if the fencing blocked all prey fish movement. The second observational study determined White Ibis foraging activity was primarily driven by a down-gradient crayfish flux from ridge to slough, with the majority of foraging activity occurring at much deeper slough depths than previously suggested water depth limitations for White Ibis. Results from both of these studies support the importance of preserving the ridge-slough landscape of the Everglades to sustain high prey availability for wading birds.

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CHAPTER 1: GENERAL INTRODUCTION

Wetlands are complex ecosystems with high levels of biodiversity, and they play a vital role in sustaining healthy environments (Gibbs 2000) and human communities (Costanza et al. 1997, Mitsch and Gosselink 2000, Keddy et al. 2009). Wetlands are subject to water level fluctuations caused by seasonal flooding, tidal changes, and flood management practices (Brinson 1993, Ma et al. 2010). The fluctuations in water levels paired with microtopographic variation in the landscape provide diverse habitats that change spatiotemporally, creating high biodiversity (Ma et al. 2010). However, wetlands around the world have greatly declined throughout the 20th century (Davidson 2014) due to degradation and loss of wetlands to provide anthropogenic resources (Keddy et al. 2009, Davidson 2014).

One of the largest freshwater wetlands in the world is the Florida Everglades in south Florida, U.S.A. Much of the central portions of the Everglades is a mosaic of two interspersed habitats: higher elevation ridges and lower elevation sloughs (i.e., the ridge-slough landscape) (Larsen et al. 2011). The ridges are higher in elevation and generally dominated by dense, grassy vegetation, while sloughs are 20-30 cm lower in elevation (i.e., commonly 70-100 cm deep in the summer) and covered with sparse emergent or floating vegetation (Jordan et al. 1997, Sklar et al. 2000, Larsen et al. 2007). This subtle topographical variation provides a dynamic habitat for aquatic fauna and their predators as water levels seasonally rise and recede. Due to anthropogenic manipulations to the hydrology and topography of the Everglades, approximately 50% of the historic

Everglades has been drained and developed into agricultural and urban areas (Davis et al. 1994, Harvey et al. 2010). The Everglades has been impounded and managed by a system of levees and canals to control flooding and water supply for human communities (Richardson 2010), and it has also been subjected to ridge and slough flattening because of manipulations to water flow, length of inundation, and water depth gradients (Ogden 1994, Larsen et al. 2007, Frederick et al. 2009), resulting in a loss of at least 25% of the ridge-slough landscape since pre-drainage times (Ogden 2005).

The health of nesting long- legged wading bird (Ciconiiformes and Pelecaniformes) populations is frequently considered as a measure of the health of the Everglades, and the loss of critical habitat and hydrological processes that create high aquatic prey availability has caused total wading bird nests in the Everglades to decline by at least 70% from the 1930s to 2001 (Crozier and Gawlik 2003). Prey availability is the combination of prey density, prey quality and prey vulnerability (Gawlik 2002). Several environmental influences, including wetland hydroperiods (the amount of time an area is inundated), landscape configuration, and water depth impact prey density and vulnerability (Gawlik 2002, Pierce and Gawlik 2010, Lantz et al. 2010). Some of these influences have been better studied than others, but two of the most important interacting factors that influence prey availability for wading birds are water depth and prey density (Gawlik 2002).

Downgradient prey movement following water-level recession makes prey highly available for wading birds because prey concentrate in high densities at shallow water depths in the sloughs (Gawlik 2002, Klassen et al. 2016, Botson 2016). Spatiotemporal changes in hydropattern that prevent the formation of shallow, concentrated pools of prey during the wading bird breeding season are considered to have caused the historic

declines in the Everglades' wading bird nesting populations (Gawlik 2002, Frederick et al. 2009). The major hydrological problems are untimely wetting or drying, shortened hydroperiods and lack of wetland depth fluctuation. However, deep canals adjacent to sloughs potentially limit the formation of fish prey concentrations further by introducing uncharacteristic channels of deep water to an otherwise topographically flat wetland, giving prey a possible refuge from wading bird predation (Harvey et al. 2010). The close proximity of this additional refuge to sloughs in the Everglades has been suggested to weaken the magnitude of prey concentration during the dry season and thus lower prey availability for wading birds (Rehage and Trexler 2006). Other hydrological alterations have produced a flattening of the microtopographic ridge-slough system (Fleming et al. 1994, Ogden 1994, Larsen et al. 2007, Frederick et al. 2009), and the importance of the microtopographic variation is only partially understood. Flattening may limit the concentrations of some prey for wading birds, if prey move between habitats as the wetland dries.

In my thesis, I addressed both the impacts of proximate deep water on fish prey concentrations in the sloughs for piscivorous wading birds, and the importance of an inter-habitat slough crayfish (*Procambarus fallax*) prey flux, for White Ibis (*Eudocimus albus*) prey availability. For both studies, I used repeated quantifications of wading birds and prey in a drying ridge and slough wetland landscape. In chapter 2, I report on a two-year experimental study in the sloughs of four replicated wetland macrocosms at the Loxahatchee Impoundment Landscape Assessment (LILA) over two dry seasons from January – April (2017 and 2018). I manipulated connections between shallow slough habitat and deep water habitat (akin to canals) to compare fish biomasses and densities as well as wading bird foraging activity. To determine if fish prey were moving to adjacent

deep water (i.e., canals) and thus weakening concentration effects in the shallow sloughs, I inhibited fish movement into adjacent deep water by placing seine fencing across the ends of two of the four wetland sloughs each year. I took 1-m² throw trap samples for invertebrates and fish, three times during the dry down at important depths related to concentration effects in the ridge and slough landscape. I ran analyses to compare prey fish densities in order to see if the fence treatment prevented escape and increased densities in the sloughs. I also quantified and compared wading bird densities under fenced and control conditions to determine whether wading bird activity was significantly higher in the fenced sloughs. I quantified average daily wading bird densities using game cameras with time-lapse imagery, providing continuous images from February – April.

In chapter 3, I report on a second study using the same wading bird images from 2017 for White Ibis only, and I used the slough crayfish biomass and density measurements from 2017 throw trap samples to quantify White Ibis foraging responses to slough crayfish movement in each slough. In this way, I was able to examine conditions (water depth and prey density dynamics) that promote White Ibis foraging in the ridge and slough landscape. In particular, I tested two hypotheses about the depth conditions under which White Ibis would forage: the depth-limited foraging hypothesis posits that the majority of White Ibis foraging during the dry season will occur when sloughs reach previously suggested optimal foraging depths for White Ibis (9-19 cm; Gawlik 2002, Heath et al. 2009, Lantz et al. 2010). Alternatively, the prey flux hypothesis posits that White Ibis feed when high concentrations of crayfish are produced by a crayfish flux elicited by down-gradient migration (> 19 cm depths) off ridges.

CHAPTER 2: WADING BIRD FORAGING AND PREY CONCENTRATION: EFFECTS OF PROXIMATE DEEP WATER

ABSTRACT

The hydrological and topographical variation of wetlands can affect the behavior, population growth and densities of small aquatic animals, which in turn can affect foraging opportunities for larger wetland predators. Canals and ditches used to manipulate shallow, flat wetlands may potentially limit the formation of prey concentrations and thus lower prey availability for nesting wading birds. In the freshwater wetlands of the Florida Everglades, U.S.A., nesting wading birds are top predators highly influenced by prey availability. Some of their fish prey concentrate in flat, shallow wetland sloughs during dry season, increasing prey availability and supporting large colonies of nesting birds. I examined the effects of proximate deep water habitat on fish prey concentrations and wading bird foraging activity by experimentally manipulating large, replicated wetlands at the Loxahatchee Impoundment Landscape Assessment (LILA), Boynton Beach, Florida, in the 2017 and 2018 dry seasons. Fish prey access to deep water was minimized by placing seine fences across the ends of two of the four shallow sloughs each year, when the water was relatively deep. Recession rates were equalized across wetlands to mimic natural recession rates. Prey-sized fish abundances were quantified using various trapping methods in sloughs and

small alligator holes throughout the dry-down, and wading birds were quantified with time lapse photography over 61 days of observations.

Sunfish (*Lepomis* spp. and *Enneacanthus gloriosus*) were caught moving toward deep water refugia at a higher rate in control sloughs than in fenced sloughs, but average fish abundance and concentrations throughout the sloughs did not differ by treatment. The biomass of larger prey fishes (> 3 cm standard length) caught in the alligator holes when the sloughs were nearly dry, was higher in fenced sloughs. Wading bird activity was unaffected by treatment. The results suggest that canals and ditches may be an attractive refuge for relatively larger prey fishes in sloughs, but the abundant 2-3 cm fishes did not appear to use the deep water. Concentrations of larger prey fishes in sloughs with connected deep water canals may be limited, but the scale and importance of the effect will require further study.

INTRODUCTION

Wetlands are complex ecosystems home to a diverse assemblage of flora and fauna, and they play a vital role in sustaining healthy environments and human communities (Brinson 1993, Costanza et al. 1997, Keddy et al. 2009). The world's wetlands have declined by 64-71% on average since the 1900s (Davidson 2014). This is partly due to the construction of canal and levee systems both directly by dredging and indirectly by affecting hydrological processes (Turner 1997, Day et al. 2000, Sokol et al. 2014). Wetlands are key components of watersheds, and degradation or destruction of wetlands can negatively impact both wetland ecosystem functions as well as the function and health of connected lakes, streams and rivers (Meyer et al. 2003). Wetlands are subject to water level fluctuations caused by seasonal flooding, tidal changes, and flood

management practices (Brinson 1993, Ma et al. 2010). The fluctuations in water levels paired with variation in the landscape create diverse habitats that change spatiotemporally (Ogden 2005, Ma et al. 2010). The hydrological and topographical variation of wetlands affects the behavior, population growth and local densities of aquatic species, which in turn can drive behavior and population dynamics of gleaning predators such as waterbirds (Ma et al. 2010).

One prominent group of waterbirds influenced by hydrological and topographical variation in wetlands is long-legged wading birds (Ciconiiformes and Pelecaniformes). Wetlands provide vital support for wading bird nesting populations by providing nesting habitat and dense abundances of prey. Nesting wading birds are generally considered to be food limited (Martin 1987, Martin 1995, Butler and Vennesland 2000, Fredrick et al. 2009). The energy demands for egg production, incubation, and rearing of chicks (Martin 1987, Herring et al. 2010, Beerens et al. 2011) require sufficient food for wading birds during the breeding and nesting season (Fredrick et al. 2009, Lantz et al. 2010, Herring et al. 2010, Borkhataria et al. 2012). Insufficient food for wading birds can cause delayed initiation of breeding (Beerens et al. 2011) and decreased clutch sizes, nestling growth rates, and survival (Martin 1987, Herring et al. 2010). A variety of wetlands around the world support colonies of nesting wading birds (Erwin and Spendelov 1991, Ma et al. 2010), including the freshwater Florida Everglades in the United States.

The Everglades is a large, oligotrophic wetland in southeast Florida that covered over one million hectares of land (Richardson 2010, Gunderson and Loftus 1993) in the 19th century. Prior to drainage, the Everglades supported colonies of nesting wading birds that could surpass 100,000 pairs per year (Ogden 1994, Frederick and Ogden 2001). The most abundant nesting wading bird species found in the freshwater portions of the

Everglades include White Ibis (*Eudocimus albus*), Snowy Egret (*Egretta thula*), Tricolored Heron (*Egretta tricolor*), Little Blue Heron (*Egretta caerulea*), Great Egret (*Ardea albus*), and Wood Stork (*Mycteria americana*) (Frederick and Ogden 2001). Most of the historic Everglades could be described as a large, shallow sheet of slow-flowing water over a topographically flat landscape with subtle elevation changes, producing an array of shallow spike rush marshes, lily sloughs, higher elevation hammocks and sawgrass (*Cladium jamaicense*) ridges, and forested uplands (Perry 2008, Richardson 2010). Small aquatic animals in the Everglades that could become prey for wading birds include small-bodied marsh fishes (small fishes) such as eastern mosquitofish (*Gambusia holbrooki*) and bluefin killifish (*Lucania goodei*), larger fishes (e.g., sunfish; *Lepomis* spp.), as well as crayfish (*Procambarus* spp.), grass shrimp (*Palaemonetes paludosus*), and aquatic insects (Dorn et al. 2011, Boyle et al. 2012, Klassen et al. 2016).

The landscape of the Everglades is an important feature contributing to the concentrations of prey that sustain nesting wading birds. The Everglades is subjected to high amounts of rainfall in the wet season (May through October), and the water then recedes over the dry season (November through April) (Davis et al. 1994). Much of the central portions of the Everglades is a mosaic of two interspersed habitats: higher elevation ridges and lower elevation sloughs (i.e., the ridge-slough landscape) (Larsen et al. 2011), and nesting wading birds almost exclusively forage in slough habitats during the dry season (Bancroft et al. 1992, Hoffman et al. 1994, Bancroft et al. 2002). This is because some types of wading bird prey concentrate in sloughs or become trapped in isolated pools as they move down from higher elevation habitats (short hydroperiod marshes and ridges), following water recession (Trexler et al. 2002, Botson et al. 2016). Evidence suggests slough crayfish (*P. fallax*) and some fish species move directionally

towards lower elevations as water levels decline in the dry season (Cook et al. 2014, Hoch et al. 2015). In addition, a study of prey fish concentrations in the Everglades found that modeled dry-season fish biomass in sloughs increased by 55% with a three-fold increase in the corresponding water recession rate (0.2 cm/day to 0.6 cm/day) (Botson et al. 2016). After prey is depleted, the Everglades re-floods in the wet season and prey populations replenish by reproduction (Trexler et al. 2005, Dorn and Cook 2015). Wading birds and their prey are therefore dependent upon and responsive to periods of drying and flooding in the heterogenous slough and ridge landscape.

The mechanisms by which wetlands make food available for long-legged wading bird breeding populations are conceptually incorporated within the Prey Availability Hypothesis (Gawlik 2002). Prey availability is the combination of prey density, prey quality and prey vulnerability (Gawlik 2002). Several environmental influences, including wetland hydroperiods (the amount of time an area is inundated), landscape configuration and water depth impact prey density and vulnerability (Gawlik 2002, Pierce and Gawlik 2010, Lantz et al. 2010). Some of the environmental factors in the conceptual model have been better studied than others, but one of the most important factors that influence prey availability for wading birds is water depth. Downgradient movement with water-level recession (and shrinking wetland habitat) makes prey available for wading birds because there are higher concentrations of prey and shallow, easily accessed water depths (Gawlik 2002, Klassen et al. 2016, Botson 2016).

All wading bird foraging is limited by water depth, but there are species-specific differences in water depth preference, foraging strategy and prey use that influence a wading bird's ability to forage efficiently (Gawlik 2002, Boyle et al. 2012, Klassen et al. 2016). Morphology (i.e. neck and leg length) determines preferred water depths for each

wading bird species, though all seem to prefer foraging in water between 5-30 cm deep (Gawlik 2002). Shorter legged wading birds such as White Ibis are thought to forage in shallower conditions, and taller wading birds such as Great Egrets forage in deeper water (Gawlik 2002; Beerens et al. 2011). Different foraging strategies also influence water depth preferences for wading birds. Some wading birds are categorized as exploiters, which display more behavioral flexibility by efficiently foraging for fish at sites where fish availability is lower (often low densities and deep water) and staying at low-quality foraging patches longer (Gawlik 2002). Wading birds categorized as searchers seek out high-quality patches with high concentrations of fish and shallower water depths, and they leave as soon as prey availability drops. While all wading birds may consume some fish, not all wading birds predominantly feed on fish. Prey preference differs depending on the species of wading bird and the prey composition in the available foraging habitat. White Ibis generally provision crayfish to their young (Boyle et al. 2012) and Glossy Ibis are generalist consumers of aquatic invertebrates, insects, and some amphibians (Taylor and Taylor 2015). In contrast, Wood Stork and Snowy Egret prey consists primarily of fish (> 2 cm SL) (Gawlik 2002, Boyle et al. 2012, Klassen et al. 2016).

Wading bird nests in the Everglades declined by at least 70% from the 1930s to 2001 (Crozier and Gawlik 2003), and the historic decline is attributed to anthropogenic alterations to the Everglades. A century of wetland drainage and altered water management practices in the Everglades has stopped the natural sheet flow, altered hydroperiods, and limited the extent of natural hydrological pulses. Approximately 50% of the historic Everglades has been drained and/or developed into agricultural and urban areas (Davis et al. 1994, Harvey et al. 2010). In addition to wetland loss, the Everglades has been impounded and the hydrodynamics are largely controlled by a system of levees

and canals (Richardson 2010). These canals and levees are a vital part of flood management in south Florida, but they compartmentalize the Everglades, which blocks the natural sheet flow and alters water depths and hydroperiods by ponding, draining, and redirecting excess water to the coasts (Harwell 1997, Ogden 2005, Harvey et al. 2010, Borkhataria et al. 2012).

Spatiotemporal changes in hydropattern that prevent the formation of shallow, concentrated pools of prey during the wading bird breeding season are considered to have caused declines in the Everglades' wading bird nesting populations (Gawlik 2002, Frederick et al. 2009). The major hydrological problems are untimely wetting or drying, shortened hydroperiods and lack of wetland depth fluctuation. In addition, deep canals adjacent to sloughs potentially limit the formation of prey concentrations further, as they connect deep water habitats to an otherwise topographically flat, shallow wetland (Harvey et al. 2010). The close proximity of canals to sloughs in the Everglades could weaken the magnitude of prey concentration during the dry season and thus lower prey availability for nesting wading birds (Rehage and Trexler 2006). Some observations indicate there are significant increases in the density of all small aquatic fauna within five meters of canals during the dry season, regardless of predation risk from larger predatory fish (> 8 cm SL) inhabiting canals (Rehage and Trexler 2006). With over 1,600 km of canals and remnant canals currently bisecting, fragmenting and surrounding the Everglades (Light and Dineen 1994), it is possible that a substantial quantity of prey produced in the wetlands escapes into adjacent deeper water instead of concentrating in sloughs during the dry season. Nevertheless, the potential impacts of prey fish (2-5 cm SL) movement into deep water refugia on prey availability for wading birds has not been studied (Harvey et al. 2010). In this chapter, I tested the potential impacts by

experimentally examining the effects of connected deep-water habitat on prey availability for wading birds in four adjacent wetland habitats.

I manipulated connections between four shallow spike-rush sloughs and adjacent deep water habitats with seine fences to compare fish prey densities and wading bird foraging activity between connected and non-connected sloughs. The study took place over the dry seasons of 2017 and 2018 (February through April). I hypothesized that fish prey densities would be higher in the wetlands where fish prey movement to adjacent deep water was inhibited by the fence treatment. This hypothesis assumed that prey fish movement occurred over a 100 to 200 m scale (Hoch et al. 2015). I used data from two years of controlled recessions and fence treatment conditions. Between the two years, I swapped the treatments among the four wetland sloughs so that each wetland had a fence condition for one year and a control condition for the other year. I test the following five specific predictions related to fish concentration and wading bird foraging:

Prediction 1: Sloughs under fenced conditions will have significantly lower catch rates of fish moving out of the slough towards deep water than sloughs under control conditions, because the seine fences blocked fish movement out of the sloughs.

Prediction 2: The average biomass of prey fish (> 2 cm SL) will be significantly higher in fenced sloughs than in control sloughs, specifically during the second sampling session when the ridges were almost dry (7-11 cm on average) and sloughs were still 30-35 cm deep.

Prediction 3: The proportional increase of fish biomass from the first to the second sampling session as wetlands dry down (effect size), will be significantly greater under fenced conditions.

Prediction 4: At the end of the dry season, the abundances of the largest prey fish (> 2 or >3 cm SL) will be higher in the alligator holes when they are embedded in fenced sloughs rather than control sloughs.

Prediction 5: Piscivorous wading bird densities will be higher in fenced sloughs, if fish prey densities are higher in fenced sloughs.

METHODS

Area of Study

I conducted a two-year study in the sloughs of four replicated 8 ha wetlands (denoted as M1-M4, north to south) at the Loxahatchee Impoundment Landscape Assessment (LILA), Boynton Beach, Florida (lat. $26^{\circ}17.99'$ N, long. $80^{\circ}13.97'$ W) during the winter-spring dry season from 2 February 2017 - 28 April 2017, and 2 February – 27 April 2018, in order to examine the effects of proximate deep water (akin to canals) on wading birds and their prey concentrations in the sloughs. The wetlands (each 8 ha) contain habitat and elevation features characteristic of the Everglades and include higher elevation ridges and tree islands, a shallower and a deeper slough, alligator holes, and deep collection ponds (Fig. 1). All are similar in arrangement and have an assemblage of fish, invertebrates, and vegetation types that are characteristic of the Everglades ecosystem. The wetlands were separated by levees, and water levels were controlled in a connected flow-through system. Each wetland contained largely independent prey populations and water levels were controlled independently. Common macrophytes in the wetlands included spikerushes (*Eleocharis* spp.), white water lily (*Nymphaea odorata*), panic grass (*Panicum* spp.), duck potato (*Sagittaria lancifolia*), pickerelweed (*Pontederia cordata*), and sawgrass (*Cladium jamaicense*). Common

submerged aquatic vegetation includes bladderworts (*Utricularia* spp.) and muskgrass (*Chara* spp.). The aquatic faunal community included slough crayfish (*Procambarus fallax*), grass shrimp (*Palaemonetes paludosus*) and small fishes such as the eastern mosquitofish (*Gambusia holbrooki*), bluefin killifish (*Lucania goodei*), flagfish (*Jordanella floridae*), golden topminnow (*Fundulus chrysotus*), pigmy sunfish (*Elassoma evergladei*), sailfin molly (*Poecilia latipinna*), and least killifish (*Heterandria formosa*), as well as the somewhat larger sunfishes (*Lepomis* spp. and bluespotted sunfish (*Enneacanthus gloriosus*). I focused on quantifying wading birds and their fish prey in the smaller and shallower of the two sloughs in each wetland (Fig. 1). Each slough was 18 – 20 m wide by 360 m long with higher elevation ridges to the north and the south. The elevation differences between the ridges and sloughs that I studied were 20-26 cm and water depths fluctuated up to 1.2 m between seasons such that ridges become dry most years and sloughs may remain wet or else become dry at a later date. Each slough contained two constructed “alligator holes” separated by ~120 m that ranged in area from 29-80 m². Some of the alligator holes seem to have been maintained by alligators while others were only slightly deeper (~20 cm) than the sloughs and have become somewhat overgrown with dense emergent vegetation.

Hydrograph and Timeline

The hydrology of each wetland was controlled by South Florida Water Management District managers and were operated independently to regulate depth and recession rates. The recession rate and stage controls were designed to create a synchronized gradient of optimal foraging depths (5-30 cm) in every slough over the period of time each year. The target hydrograph and work timeline for the two years can be seen in Fig. 2. The water levels receded in each wetland with an average recession rate

of $0.55 - 0.56 \text{ cm} \cdot \text{day}^{-1}$ in 2017 (mean from 2 February. – 27 April) and $0.51 - 0.52 \text{ cm} \cdot \text{day}^{-1}$ in 2018 (mean from 2 February to 20 April, 2018) (Fig. 3). I chose this recession rate because both White Ibis and Great Egrets have been observed to select foraging locations across the Everglades landscape with recession rates of $0.52 - 0.59 \text{ cm} \cdot \text{day}^{-1}$ (Beerens et al. 2011). Continuous recording devices tracked water surface elevations in the wetlands and were reported on the DBHYDRO database (South Florida Water Management District 2018). I used measured water depths (cm from water surface to sediment surfaces) in the sloughs to create hydrographs for the sloughs in each year (Fig. 3). Accurate water depths (in cm) in wading bird foraging observation areas (0.13- 0.14 ha within each shallow slough) for each year were calculated based off of reported DBHYDRO depths and depth transects in each shallow slough that I completed on 5 February., 2018. I measured depths (cm) along six evenly spaced transects (13.3 m apart), perpendicular to the length of each slough. On each transect, I measured depth at 13-16 points (1.5 m apart). Altogether I made a total of 51-61 measurements in each slough. The average slough water depths were compared with the water surface elevations from DBHYDRO on the same day to calculate a differential for each wetland, which was applied to daily average surface water elevations from DBHYDRO for each day of the 90-day experiment, providing ridge and slough hydrographs for each wetland.

Treatment

To test the hypothesis that fish prey are moving to adjacent deep water and thus weakening concentration effects in the sloughs, I first inhibited prey movement to adjacent deep water in two of the four sloughs each year by placing seines across the ends of the sloughs. In 2017, wetland macrocosm 2 (M2) and wetland macrocosm 3 (M3) were fenced, and I reversed the treated wetlands in 2018, with M1 and M4 as the fenced

wetlands. The seines were tar-coated mesh (4.76 mm mesh) supported by PVC pipes and metal posts, extending 50 m across the shallow sloughs (~20 m) and up onto the ridges (Fig. 1). They were installed from 30 January– 3 February 2017 and 24 January - 26 January 2018, when the ridges were still flooded (13-15 cm deep, on average) and the shallow sloughs were 50- 54 cm deep (Fig. 2). The bottoms of the seines were lined with bricks and partially buried in the sediment to keep fish from swimming or burrowing under the seine. This formed two stranding sloughs (i.e., fence treatment) that I considered similar to dead ends or local low elevation points in the ridge and slough landscape. Although some fish may have moved over the ridges into the adjacent deeper slough while the water levels were still high, the seines should have prevented larger prey (e.g., > 2-3 cm SL fish, depending on the body width of the fish) from moving directly from the slough into the deep water collection ponds adjacent to the east and west ends of the slough (Fig. 1). At the end of the seines, a silt fence (erosion control construction fencing) was attached at a perpendicular angle and ran lengthwise through the ridge for 50 m in order to discourage fish that encountered the seines from crossing back over the ridge into the other slough to the north (Fig. 1), when the water started to become low on the ridge. Once the seines and nets were placed, I checked the condition of the fencing at least two to three times per week to confirm the barriers remained intact. I also placed extra silt fencing along two deep ditches running perpendicular through the ridges in M1 and M4 during the fencing treatment year, to prevent fish from escaping the sloughs through these ditches.

Prey Emigration from Sloughs

To assess whether the fence treatment conditions were effective at obstructing prey movement, I estimated and compared fish movement into the adjacent deep water

collection pond to the east by setting out two fyke nets next to each other at the eastern end of each of the four shallow sloughs. Data from the fyke nets allowed me to compare the capture rate of fish >2 cm SL in the sloughs under fenced and control conditions. If capture rates were found to be significantly lower in the sloughs under fenced conditions, it would suggest that some fraction of fish were prevented from moving directly into deep water by the seine fencing. Fyke nets were not available immediately because they had to be purchased by the SFWMD and thus could not be set out for more than two nights in 2017. The fyke nets were set out over two nights (6 and 7 March) when water levels were 30 - 38 cm on average, across the sloughs. In 2018, the nets were set out for three trap nights (28 February – 2 March) when water levels were 35 - 42 cm across the sloughs. Two nets were placed side by side, 10 m east of the seines in the fenced wetlands and placed in equivalent locations in the control wetlands. The net openings faced west in order to capture fish moving directionally west to east towards deep water. The lead lines for each net were set across the slough to completely cut off the sloughs (Fig. 1). Due to limitations in the lead line length, the lead lines did not fully stretch across the sloughs, and the last 10 m on the south side of the sloughs were not covered by the lead lines. Fish > 2 cm SL were identified and counted because wading birds select for fish this size (Gawlik 2002), and the seines were only expected to limit movement of fish with a standard length greater than 2 or 3 cm, depending on the species' body width. All animals were released on the east side of the fyke nets to prevent them from getting caught and recounted the next day.

Prey Density in the Sloughs

Prey densities in the slough were sampled using a 1-m² throw trap (Dorn et al. 2005, Dorn and Cook 2015), at three separate time periods during the dry-down in 2017

(8 February – 10 February, 13 March -17 March, and 3 April – 7 April) and 2018 (5 February – 7 February, 12 March – 16 March, and 2 April – 6 April) (Fig. 2). The throw trap consisted of a 1-m² area (90 cm deep), with a copper frame covered in 1.5-mm nylon mesh, which was open on the top and bottom. The trap was thrown into the slough from 1-2 m away, enclosing the fish (for methods see Dorn et al. 2005, Dorn and Cook 2015). I created a stratified random sampling method in QGIS 2.18 to sample seven locations within each shallow slough during each of the three sampling periods for a total of 28 throw traps per sampling period, each year. Each sampling point was at least 5 m away from the next in order to increase the independence and spatial coverage of the point estimates.

I created three distinct sets of random points for each of the three sampling sessions, for each of the four wetlands. The sampling took place only within the seined area of the shallow slough in wetlands under fenced conditions (M2 and M3 in 2017; M1 and M4 in 2018) and an equivalent area in wetlands under control conditions (M1 and M4 in 2017; M2 and M3 in 2018). All of the sampling took place outside of the camera observation areas used to monitor wading bird activity and only after the cameras were turned off each day at 2:00 pm in order to reduce disturbance to foraging birds. Seven to eight traps were completed each day, with samples collected between 2:00 pm and 8:00 pm. Each sampling session was completed within three to five consecutive days. The throw trap sample size was based on previous experience throw-trapping in the sloughs and time constraints for obtaining comparable snapshots of density (i.e., depths are continuously falling, and birds may be regularly foraging). The timing of the samplings focused on expected important depths that potentially affected prey density and wading bird activity.

Sampling dates were spaced out roughly evenly and chosen in order to capture prey dynamics at fundamentally different water depths. The deepest water depths (48 – 50 cm, on average) corresponded to a period when water in the shallow slough was too deep for wading bird foraging, the ridges were flooded, and prey moved freely. This produced information about prey standing stocks before they concentrated in the sloughs. At 30 – 35 cm, the water depth was near the ridge elevation, and prey should have been forced to move into the sloughs (Cook et al. 2014). However, 30 - 35 cm is still considered too deep for most wading birds to forage (Gawlik 2002). This provided a measurement of prey density before wading birds depleted prey populations. At the final depth stage (18 - 23 cm on average), I expected that prey would be highly vulnerable to wading bird foraging, and that prey densities would be declining or somewhat depleted from wading bird predation and/or prey movement to deeper water. Average fish (>2 cm SL) densities and biomass (per m²) for each of the three sampling periods were calculated to determine the absolute increase in fish densities and biomass in all wetlands (Cook et al. 2014, Dorn and Cook 2015). Fish were euthanized with MS222, preserved in formalin and returned to the lab. All prey items were identified, counted and measured in the lab. The fish biomass was calculated for each trap using lengths and length-dry mass regressions (Dorn et al. 2011, unpublished data). Total biomass per trap was quantified as g dry mass/m². Fish > 2 cm SL (i.e. sizes capable of being trapped by fences) were the focus of statistical analyses.

Prey Abundance in Alligator Holes

Whether or not a slough was fenced, some fish were expected to move into smaller local refuges; specifically, the two alligator holes in each slough (Fig. 1). To sample fish in alligator hole habitats, I set out four un-baited minnow traps (0.32 cm

mesh size and 2.54 cm openings) ≥ 2 m apart over one night in each of the two alligator holes in each wetland. Traps were set spread out relatively evenly within each alligator hole, three separate times during the dry down: at 38-46 cm slough depths over the week of 23 February, at 21 - 30 cm depths the week of 23 March, and 3 - 11 cm slough depths the week of 20 April in both years (Fig. 2). Fish were counted, identified, measured and released in the same location. Fish abundances were quantified as mean catch-per-unit-effort where one trap night counted as one effort. One trap in 2017 and another trap in 2018 were dropped from the analyses because the openings were out of the water on the recovery day.

Other Observations of Prey Movement and Concentration

To further analyze fish abundance patterns in alligator holes, I graphically compared catch rates (fish per trap night) in each hole ($n=8$, 2 holes per wetland) through time to determine whether catch rates varied in alligator holes as the water level declined in the sloughs. Holes within the same wetland were graphed individually because of high variation in depth and vegetation cover between holes. In addition, assemblage compositions of fish > 2 cm SL on the final sampling date in 2017 and 2018 were compared in order to determine if there were indications of fish composition differences between treatments. Species composition was summed over holes to create a percent composition for each wetland, which was then averaged to determine the mean percent composition for alligator holes under fenced and control conditions in each year. Data summaries and analyses can be found in Appendix A.

Wading Bird Density in Sloughs

To quantify wading bird foraging responses in each slough, I calculated average

daily wading bird densities over 0.13 – 0.14 ha of the slough in each wetland with game cameras (Reconyx PC800 Hyperfire) using time-lapse imagery (position in Fig.1). Only wading birds within the slough observation area were counted, and the edges of the sloughs were visually identifiable by vegetation shifts from slough to ridge. The cameras took a photo every 3 minutes from 6:00 am to 2:00 pm. These eight hours typically contained 80-90% of all daily activity in a 2015 pre-study. The cameras provided 160 images for each wetland, each day, continuously for a 60-61-day period of observation (27 February 2017 – 28 April 2017 and 27 February – 27 April 2018).

The images were individually inspected, and bird counts were recorded to calculate the time-integrated daily average bird densities in each slough. Most birds, especially those in the nearest 70% of the viewing area, could be identified to species so that composition was recorded as well. Overall > 93% of the birds could be identified except in M4 where densities were low in both years and only ~75% could be identified. This was partly caused by small numbers of singletons towards the back of the images that could not clearly be distinguished as egrets or ibis. Although each wetland is similar in landscape features and size, each camera area was slightly different at different times during the camera observation period. Adjustments in the total image area observed for each wetland were made to calculate density (per-hectare) between wetlands and over time.

I calculated the mean density of wading birds for each day of the 60-day period in each year by dividing the average count of all wading birds in the slough per frame by the viewing area of the slough. Early in the dry down in both years (February to mid-March), there were almost no wading birds in the sloughs so that our summary data are focused on days after the first flush of wading birds (after 10 March). Frames each day that were

too dark, foggy or rainy to distinguish birds were discarded; thus, and range of 100-155 frames per day were used.

From 6 - 14 March 2017, the camera observation area in M4 was reduced because the camera loosened from its support and rotated. The data from this portion of the study was considered less valuable because the viewing area was so small. The camera angle in M3 was initially set a bit smaller than desired and it was adjusted partway through the study. In 2018, no images were taken in M3 due to a camera malfunction, so only images from three wetlands were usable. Individual area measurements were taken for each slough at each camera angle in order to calculate a standard average daily bird density per hectare in each wetland, for both years.

Due to differences in the slough depth and water recession rates between wetlands, the depths did not align perfectly with the dates across wetlands. However, to compare time-integrated densities, I needed to calculate a summary response over a similar frame of reference in each wetland. I summarized average time-integrated bird densities two different ways for initial inspection: windows of equivalent dates (36 days starting on 15 March) and equal water depths (variable days, but depths from 33 down to 11 cm) for each year. The daily averages were calculated as a single mean wading bird activity metric for each wetland over the date range of 15 March - 19 April and separately over the depth range of 33 cm - 11cm within the 60 to 61-day observation period. The specific depth and date ranges were chosen to start during the initial flush of activity in mid-March. Means were calculated for total wading bird density (including unknowns), piscivorous wading bird density (sum of Little Blue Herons, Tricolor Herons, Snowy Egrets, Great Egrets, Roseate Spoonbills, Great Blue Herons) White Ibis density, and Glossy Ibis density.

ANALYSES

All analyses were conducted in R (v.3.4.0). I hypothesized that densities of larger prey fish would be higher in wetlands when the ends were fenced (i.e., treatment conditions) because fish would not be able to swim into the deep water refugia as the water receded. I tested the following three specific predictions related to fish concentration in the analysis and results:

Prey Emigration from Sloughs

The mean CPUE from the paired fyke nets were averaged across all trap nights in each wetland, each year. The average CPUE of all fish > 2 cm and the CPUE of all sunfish were initially graphically displayed separately as mean CPUE per wetland under both fenced and control conditions. Directional movement to deep water is species-specific, and sunfish were specifically chosen for separate analysis due to previously observed down-gradient directional movement in one species of sunfish (*Lepomis marginatus*) (Hoch et al. 2015). In addition, they have deeper bodies that make them more likely to be impeded by the small holes of the seine nets than other common prey species. Only mean CPUE for sunfish was analyzed with an ANOVA between years, blocked by wetland (n=4) to compare catches between 2017 and 2018 within the same wetland.

Fish Density and Concentration in the Sloughs

Mean fish densities (#/m²) and biomass densities (g dry mass/m²) (> 2 cm SL) in each of the four sloughs were determined for each wetland (n=4), for each sampling session. Fish prey density and biomass from the first sampling session in each year were first compared between wetlands with an ANOVA, in order to determine if initial fish densities between wetlands were relatively similar. I then compared biomass in each

wetland separately, between years ($n=2$), in order to determine if initial fish biomass for an individual wetland was significantly different from one year to the next.

After establishing if fish densities were similar at the start of each dry season, I tested for the effects of seine fencing on fish prey > 2 cm SL in the sloughs (prediction 2). The mean biomass of fish (> 2 cm SL) during the second sampling session for each wetland were compared between years with an ANOVA blocked by wetland. Though initial fish abundances at high water (February) were similar between years and wetlands, they were not exactly equal. To control for initial biomass variance, I calculated a proportional effect size (prediction 3) as a proxy for fish biomass concentration using mean biomass densities from the first and second sampling sessions in each wetland each year (concentration effect size = $\ln(\text{mean biomass session 2} / \text{mean biomass session 1})$). The effect size for each wetland was compared between years by an ANOVA, blocked by wetland ($n=4$).

Fish Abundance in Alligator Holes

Mean catch rates and biomass (g dry mass) for fish > 2 cm SL and fish > 3 cm SL in each alligator hole were compared between years with an ANOVA, blocked by hole ($n=8$), on the last sampling session (when the sloughs were shallowest). Although pairs of alligator holes are embedded inside each slough/wetland, alligator holes were treated as independent replicates within each wetland because they were separated by ~ 200 m and were highly variable in area, water depth and vegetative structure.

As an additional analysis of the fence treatment effect on fish in the alligator holes, the size structure of fish ≥ 2 cm SL was compared between sloughs under fenced and control conditions with non-parametric Kolmogorov-Smirnov tests. The fish sizes (irrespective of species) from each pair of alligator holes in each slough were combined

(n=4) to provide larger numbers for the statistical analysis of size frequency. The size structure for each wetland in each year was compared directly using each wetland as its own control (four tests). For graphical examination, fish were binned by 0.2 cm increments from 2.0 cm up to > 5.4 cm fish. The specific maximum-length cutoff was chosen because few fish were caught in minnow traps above 5.4 cm.

Wading Bird Density in Sloughs

Piscivorous (Little Blue Herons, Snowy Egrets, Roseate Spoonbills, Tricolored Herons, Great Egrets, and Great Blue Herons) and total (all piscivorous birds plus White Ibis and Glossy Ibis) wading bird activity was evaluated and tested as a density index. The treatment effect on wading birds was determined with paired t-tests for three of the four wetlands (n = 3 per treatment; each wetland serves as its own control). Only M1, M2 and M4 were used, as wading bird data from M3 was unavailable in 2018. The index was standardized by annual mean density to account for differences in overall wading bird activity between years. Wetland indices were calculated as the average annual density per wetland divided by the sum of average annual densities from all wetlands; the index was a relative density in each wetland in each year (control and treatment for each wetland). The indices were then compared with paired t-tests (treatment vs. control).

RESULTS

Hydropattern and Hydrographs

The 2017 and 2018 hydrographs for the mean depths across wetlands can be seen in Fig. 3. The water levels receded in each wetland with an average recession rate of 0.55 - 0.56 cm · day⁻¹ in 2017 (mean from 2 February – 27 April) and 0.51 – 0.52 cm · day⁻¹

in 2018 (mean from 2 February to 20 April 2018). In 2017, water levels reached an average of 2 – 8 cm across the sloughs by 28 April. In 2018, water levels reached an average of 5- 11 cm on 21 April, but increased to 22-29 cm by 27 April because of a pump failure. Thus, the average recession rate was calculated from 2 February - 20 April. Water levels were more variable in 2018 because of several water pump malfunctions that allowed water levels to temporarily rise.

Prey Emigration from Sloughs

A total of 1,707 fish were captured and counted in the fyke nets set at the end of the sloughs in 2017 and 2018 combined. Fish counted in the fyke nets ranged in size from 20 to 890 mm SL. The majority of fish caught were eastern mosquitofish, bluefin killifish, golden topminnows, and dollar sunfish. Catch rates of fish > 2 cm SL did not show a consistent fence treatment effect (Fig. 4a). Catch rates of all sunfish were lower in wetlands under fenced conditions than control conditions ($F_{3,4} = 7.80$, $p = 0.046$; Fig. 4b).

Prey Density in the Sloughs

Fish captured in the throw traps ranged in size from 3 to 111 mm SL, with 0 to 64 fish per m² trap over the two years of data collection. Initial mean fish (> 2 cm SL) biomasses and densities did not significantly differ between wetlands within the year 2017 or 2018 (biomass: p -values > 0.22 for both years; density: $p \geq 0.08$ for both years). Initial mean fish biomasses and densities also did not qualitatively differ between years within the wetland (biomass p -values > 0.51 for all wetlands; density: p -values > 0.12 for all wetlands).

Fish biomass did not differ between the fenced and control conditions after the ridges dried ($F_{1,3} = 5.05$, $p = 0.11$; Fig. 5a). The concentration effect sizes (proportional biomass change from the first to second sampling session) did not differ between fenced

and control sloughs ($F_{1,3} = 1.13$, $p = 0.37$; Fig. 5b). Fish > 3 cm SL biomass and density had similar trends visually, but the data was not statistically analyzed.

Prey Abundance in Alligator Holes

Abundances of fish in alligator holes varied through time and between holes (see interaction plot in Appendix A; Fig. A3). On the final date, when the sloughs were shallowest, there was no fence treatment effect on the trap catch numbers or biomass of all fish > 2 cm ($F_{1,7} = 1.99$, $p = 0.20$). Larger fish (> 3 cm SL) catch rates suggested a possible difference between treatments ($F_{1,7} = 4.0$, $p = 0.09$), and when converted to biomass, the alligator holes in wetlands under fenced conditions had significantly greater fish > 3 cm SL biomass ($F_{1,7} = 7.36$, $p = 0.03$; Fig. 6). Population size structure differed for all wetlands ($D > 0.36$, p -values < 0.05) between fence and control conditions except in M2 ($D = 0.086$, $p = 0.84$). In all three cases of significant size structure differences, the wetlands had higher frequencies of larger fishes (>3 cm SL) when they were fenced (Fig. 7). The fenced conditions seemed to produce alligator hole assemblages with more flagfish (2017) or sunfishes (2018) in the respective years (Appendix A; cumulative catches in Table A1).

Wading Bird Density in the Sloughs

Most of the identifiable wading birds in the sloughs in both years were Glossy Ibis. White Ibis, Little Blue Herons and Snowy Egrets were fairly common, Great Egrets followed with relatively moderate densities, and Great Blue Heron, Great Egret, and Roseate Spoonbill densities were consistently low. The wading bird densities did not display a gradual rise and fall of activity as the water dried down in either year. Rather, in all of the wetlands, foraging birds exhibited an oscillating pattern of peaks and valleys of activity over 30 or more days, starting in early to mid-March (Fig. 8). Total wading bird

densities for each wetland were variable through time and depths in both years. Generally, there were higher densities of wading birds in 2017 than in 2018 (Fig. 8a vs. 8b). M4 did not contain high numbers of any wading bird species in either year (Fig. 8). Some peaks in wading bird density in one wetland followed the peak in an adjacent wetland by a day or two, perhaps suggesting that a similar flock of wading birds moved between the LILA wetlands from day to day. In 2018, data were only available for three of the four wetlands (Fig. 8b). M2 had a peak in activity in late April of 2018 (Fig. 8b) that was absent in 2017.

Fences had no effect on total wading bird density (Paired t-test on density indices; $t = -1.70$, $p = 0.23$; Fig. 9a) or piscivore density indices ($t = 0.15$, $p = 0.89$; Fig. 9b). M1 had the highest average total daily wading bird densities and highest Glossy Ibis densities under both fenced and control conditions (Tables 1 and 2). Total and Glossy Ibis densities in the remaining wetlands declined north to south in both years. M1 and M2 contained similar densities of piscivorous wading birds and White Ibis (Tables 1 and 2), and both had more than M3 and M4. The one exception is for White Ibis densities in 2018, where M4 had a slightly higher density than M2 when averaging for date (Table 2b). Overall bird densities from 2018 were much lower than 2017 (Table 1 and 2), regardless of whether observation periods were standardized by equivalent dates (36 days from 15 March -19 April) or depths (33 cm down to 11 cm).

DISCUSSION

Results from this experiment indicated that the fence treatment may have successfully blocked larger prey fish (sunfish and fish > 3 cm SL) from emigrating to deep water refugia, but not necessarily all fish > 2 cm SL. Results from fyke net sampling

indicated the seine fencing was successful in inhibiting sunfish movement, but not all fish > 2 cm SL movement. Biomasses and densities of fish > 2 cm SL in the sloughs seemed to increase over the first two sampling sessions (while ridges dried) (e.g., M1 and M4; Fig. A4), but biomass and concentration effect sizes for fish > 2 cm SL did not show a significant effect of the fence treatment during the second sampling session. There were mixed results pertaining to fish CPUE in alligator holes on the last sampling date, with only fish > 3 cm SL biomass responding to fence treatment, and there was no evidence for a fence treatment effect on wading bird activity; despite dramatic oscillations in activity over 30+ days. Explanations for each of these results will be explored further.

There could have been a lack of concentration in the sloughs if the experimental setup failed to fence in all the fish. An inability to fence in the fish could have been due to a failure of the fence itself, or an unexpected amount of fish movement up and over the ridges (to the north or south; Fig. 1) prior to the ridge drying. The fence failure is a poor general explanation for the following reasons: the fences were checked two to three times per week by feeling along the bottom of the seines to make sure it was flush with the ground, and the rest of the net was also inspected for holes. The seine fences across the sloughs appeared undamaged in almost all cases, except perhaps in M1 in 2018, when several small holes were found in that seine along the area within the slough. Fewer than 10 small holes total were found and patched in the seines over both years. Most of the holes were in the ridge portion of the seines and seemed to appear after the ridges were dry or nearly dry, most likely due to rodents. I have no direct information about fish movement out of the sloughs over the ridges to the north and south, but I did conduct a small minnow trapping effort in 2018 along the corners where the seine and the drift fences were connected (n=8 corners). I found that in six out of eight corners, the CPUE of

fish inside the fence corners was lower than the CPUE around the outside of the corners, suggesting that captured fish were not following the fencing up onto ridges in an attempt to exit the fenced area (i.e., piling up in the corners on the ridges).

One ecological explanation for a lack of fence treatment effect on fish density relates to a fundamental premise of my hypothesis; fish 2-5 cm SL will move into the deepest available habitats when wetland water depths are receding. In fact, it is possible that such fish may not extensively move into deep canal-like habitats when ridges dry or when the sloughs have only 5-10 cm of water. I found no effect of fencing on the biomass of fish in the sloughs during the second sampling session, when the ridges were dry. One explanation is that the fish community was not substantially moving into deep water habitats when the sloughs were still 30 cm deep. I did find greater catches of sunfishes in the fyke nets that were set at the end of the sloughs between the first two time periods, but the results did not clearly hold for all larger fish. With even lower depths in April, I only observed a modest increase in the biomass of the largest fishes (> 3 cm SL), suggesting that some of the 2-5 cm fish may not have used the deep water collection ponds, instead using smaller alligator hole habitats even when adjacent deep habitats were available (i.e., control conditions). I have little other information to assess this explanation, but it seems a viable explanation, contrary to the basic premise of the study.

Another ecological explanation is that the experiment did not fence a large enough area to produce large concentrations of fish across the whole slough. It may be that high fish densities are only discerned by concentrating at a much larger spatial scale (e.g., a 10- or 20-fold decrease in area) during the dry down (Trexler et al. 2002). The fencing in this experiment concentrated fish from ridge to slough with perhaps only

halving the flooded wetland area. It may also be that our focus on the mean density combined with random trap locations did not necessarily capture the heterogeneity in the sloughs, and the fish may have been aggregating in a few deeper points within the sloughs by the second sampling session. I cannot assess this explanation directly, but I did examine the highest density throw in each wetland during the second sampling session and found little support for this explanation; the highest density throw traps during the second sampling session did not appear to be consistently higher when the sloughs were fenced (data not shown).

I found mixed results comparing differences in CPUE of prey fish (> 2 cm SL) in alligator holes on the last sampling date. The only clear indication of a fencing effect was shown when considering the biomass of the largest size class (> 3 cm SL) of fish in the alligator holes (Fig. 6b). The fencing effect on larger fish (> 3 cm SL) biomass in the alligator holes was consistent with fyke net results, which showed that sunfish (generally larger prey fish > 2.5 cm SL) were prevented from moving out of the sloughs by the fencing. However, these results seem initially inconsistent with the lack of a fencing treatment effect on fish throughout the sloughs on the second sampling session. It is likely that largest prey fish may be sparse enough in the sloughs ($< 1/\text{m}^2$) to make density detection in sloughs unlikely, but when they concentrate in the smaller alligator holes later in the season, the density differences may be detectable. When a smaller cutoff size was used to compare fence treatment in alligator holes, the same pattern did not emerge. The catch rates of fish > 3 cm were not affected by the fence either, though results were close to significant ($P = 0.09$). It is also worth noting that the fence treatment effect on fish biomass accumulating in the alligator holes was strong and consistent in the holes in M3 and M4 and rather weaker in M1 and M2 (Fig. 6b).

The emerging pattern from graphical analysis of fish size structure in alligator holes indicated that there was a switch from a majority of fish < 2.5 cm SL under control conditions to a majority > 2.5 cm SL under fenced conditions (Fig. 7). Analysis showed a significant difference in size structure between fenced and control conditions for all wetlands except in M2. M2 also had low overall biomass within the alligator holes for larger fish (> 3 cm SL). A smaller overall size structure may explain the lack of a shift in size structure under fenced conditions in M2.

The lack of a fence treatment effect on small fish (> 2 cm SL) may be due to differing fish body depths or lengths. Some fish species with shallower bodies (i.e. bluefin killifish) that are 2 cm SL may have escaped through the seine holes. Though the seine mesh size was chosen based off of the average depth of 2 cm SL bluefin killifish, it may be that mainly larger fish (> 3 cm SL) congregated in the deeper alligator holes and excluded smaller-sized fish that can be sustained in the shallower sloughs for longer. Smaller fish (> 3 cm SL) may not have been moving into deep water refugia as quickly as larger fish (> 3 cm SL), or at all. Differences in immigration patterns for small fishes based on size (depth or length) in the Everglades are relatively unstudied, but literature generally supports that there are species-specific differences in when fish move into deeper water and how quickly. This is based on a number of factors including the distance of the refugia to the animal, the preceding hydroperiod, water depth, and the rate at which water recedes (Hoch et al. 2015, DeAngeles et al. 2013, Kobza et al. 2004, Trexler et al. 2002). A recent study found that dollar sunfish (*Lepomis marginatus*), a deeper-bodied fish species, was the only species sampled to show rapid and directional movement to deep water refugia as water levels declined (Hoch et al. 2015). This is also consistent with fyke net data, that showed sunfish were particularly blocked by the

fencing when all fish > 2 cm SL were not. Although there are other species-specific factors that influence movement patterns of fish, our size structure comparisons and the fence treatment effect on fish > 3 cm SL biomass in alligator holes suggest it is possible that the size of the fish influences movement to deep water refugia during the dry season.

It may be that there were additional piscivorous predators present in the sloughs that predated the smaller size class of prey fish. (2-3 cm SL) to the point where I could not determine a fencing effect. The larger sunfish (> 4 cm SL) can potentially consume the smaller fish. However, I did not find large numbers of the larger predatory fish in minnow traps, throw traps, or fyke nets, with 1-2 larger fish caught per year. In addition, there are some piscivorous snake species and piscivorous amphibians within the sloughs. Although they were caught during trapping, I did not collect more than 10 – 15 of these individuals per year. It is unlikely that these additional predators would substantially decrease small fish (2 -3 cm SL) biomass, especially in comparison with large groups of foraging wading birds.

In addition to the fish predictions, I predicted that the average daily piscivorous wading bird density would be significantly higher in sloughs under fenced (treatment) conditions, if the fence treatment limited fish movement and increased fish abundances in sloughs. Statistical analyses and graphical interpretation did not reveal any pattern of increased piscivore densities under fenced treatment conditions. Piscivorous wading bird densities were relatively low in all wetlands compared with Glossy Ibis densities alone, especially in 2018. The lower overall activity in 2018 may be a function of regional nesting patterns across the greater Everglades ecosystem, because nesting was highly successful much further south of LILA with little nesting near our impounded wetlands.

Glossy Ibis (insectivores) primarily drove wading bird densities in both years, with a consistent gradient in mean density from M1 to M4 (north to south), which could not be explained by invertebrate prey densities nor vegetation densities. Data summaries and analyses can be found in Appendix B. In both years, Glossy Ibis, occasionally accompanied by other species (mainly Little Blue Herons), seemed to sweep through a slough several times with intervening days of no activity, until near the end of the observation period. The oscillations may indicate that the sloughs became relatively good for foraging several times in a single dry down as prey concentrated across micro-topographic gradients; starting with the ridge-slough interface and then moving to gradients within the sloughs.

Results from this study suggest that large canals might be an attractive refuge for relatively large prey fishes (> 3 cm SL) in sloughs, but there is little evidence to support that all prey fish were affected by the fencing treatment. The wading birds did not respond to the fence treatments, but the underlying N-S gradient in wading bird responses and the lower foraging and nesting activity around Loxahatchee National Wildlife Refuge (adjacent to LILA) in 2018 made it difficult to make strong conclusions on wading bird foraging patterns.

On average, the world's wetlands have declined by 64-71% since the 20th century (Davidson 2014), partly due to the construction of levees and canals to manipulate hydrology (Turner 1997, Day et al. 2000, Sokol et al. 2014). It was thought that deep canals connected to sloughs may further limit the formation of prey concentrations by carving channels of deep water into flat, shallow areas (Harvey et al. 2010). Although some results from this study are unclear, there is some evidence that deep canals running through the sloughs of the Everglades can affect prey availability for wading birds. It is

still important to consider the costs of introducing canals into the Everglades wetlands. The microtopography of the Everglades is imperative to the health and functionality of the ecosystem (Trexler et al. 2002, Botson et al. 2016), and manipulations to this landscape have drastically decreased nesting wading bird populations in the past (Crozier and Gawlik 2003). Future management decisions should therefore take precaution when employing additional landscape manipulations to the Everglades.

Table 2.1. Mean (\pm SE) daily wading bird densities ($\# \cdot \text{ha}^{-1}$) from 6:00 am to 2:00 pm for days with slough water depths between 11 and 33 cm water depth in the sloughs. The number of days varied somewhat between wetlands. M2 and M3 (bold) were fenced in a) 2017, and M1 and M4 (bold) were fenced in b) 2018. In 2018, there was no data available for M3 because of a camera failure. The number of days of water depths within the range is listed below the wetlands. Piscivores included Little Blue Herons, Snowy Egrets, Roseate Spoonbills, Tricolored Herons, Great Egrets, and Great Blue Herons.

2017

	M1	M2	M3	M4
# days examined	35	36	41	36
Total Density	18.24 (± 3.87)	15.09 (± 5.40)	9.60 (± 2.28)	2.40 (± 0.49)
Piscivores	2.03 (± 0.42)	2.28 (± 0.97)	1.66 (± 0.27)	0.84 (± 0.13)
White Ibis	1.38 (± 0.75)	1.40 (± 0.67)	0.71 (± 0.47)	0.09 (± 0.06)
Glossy Ibis	13.74 (± 3.11)	11.11 (± 4.05)	6.57 (± 1.95)	0.80 (± 0.41)

2018

	M1	M2	M3	M4
# days examined	38	40		40
Total Density	5.66 (± 1.32)	4.03 (± 0.84)	NA	2.24 (± 1.00)
Piscivores	1.87 (± 0.41)	0.80 (± 0.15)	NA	0.31 (± 0.03)
White Ibis	0.25 (± 0.07)	0.03 (± 0.02)	NA	0.03 (± 0.02)
Glossy Ibis	3.45 (± 1.20)	3.05 (± 0.73)	NA	0.192 (± 0.98)

Table 2.2. Mean (\pm SE) daily wading bird densities ($\# \cdot \text{ha}^{-1}$) from 6:00 am to 2:00 pm for 36 days while sloughs were drying (March 15 through April 19) at LILA. M2 and M3 (bold) were fenced in a) 2017 and M1 and M4 were fenced in b) 2018. In 2018, there was no data available for M3. Average daily depth during the observation period is listed below the wetlands. Piscivores included Little Blue Herons, Snowy Egrets, Roseate Spoonbills, Tricolored Herons, Great Egrets, and Great Blue Herons.

2017				
	M1	M2	M3	M4
Avg. water depth (cm)	22.00	20.50	25.60	18.40
Total Density	17.88 (± 3.78)	15.24 (± 5.39)	10.47 (± 2.56)	2.26 (± 0.49)
Piscivores	1.97 (± 0.41)	2.24 (± 0.97)	1.65 (± 0.28)	0.76 (± 0.13)
White Ibis	1.34 (± 0.73)	1.37 (± 0.67)	0.79 (± 0.54)	0.027 (± 0.02)
Glossy Ibis	13.50 (± 3.04)	11.36 (± 4.05)	7.38 (± 2.19)	0.82 (± 0.41)
2018				
	M1	M2	M3	M4
Avg. water depth (cm)	22.2	23.10		17.56
Total Density	5.89 (± 1.39)	3.66 (± 0.77)	NA	2.45 (± 1.10)
Piscivores	1.94 (± 0.43)	0.80 (± 0.16)	NA	0.16 (± 0.03)
White Ibis	0.26 (± 0.08)	0.01 (± 0.01)	NA	0.04 (± 0.02)
Glossy Ibis	3.60 (± 1.22)	2.73 (± 0.66)	NA	2.13 (± 1.09)

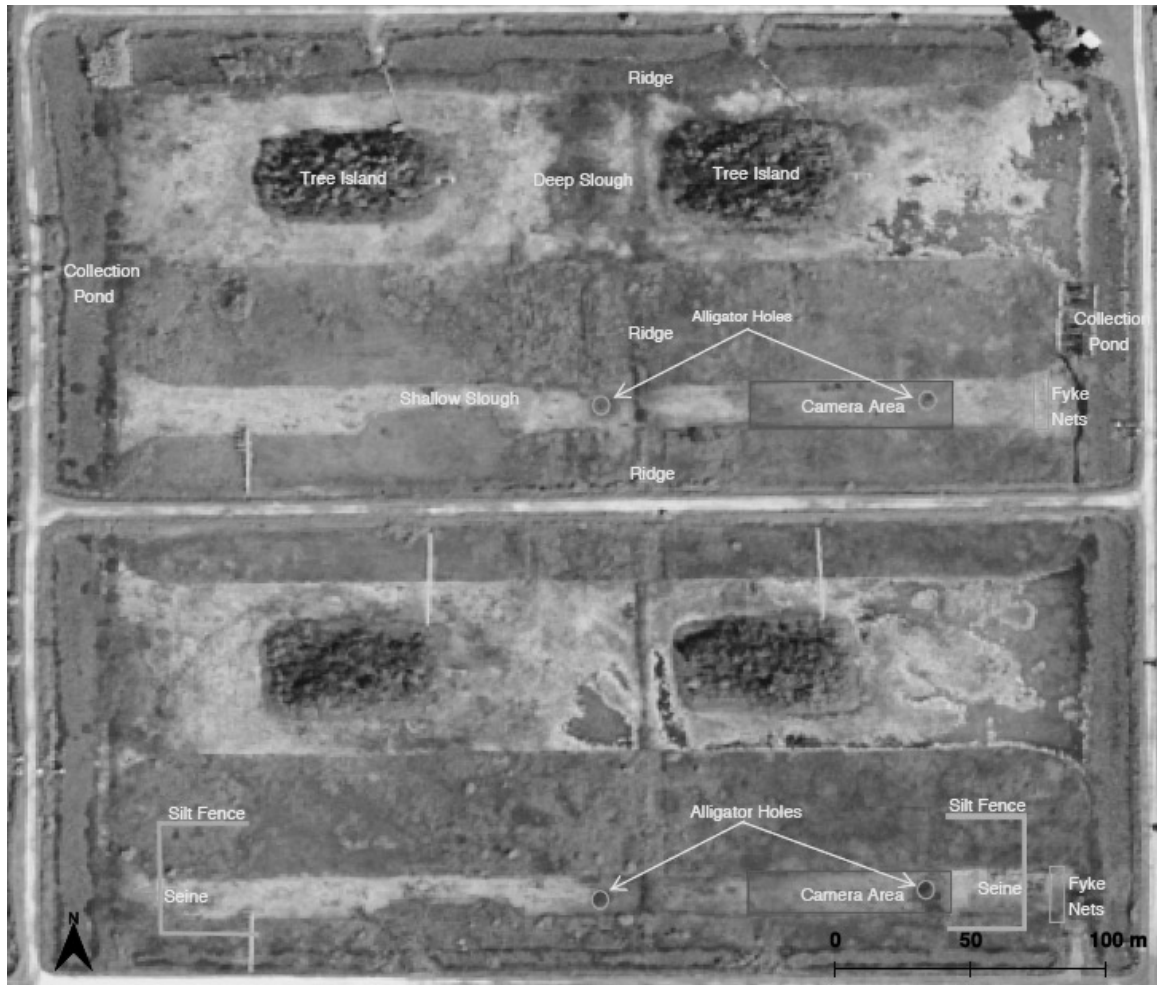


Figure 2.1. Aerial image of two of the 8 ha wetlands at the Loxahatchee Impoundment Landscape Assessment. Each replicated wetland contained tree islands, ridges and deep and shallow sloughs. Deep collection ponds bordered the east and west ends. The placement of the seines and silt fences in a fenced wetland (in the southern wetland) and the approximate camera viewing area (in both wetlands) are also pictured here. The shallow sloughs were 20 - 26 cm deeper than the ridge habitat. The collection ponds to the east and west of the shallow sloughs were greater than 1 m deeper than the sloughs.

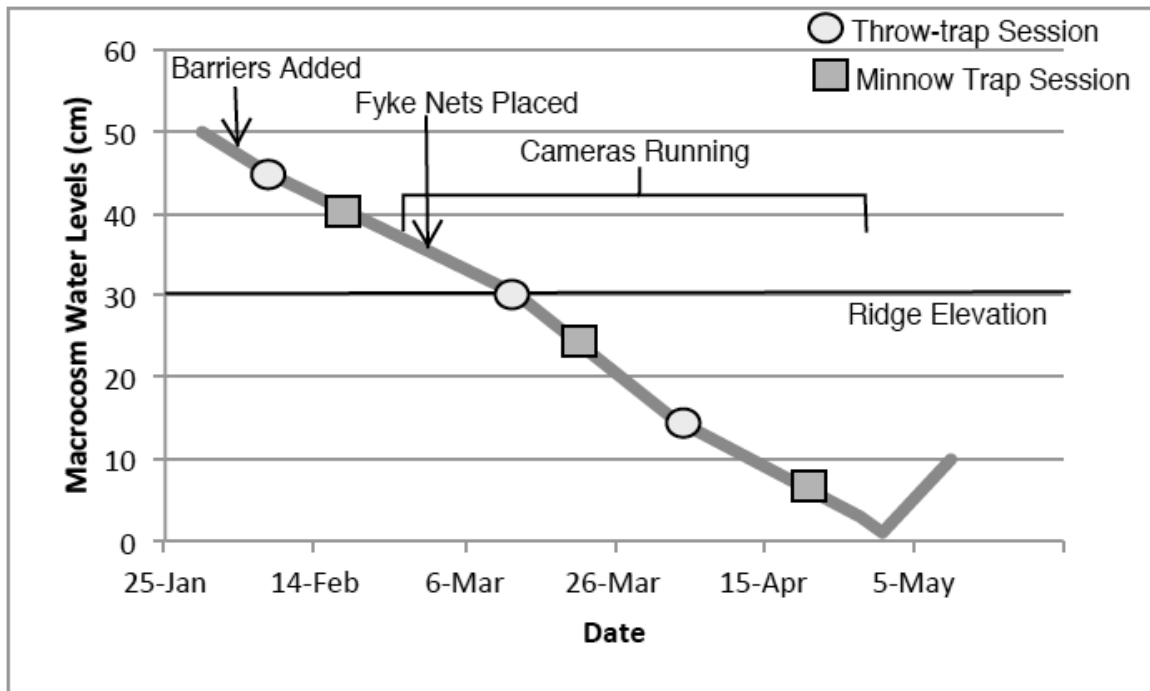


Figure 2.2. Hydrograph and timeline for the study of wading bird activity and prey stranding/escape at the Loxahatchee Impoundment Landscape Assessment. Images of wading birds in the slough were taken from late February through late April. Throw trap samples of prey were taken around at 48 – 50 cm depths (February.), 30 - 35 cm depths (March), and 18-23 cm depths (April). Fyke net samples were taken just prior to the drying of the ridge habitat to attempt to document fish movement into the deep water. Minnow traps were set in the alligator holes three times during the dry down.

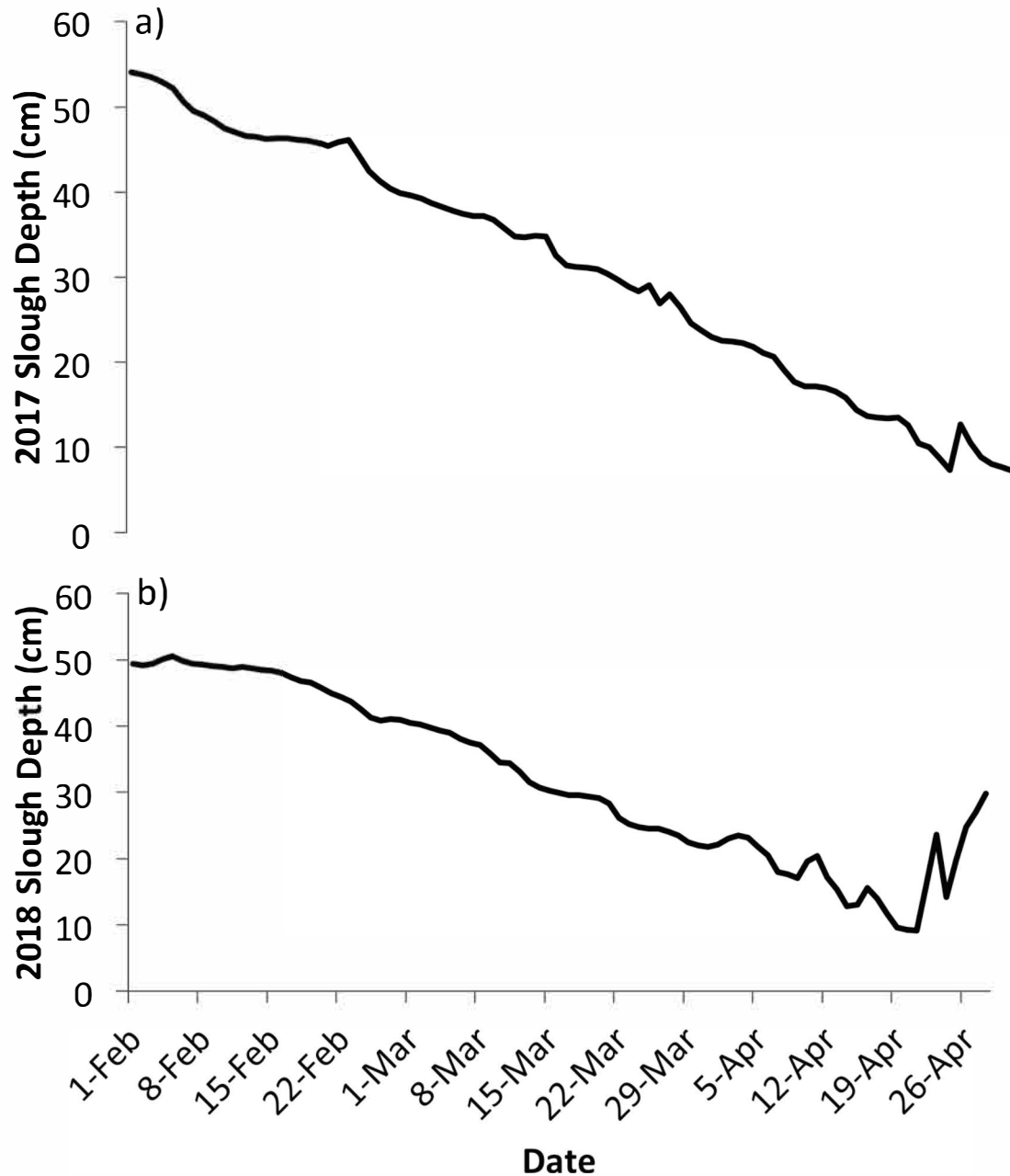


Figure 2.3. Hydrograph of the mean slough depth from all four wetlands from a) 2017 (2 February – 28 April) and b) 2018 field season (2 February – 27 April). The average difference between the deepest (M3) and shallowest (M4) wetland slough depths was between 6.63-6.71 cm day⁻¹ in both years. In April 2018, heavy rainfall and pump failures made water recession and depth control difficult.

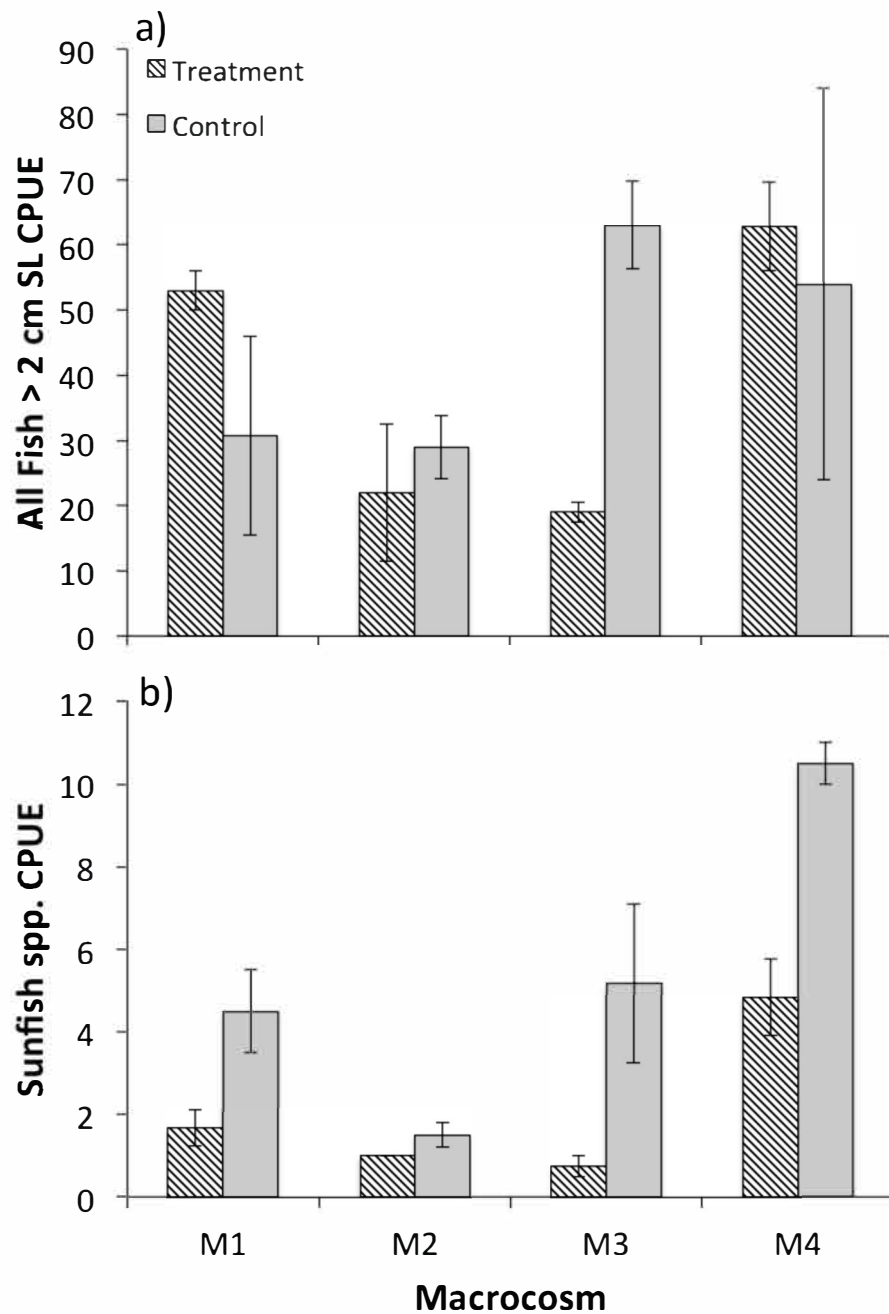


Figure 2.4. Mean CPUE (catch per night) of a) all fish species and b) mean sunfish CPUE of all sunfish species (5b). The error bars represent ± 1 standard error from $n = 2$ nights in 2017 and $n=3$ nights in 2018.

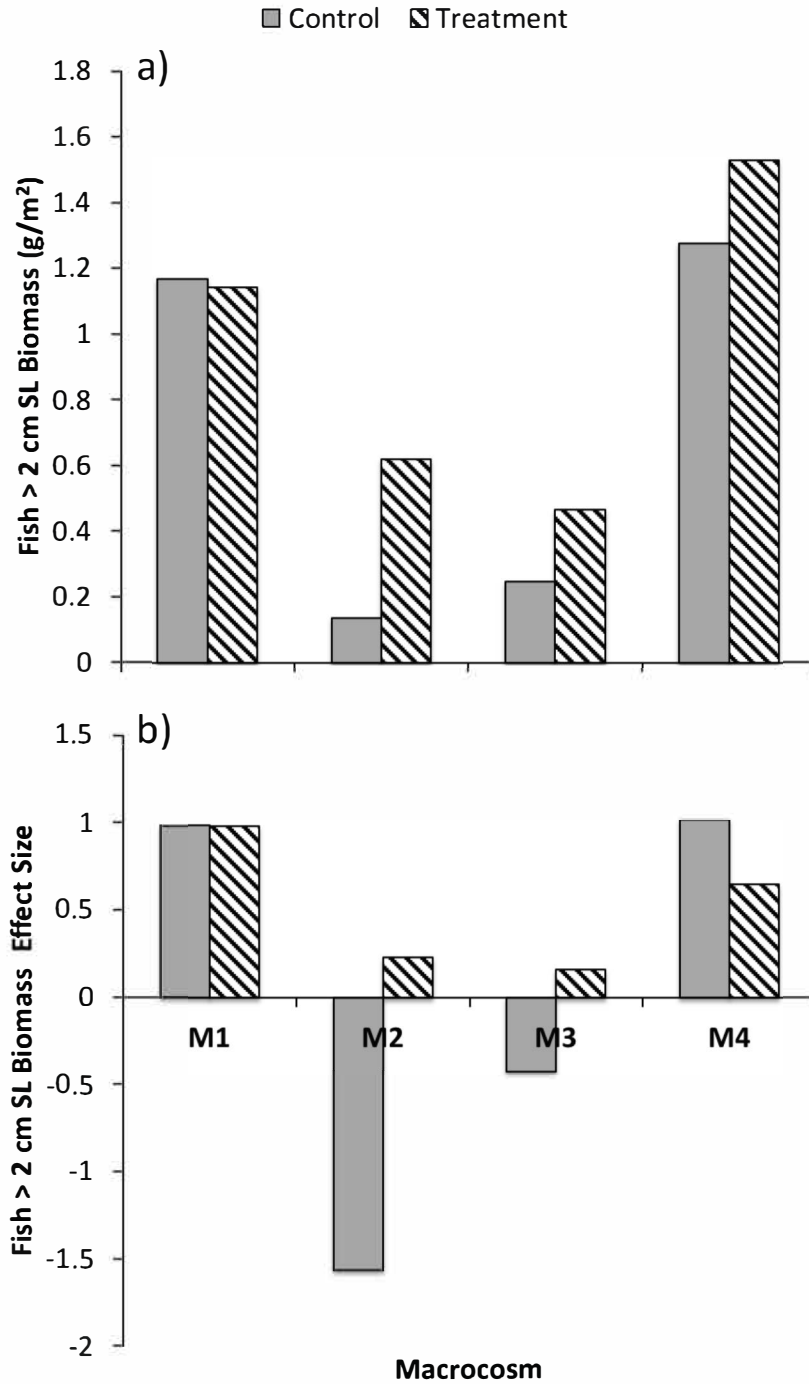


Figure 2.5. Mean fish > 2 cm SL a) biomass density ($\text{g dry mass} \cdot \text{m}^{-2}$; $n = 7$ randomly placed throw traps each session) and b) biomass effect size between the first and second sampling session from the second sampling session in fenced (black stripes) and control (solid gray) sloughs in 2017 and 2018.

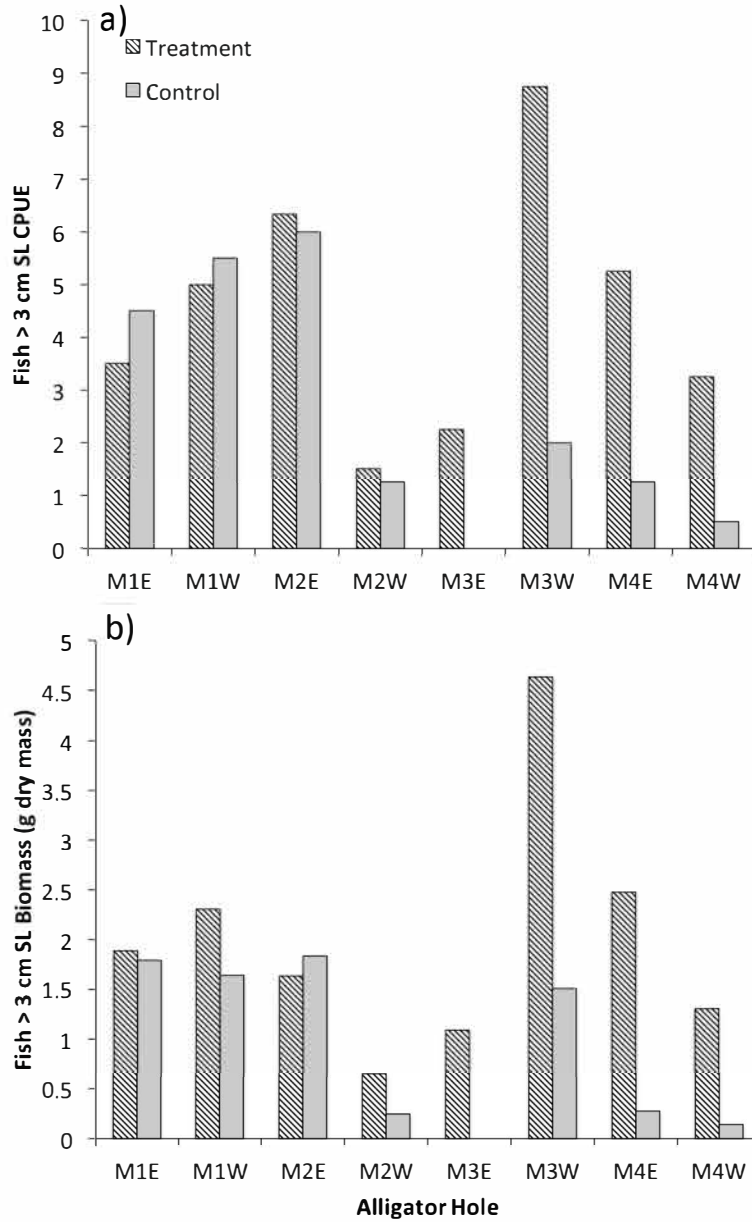


Figure 2.6. Mean fish > 3 cm SL a) CPUE and b) biomass (g dry mass · trap night⁻¹) from minnow traps (n=4 per night) in each alligator hole during the final sampling session in 2017 and 2018 when water levels were 5-11 cm in the adjacent slough. Slough means under fenced conditions are black striped and sloughs under control conditions are solid gray. Alligator holes are labeled separately by the eastern (e.g., M1E) and western (e.g., M1W) holes within each wetland.

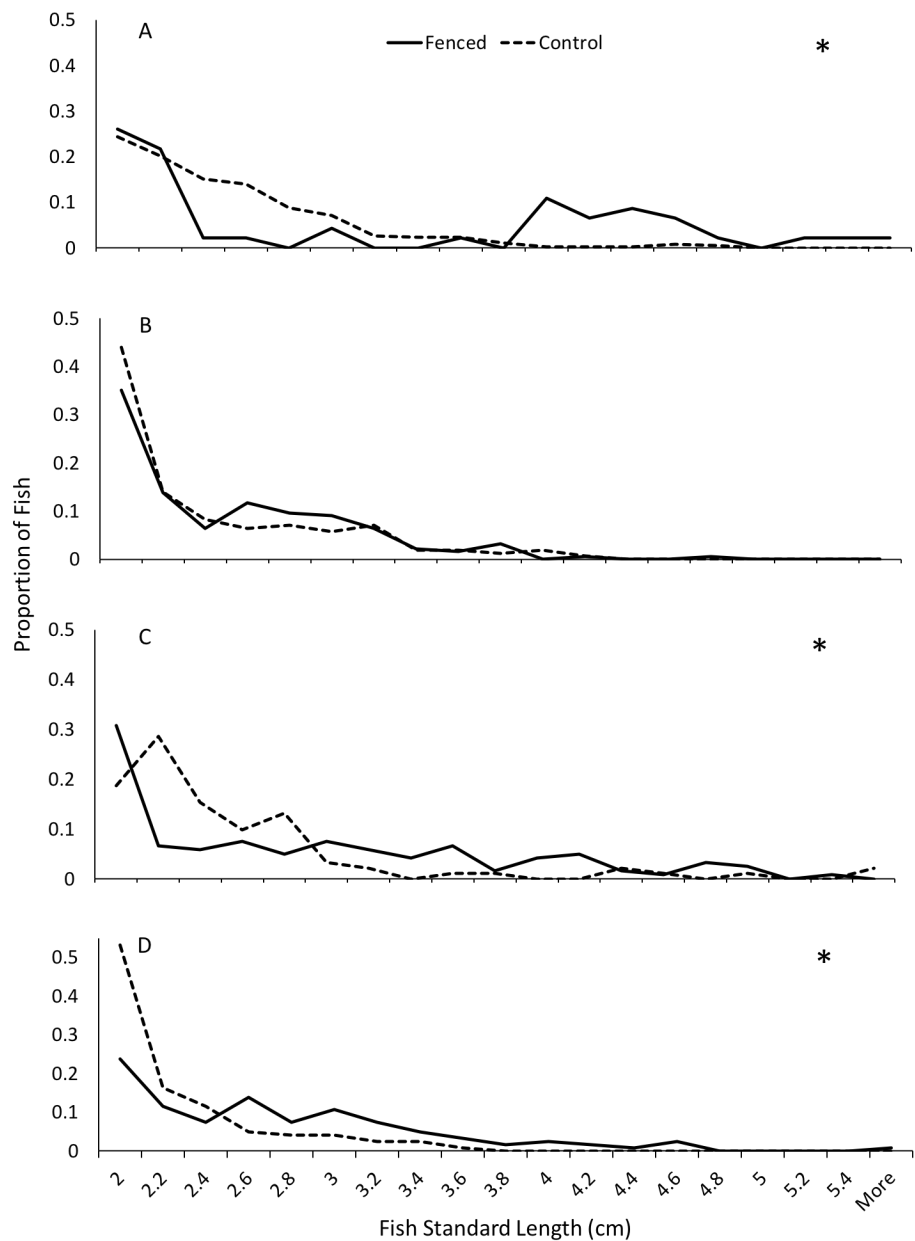


Figure 2.7. Size frequency distributions (proportion of all captured fish in minnow traps) in the sloughs of a) M1, b) M2, c) M3, and d) M4 from the third minnow trap sampling session. The 0.2 cm size increments are centered on the values listed along the Y-axis. Population size structure differed for all wetlands except M2. Asterisks indicate $p < 0.05$ from Kolmogorov-Smirnov tests.

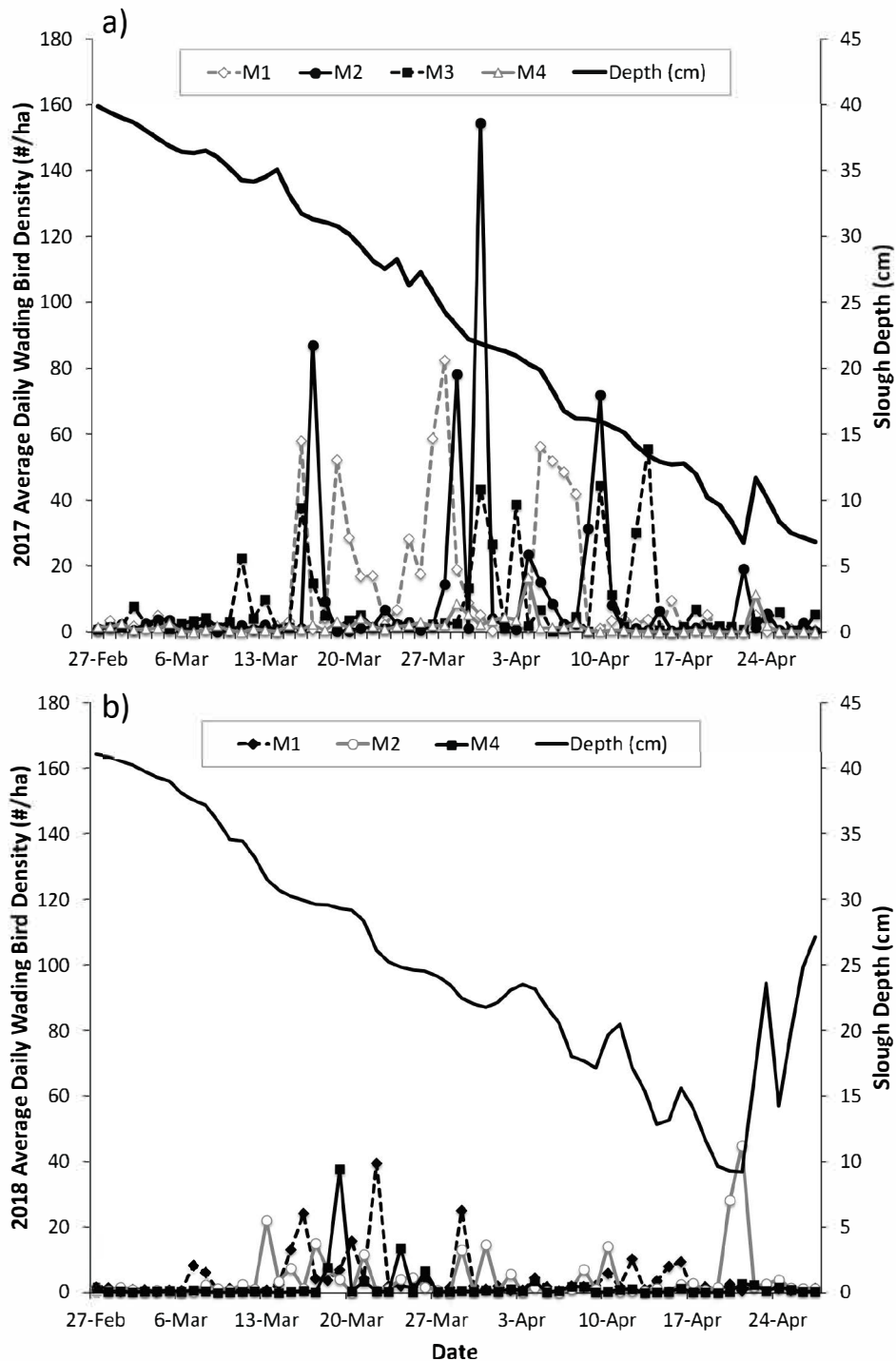


Figure 2.8. Average daily total wading bird density in shallow sloughs at the Loxahatchee Impoundment Landscape Assessment over the 60 to 61-day period of observation of four wetlands in a) 2017, and three wetlands in b) 2018. Mean water depth in sloughs is plotted on the secondary y-axis. The ridges dried around March 15th in most wetlands.

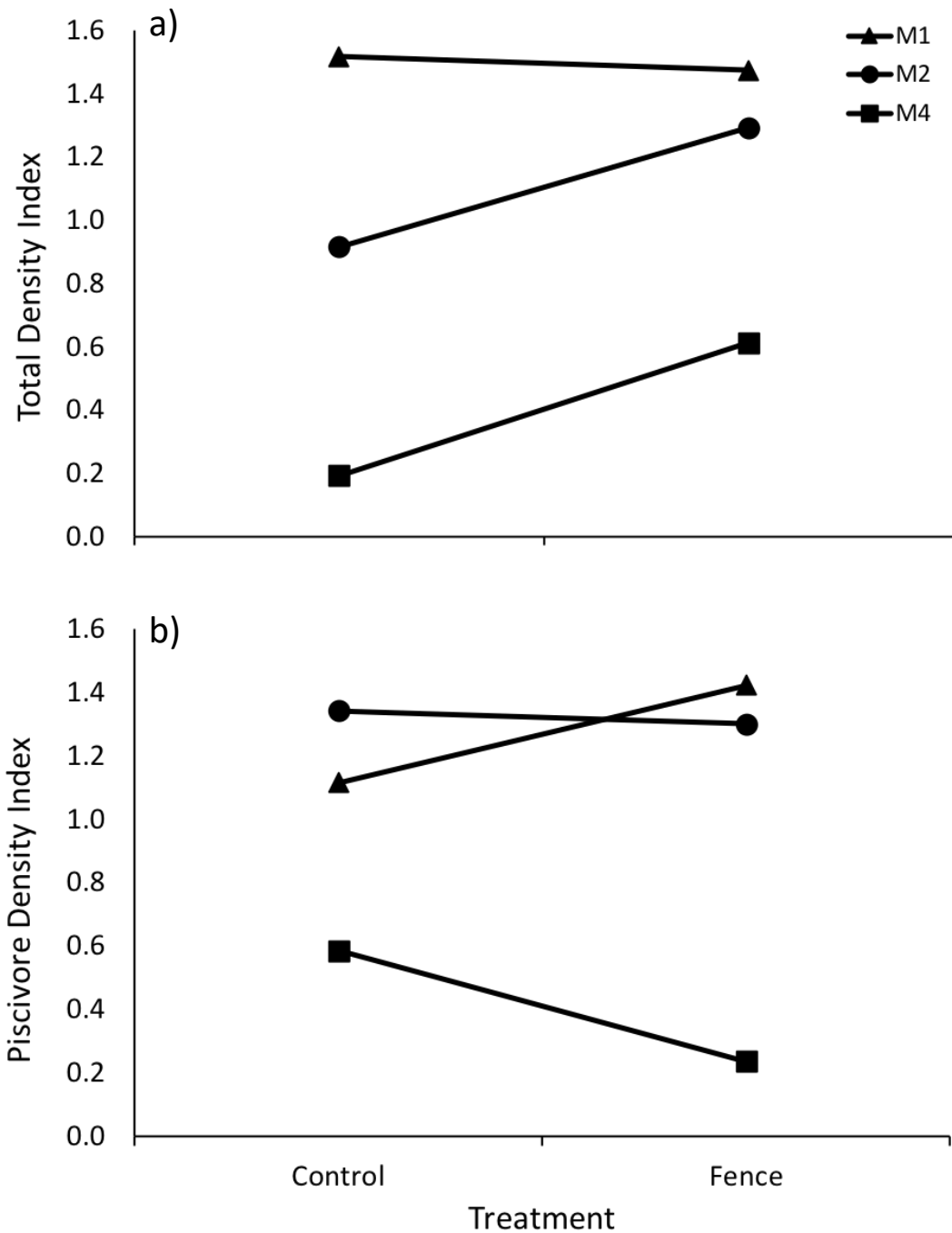


Figure 2.9. Density indices for a) total wading bird relative densities and b) piscivore relative densities for three wetland macrocosms. The index includes the average annual density per wetland divided by the total average annual density from all wetlands.

APPENDIX A

Crayfish Densities in Sloughs Through Time

As an additional analysis of non-fish wading bird prey, mean crayfish biomass densities (g dry mass/m²) were determined using throw trap sample data by calculating the mean biomass of the replicate trap samples for each macrocosm in each sampling session and graphed through time. In 2017, crayfish biomass differed through time, peaking in the March sampling session in all four macrocosms when we would expect to see prey movement down gradient from the ridges to the sloughs. Macrocosm 3 had the lowest mean densities of crayfish and weakest dynamic response (Fig. 1a). In 2018, there were lower biomass densities across all macrocosms through time compared to 2017, and the data did not show the same clear concentration pattern, with M2 and M4 consistently decreasing in biomass through time (Fig. 1b). Macrocosm 3 had the highest mean density of crayfish and strongest dynamic response.

Prey Fish Densities in the Sloughs Through Time

As an additional analysis of fish prey, we graphed fish > 2 cm SL densities for 2017 and 2018 over all three sampling sessions using throw trap sample data. In 2017, there was a visible increase in fish density in M1, M2 and M4 from February (when depths are well above the ridge height) to March, when the ridges were shallow and fish started moving into the sloughs. Densities in M3 decreased from February to March, and the concentration effect in M4 was weak (Figure 2a). Graphical examination of the final

date densities suggested that average fish densities might have been somewhat higher in the sloughs under fenced conditions, suggesting there might be a significant effect of treatment on the last session of throw trapping. However, there was no effect of treatment on density ($F_{1,2}=3.02$, $p=0.23$) in the sloughs.

In 2018 over the course of the dry season, the control macrocosms (M2 and M3) did not show a concentration effect over the second sampling session when we would expect to see a peak in fish densities in the sloughs as they move off the ridges. Graphical examination of the final date densities suggests that average fish densities did not show the same pattern from 2017 (fenced slough densities were not uniformly higher) (Fig. 2b). Thus, no statistical analyses were run for the final date in 2018. The lack of concentration in the control macrocosms may be due to the absence of the seine fencing to hold fish in the slough. No statistical analyses were run for 2018 fish densities through time.

Fish Communities in Alligator holes

To analyze fish abundance patterns through time in alligator holes, we graphically compared catch rates (fish per trap night) in each hole ($n=8$, 2 holes per macrocosm) through time to determine whether catch rates varied in alligator holes as the water level declined in the shallow sloughs. Holes within the same slough were graphed individually because of high variation in depth and vegetation cover between holes. In both years, abundances of fish in some alligator holes varied over the study (see interaction plot in Fig. 3). In 2017, there was a general increase in large fish abundance in most holes as the water levels declined in the slough and pushed fish into the deeper alligator holes. In 2018, M3 showed a different pattern of concentration, with highest abundances in both

holes occurring during the second sampling session in March when there is still water in the sloughs.

Assemblage composition of fish > 2 cm SL on the final sampling date in 2017 and 2018 was compared in order to determine if there were species more likely to use alligator holes in fenced macrocosms. Fish species composition in alligator holes were summed to create a percent composition for each macrocosm, which was then averaged to determine the mean percent composition for fenced and control macrocosms. The final sampling session provided the most significant catch and composition data because prey concentrations were highest at that time (i.e., when water levels in the slough were lowest). The fish composition in the sloughs was also calculated for the second sampling session as a comparison to the alligator hole compositions. The second sampling session was chosen because fish numbers were high enough to compare and represented fish densities after concentrating from the ridges and before concentrating in the alligator holes.

The composition of fishes refuging in the holes in both 2017 and 2018 seemed to differ between treatment and control macrocosms when aggregated across holes (Table 1). Generally, there was greater species diversity in the holes under fenced treatment conditions. In particular, sailfin mollies, bluespotted sunfish and flagfish made up larger fractions of the refuging assemblages in the alligator holes in the fenced macrocosms in both years (Table 1). Eastern mosquitofish dominated (80% in 2017, 58% in 2018) the assemblage in alligator holes under control conditions, but holes under fenced conditions contained only 16-35% mosquitofish. Sailfin mollies constituted 4-12% of the catch in holes under control conditions, but 22-38% of the catch in holes under fenced conditions. Flagfish were 20% of the catch in the holes under fenced conditions and 0% in holes

under control conditions in 2017 only, and bluespotted sunfish constituted 38% of composition in the holes under fenced conditions and 6% in holes under control conditions in 2018 only. Golden topminnows were present and constituted 4% of catch in fenced macrocosms in both 2017 and 2018, with only 0-1% in holes under control conditions. The fish composition in the sloughs for the second throw trap sampling session did not clearly reflect the differences in composition of the alligator hole catch for either year. Over the course of the study flagfish, bluespotted sunfish, mollies and topminnows were captured with throw traps in sloughs of all four macrocosms (data not shown).

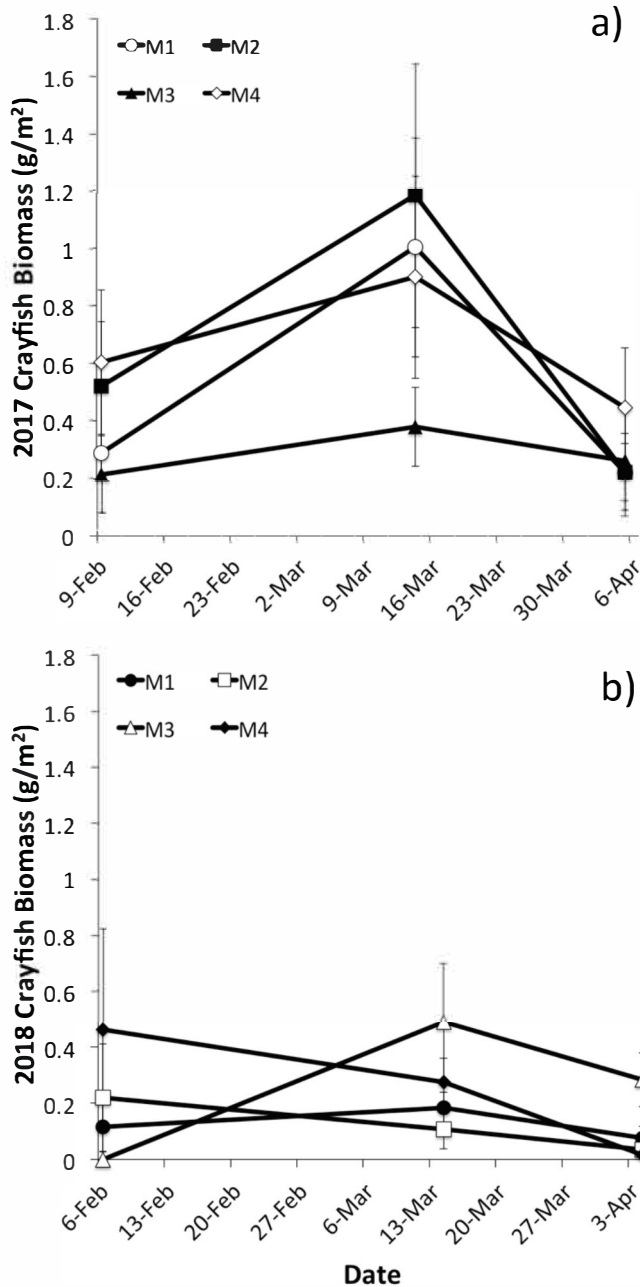


Figure 2.1.A. Mean crayfish biomass density (g dry mass · m⁻²; n = 7 randomly placed throw traps each session) in fenced (black symbols) and control (open symbols) sloughs over all three sampling sessions in a) the dry season of 2017 and b) the dry season of 2018. The ridges dried just before the second sampling session in all macrocosms except perhaps in M3. The error bars represent ±1 standard error from n = 7 traps.

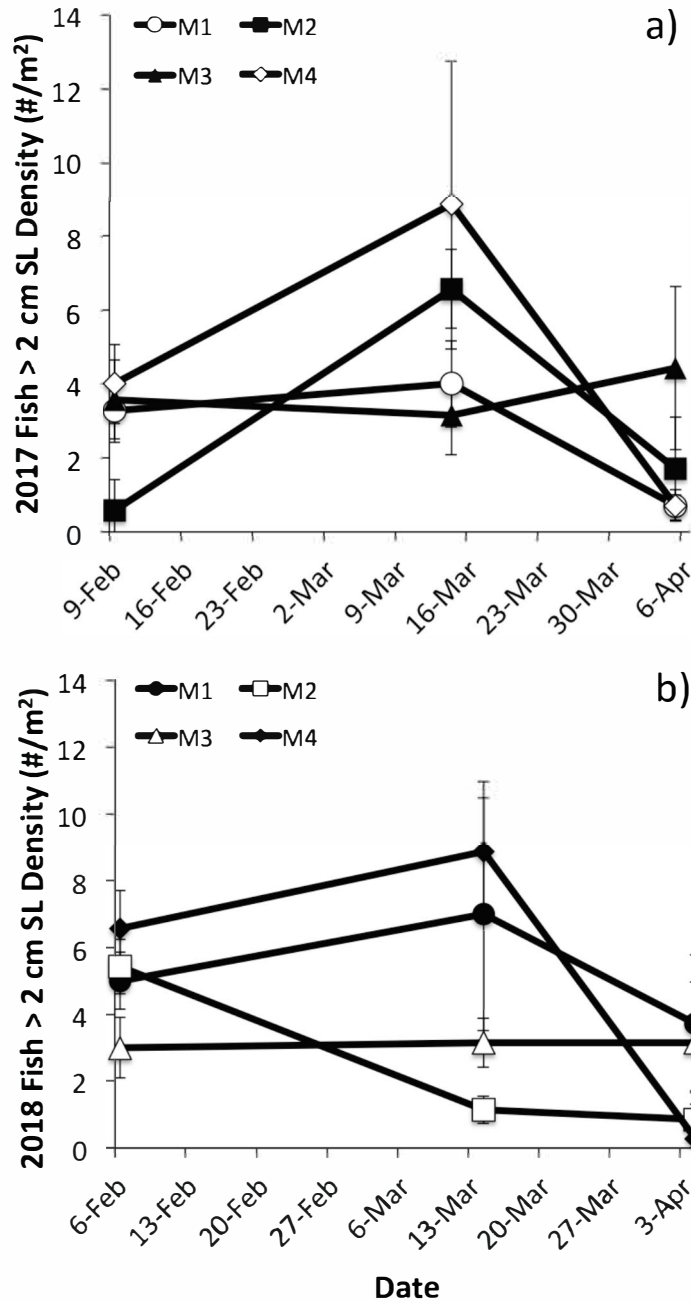


Figure 2.2.A. Mean fish density (no. · m⁻²; all fish > 2 cm SL; n=7 randomly placed throw traps each session) in fenced (filled symbols) and control (open symbols) sloughs over all three sampling sessions in the dry season of a) 2017 and b) 2018. The ridges dried just before the second sampling session in all macrocosms except perhaps in M3. The error bars represent ± 1 standard error from n = 7 traps.

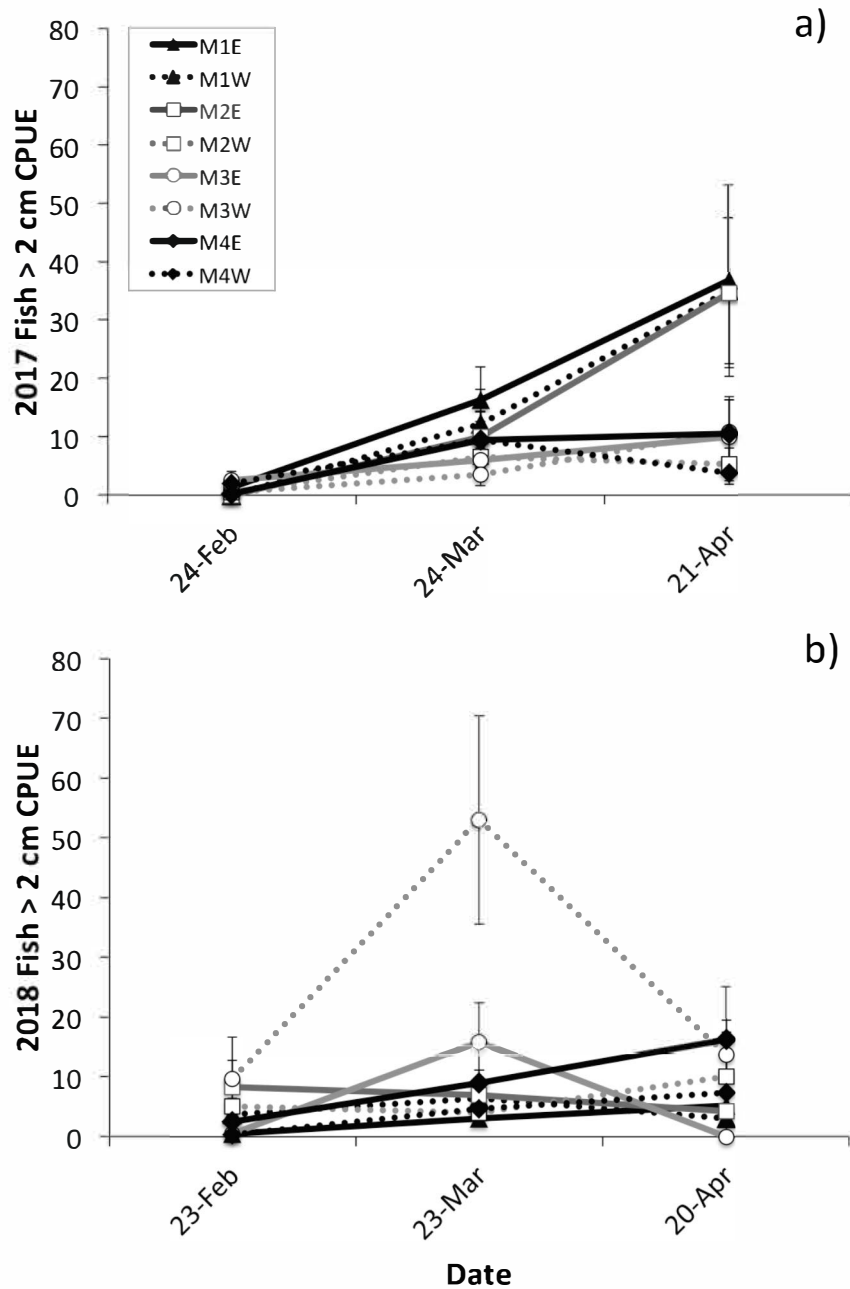


Figure 2.3A. Mean fish CPUE ($\# \cdot \text{trap night}^{-1}$) for fish > 2 cm SL caught in minnow traps ($n=4$) in each alligator hole for three sample sessions (February, March, April) over the course of the a) 2017 and b) 2018 dry season. The water depth was decreasing through time. M2 and M3 were fenced in 2017, and M1 and M4 were fenced in 2018. The error bars represent ± 1 standard error from $n = 4$ traps per hole.

Table 2.1A. Composition of fish > 2 cm SL in sloughs (i.e., caught in throw traps) in March and refuging in alligator holes (i.e., caught in minnow traps) in April 2017 and 2018.

Fish Species	Fenced Sloughs (%)		Control Sloughs (%)		Fenced Alligator Holes (%)		Control Alligator Holes (%)	
Year	2017	2018	2017	2018	2017	2018	2017	2018
Eastern Mosquitofish	21	20	15	37	16	35	80	58
Bluefin Killifish	14	15	26	17	6	3	8	12
Bluespotted Sunfish	6	6	10	10	4	23	4	6
Sailfin Molly	14	18	35	3	38	22	4	12
Flagfish	3	26	0	13	20	6	0	1
Golden Topminnow	5	7	7	10	4	4	0	1
Mayan Cichlid	0	0	0	0	5	2	1	2
Least Killifish	0	0	0	0	1	2	2	2
Pigmy Sunfish	36	6	5	3	2	2	1	1
Dollar Sunfish	2	0	0	0	2	0	0	2

APPENDIX B

Glossy Ibis are generally thought to have macroinvertebrate diets (Taylor and Taylor 2015) and were not expected to respond to fish densities. M1 contained the highest total wading bird density, followed by M2, M3 and M4. This suggested Glossy Ibis foraging may have been affected by the position of the macrocosms in the greater landscape or some other underlying foraging characteristic such as following a macroinvertebrate gradient. It was possible that total macroinvertebrate prey would show a consistent gradient N to S. Another possibility is that there were differences in micro-topographic relief inside the sloughs that concentrates macroinvertebrates more frequently (i.e., makes prey more available), but addressing that hypothesis would require additional high-resolution measurements of depth when the system is flooded.

In order to test possible factors driving the gradient in Glossy Ibis foraging activity, invertebrate biomass densities and emergent vegetation densities were calculated and compared from the second round of throw-trapping (March 13 – March 17, 2017). Mean invertebrate biomass (g dry mass/m²) were determined by calculating the mean biomass of the replicate trap samples for each macrocosm in each sampling session. Total invertebrate biomass for each macrocosm were square root transformed to reach normality assumptions and analyzed with ANOVA for the second trapping session between macrocosms using individual throw trap samples as replicates to look for significant variation between macrocosms while water levels were just low enough for wading birds to forage in the sloughs.

Total invertebrate biomass did not differ among macrocosms ($F_{3, 24} = 0.996$, $p = 0.41$) when traps were treated as the units of replication (Fig. 1a). In addition to biomass, mean density (# of individual invertebrates) and total invertebrates in each macrocosm over the second throw trap sampling session were visually inspected to look for a gradient of invertebrate abundance that followed the gradient of wading bird activity. There was no apparent gradient in invertebrate densities for either biomass or density for any taxa (Fig. 1b). Therefore, Glossy Ibis did not seem to follow a gradient of available invertebrate prey.

Wading bird activity may be related to low emergent vegetation densities in the sloughs, so we graphically inspected the average emergent vegetation stem density (#/m²) in each macrocosm. Average stem densities for each macrocosm were then analyzed with ANOVA for the second trapping session between macrocosms using individual throw trap samples as replicates to look for significant variation between macrocosms. The average stem densities did not differ among macrocosms ($F_{3, 24} = 0.725$, $p = 0.547$) when traps were treated as the units of replication (Fig. 2). In addition, emergent vegetation densities for the first trapping session were also graphed, with no gradient pattern present.

There is no evidence that either invertebrate biomass or emergent vegetation cover affected the foraging behavior of the Glossy Ibis, despite the gradient of wading bird activity. It is possible that the wading birds consistently traveled and foraged north to south, and found no reason to venture as far as M4 on the southern end of LILA. However, the relative distance between macrocosms is small, and there is no evidence that the wading birds would spend too much energy traveling to forage in M4. The

gradient may have been a stochastic occurrence for the year 2017, or due to other unmeasurable environmental factors.

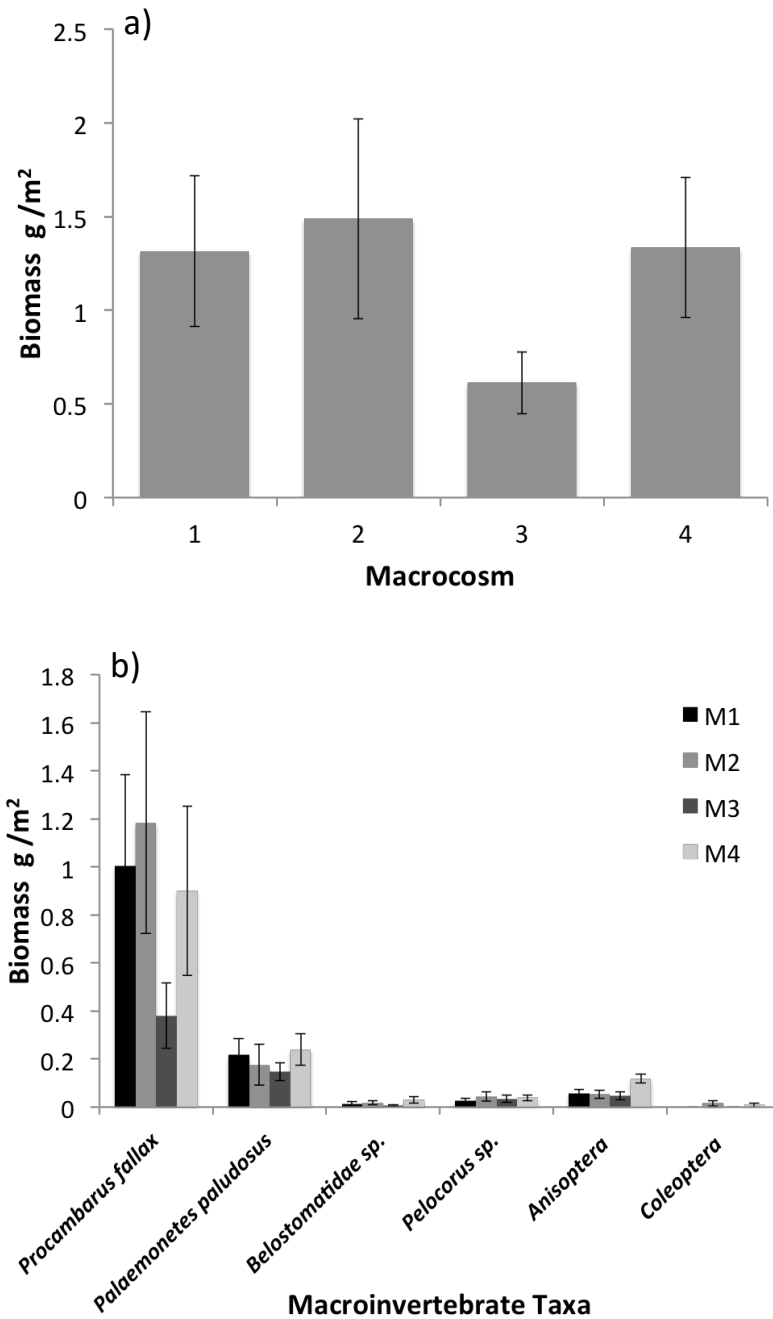


Figure 2.1.B. Mean (\pm SE) biomass per m^2 of a) total macroinvertebrate and b) taxa-specific biomass density in each macrocosm collected from throw traps from March 13 – March 17, 2017, with slough depths of 30 - 35 cm in the sloughs. Macrocosms M2 and M3 were the fenced macrocosms in 2017. Means and standard errors came from $n = 7$ throw traps per macrocosm.

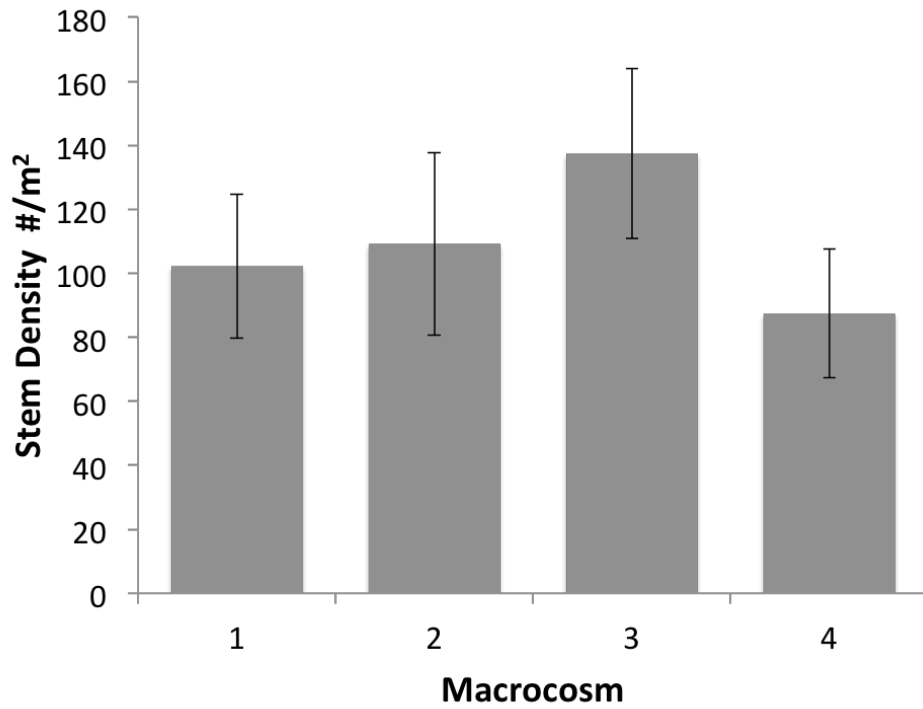


Figure 2.2.B. Mean (\pm SE) emergent vegetation stem density ($\#/\text{m}^2$) in each macrocosm counted from throw traps from March 13 – March 17, 2017, with a target slough depth of 30 cm in the sloughs. The error bars represent a standard error from $n = 7$ throw traps per macrocosm.

CHAPTER 3: FEEDING ON THE EDGE: FORAGING WHITE IBIS (*EUDOCIMUS* *ALBUS*) TARGET INTER-HABITAT PREY FLUXES

ABSTRACT

Animal population success is partly determined by the availability of spatially and temporally variable prey resources, but the conditions producing those prey fluxes or concentrations is not always clear. In the Florida Everglades, U.S.A., wading birds nest and forage in the dry season. Receding water levels in the heterogenous landscape functionally concentrate prey and make foraging efficient for depth-limited foragers. The White Ibis (*Eudocimus albus*), feeds extensively on crayfish that concentrate in relatively open and low elevation slough habitats. Previous work indicates that crayfish (*Procambarus fallax*) move from higher elevation ridge habitats down into adjacent sloughs when ridges are almost dry. While it is possible that an inter-habitat prey flux could be exploited by White Ibis, the water is generally considered too deep (> 19 cm) for efficient foraging. I conducted an observational study of White Ibis foraging activity and crayfish biomass in replicated drying wetlands to examine this predator-prey interaction and determine the conditions under which White Ibis exploit their prey. I used time-lapse imagery to continuously quantify White Ibis foraging activity for 61 days, and I quantified crayfish biomass three times while the wetlands dried. Crayfish biomass in sloughs peaked when ridges were almost dry. More than 54% of White Ibis foraging occurred when the ridges were almost dry, crayfish were abundant in sloughs,

and sloughs were relatively deep (> 29 cm). The average White Ibis fed in slough water depths of 26 – 32 cm - depths that have generally been considered too deep for efficient prey capture. White Ibis frequently selected slough edges, suggesting they captured crayfish that migrated off the ridge habitat. My results support that White Ibis foraging activity was primarily driven by crayfish biomass and an inter-habitat prey flux rather than a narrow range of optimal foraging depths. The results suggest that costs of foraging in deep water depend on characteristics of predator and prey pairs, and that an inter-habitat prey flux driven by elevational differences may provide substantial opportunities for wetland predators.

INTRODUCTION

Prey availability is a fundamental ecological concept related to optimal foraging and patch use, and it is important for understanding predator-prey dynamics that affect populations (Hutchinson 1959, MacArthur and Pianka 1966). Prey availability is the combination of prey density and vulnerability to predation, the latter influenced by species-specific predator-prey dynamics and the environment (Sutherland 1996). More specifically, prey density is determined by local in situ prey production and movement (i.e., inter-habitat flux, concentration, migration, or emergence (Allen and Wesner 2016)). In differing habitats, inter-habitat transfers of allochthonous resources, including prey fluxes, can dramatically alter community interactions (Polis et al. 1996). Prey fluxes can be synchronous for a large portion of the population and directionally driven by environmental conditions or ontogeny (i.e., forced migration) (Walters et al. 2017), creating resource fluxes between habitats or ecosystems that provide large, quantifiable benefits to predators in recipient habitats (Nakano and Murakami 2001, Allen and

Wesner 2016). In neighboring habitats with differing elevations, prey fluxes can be influenced by down-gradient water movement to lower elevation sites (Leroux and Loreau 2008). In shallow aquatic ecosystems, this phenomenon can produce spatiotemporally distinct conditions to create high prey availability for foraging predators (Sabo and Power 2002).

In the hydro-dynamic wetland ecosystems of the Everglades in Florida, U.S.A., seasonally nesting wading birds (Ciconiiformes) take advantage of receding water levels in a heterogeneous landscape to access concentrated aquatic prey. Foraging wading birds are sensitive to variable water depth because prey availability is believed to be largely controlled by physical limitations of the birds in deep water and the abundance and behavior of prey within the dynamically changing wetland landscape (Gawlik 2002, Ma et al. 2010). Much of the central portions of the Everglades is a mosaic of two interspersed habitats: higher elevation ridges and lower elevation sloughs (i.e., the ridge-slough landscape) (Larsen et al. 2011), and wading birds almost exclusively forage in slough habitats during the nesting season (Bancroft et al. 1992, Hoffman et al. 1994, Bancroft et al. 2002). The ridges are higher in elevation and generally dominated by dense, grassy vegetation, while sloughs are 20-30 cm lower in elevation (i.e., commonly 70-100 cm deep in the summer) and covered with sparse emergent or floating vegetation (Jordan et al. 1997, Sklar et al. 2000, Larsen et al. 2007). The ratios of the two interspersed habitats can vary, but ridges can frequently make up 55% of the landscape (Larsen et al. 2011). The Everglades is subjected to high amounts of rainfall in the wet season (May through October), when prey are dispersed and growing, and dries down in the dry season (November through April). As water depths decrease during the winter dry season, prey densities increase in the sloughs or become trapped in isolated pools as they

move downgradient between habitats (Kushlan 1979, Cook et al. 2014, Botson et al. 2016).

The most abundant nesting wading bird species in the Everglades is the White Ibis (*Eudocimus albus*). White Ibis (hereafter “ibis”) are considered highly sensitive to water depths in part because of their foraging strategy, which requires tactile feeding by probing the slough bottom with a highly sensitive bill (Kushlan 1977, Kushlan 1979). Previous studies indicate that White Ibis require relatively shallow water depths (9-19 cm, with a threshold of 24 cm) for successful foraging (Gawlik 2002, Bancroft et al. 2002, Heath et al. 2009, Lantz et al. 2010). The most common aquatic prey for nesting White Ibis in the sloughs of the central Everglades are slough crayfish (*Procambarus fallax*) (Boyle et al. 2014), but White Ibis will also forage on marsh fishes and aquatic insects (Dorn et al. 2011, Boyle et al. 2014).

Aquatic prey are generally expected move downgradient within sloughs and across the ridge-slough habitat interface as water recedes in the wetlands, but movement decisions may vary between species (Cook et al. 2014, Hoch et al. 2015). A recent study of inter-habitat slough crayfish (hereafter “crayfish”) movement from ridges to sloughs determined that crayfish populations moved into the sloughs when ridge water depths reached 1-11 cm (Cook et al. 2014). Because ridges have little elevational variation, most of the crayfish population over entire ridges (sometimes multiple ha of habitat) could be migrating into adjacent sloughs over a period of < 2 weeks (Cook et al. 2014). Crayfish are produced in both habitats during summer months (van der Heiden and Dorn 2017), but a large-scale prey flux into the slough habitat in response to ridge drying could be an important behavioral phenomenon that increases prey availability for White Ibis. While an inter-habitat flux of crayfish prey could produce foraging opportunities in

sloughs, the slough depths when ridges dry may still be too deep for White Ibis foraging and the birds may need to wait until the sloughs are shallower to access the crayfish.

Using a series of prey and depth observations, Kushlan (1979) suggested as much, noting the sloughs appear to be too deep for foraging when crayfish reach peak density (25 cm).

The ridge-to-slough crayfish prey flux, the heavy use of crayfish prey by ibis during the dry season, and previous observations of depth-sensitive foraging by ibis created an apparent discrepancy about the conditions under which White Ibis access crayfish prey in slough habitats. I quantified the foraging activity of White Ibis and their crayfish prey in a drying wetland and tested two alternative hypotheses (Fig. 1) to determine what wetland conditions promote good foraging conditions (i.e., timing of predator-prey interactions) in sloughs. The depth-limited foraging hypothesis posits that the majority of White Ibis foraging during the dry season will occur when sloughs reach 9-19 cm (depth limitation, Fig. 1) (Gawlik 2002, Heath et al. 2009, Lantz et al. 2010). Alternatively, the prey flux hypothesis (Fig. 1) posits that White Ibis feed when high concentrations of crayfish are produced by a crayfish flux elicited by down-gradient migration. Movement occurs when ridges are 1-11 cm deep (Cook et al. 2014) and under such conditions sloughs will generally be > 20 cm deep in the Everglades and in my experimental wetlands. To identify the depths at which White Ibis forage in sloughs I continuously quantified ibis foraging activity over 61 days in a drying wetland using game cameras. I also quantified crayfish biomass in the same sloughs three times during the study. The procedure was replicated in multiple impounded wetlands with habitat elevation features similar to the Everglades and controlled water level recession that mimicked natural drying (from 54 cm – 7 cm in the sloughs, February – April, see hydrograph in Fig. 1). If White Ibis foraged on crayfish during the migration from ridge

to slough, I further predicted that ibis would preferentially forage close to the habitat boundary to capture crayfish while they moved into the slough. Once the ridge habitat is dry (< 0 cm) and crayfish movement ceases, preferential use of the ridge-slough boundary would not necessarily be expected.

METHODS

Area of Study

My study was conducted in the sloughs of four replicated 8 ha wetlands (denoted as M1-M4, north to south) at the Loxahatchee Impoundment Landscape Assessment (LILA), Boynton Beach, Florida (lat. 26°17.99' N, long. 80°13.97' W) during the winter-spring dry season from 2 February 2017 – 28 April 2017. The replicate wetlands (200 x 400 m) included habitat and elevation features similar to the habitats of the central and southern Everglades ecosystem, higher elevation ridges with thick vegetation are interspersed with adjacent lower elevation sloughs with emergent vegetation. Smaller high points in my study site support woody vegetation and alligator holes constitute the lowest elevation habitat (Fig. 2). The elevation differences between the ridges and sloughs that I studied were 20-26 cm and water depths fluctuated up to 1.2 m between seasons such that ridges become dry most years and sloughs may remain wet or else become dry at a later date. The wetlands were separated by levees and water levels were controlled in a connected flow-through system. All four wetlands were similar in habitat/elevation arrangement and area size, with communities of fish, macroinvertebrates, and vegetation that are characteristic of the Everglades ecosystem. Common macrophytes included spike rush (*Eleocharis* spp.), white water lily (*Nymphaea odorata*), panic grass (*Panicum* spp.), duck potato (*Sagittaria lancifolia*), pickerelweed

(*Pontederia cordata*), sawgrass (*Cladium jamaicense*), and bladderworts (*Utricularia purpurea*, *U. foliosa*). Common aquatic fauna included slough crayfish, grass shrimp (*Palaemonetes paludosus*) and small fishes such as the eastern mosquitofish (*Gambusia holbrooki*), bluefin killifish (*Lucania goodei*), sailfin molly (*Poecilia latipinna*), and bluespotted sunfish (*Enneacanthus gloriosus*). My work focused on quantifying White Ibis foraging activity and biomass densities of their primary prey (slough crayfish) in the shallower of the two sloughs in each wetland (Fig. 2). Each slough was 18 – 20 m wide by 360 m long with higher elevation ridges to the north and the south.

I made repeated observations of predator and prey within a heterogeneous landscape with receding water to examine the timing and conditions associated with the predator-prey interactions between White Ibis and slough crayfish. The water depths were controlled to mimic a natural recession and create suitable depths (5-35 cm) over similar time periods in each wetland. Recession rates and depths varied slightly between wetlands and through time, with average recession rates over the 90-day period (2 February - 28 April) between 0.55 and 0.56 cm · day⁻¹ and final water depths ranging from 2.10 - 8.14 cm in each slough on 28 April (Fig. 1). I chose this recession rate because White Ibis have been observed to select foraging locations across the Everglades landscape with recession rates of 0.52 – 0.59 cm · day⁻¹ (Beerens et al. 2011). Continuous recording devices tracked water surface elevations in the wetlands (South Florida Water Management District 2017), and I used measured water depths (cm from water surface to sediment surfaces) in the sloughs to create hydrographs for each habitat (sloughs and ridges) in each wetland (Fig. 1). Water depths varied slightly between wetlands, with M3 running an average of 1 - 7 cm deeper than the other wetlands throughout the 90-day observation period. I measured depths (cm) for the White Ibis observation areas (0.13 –

0.14 ha within each shallow slough) along six evenly spaced transects (13.3 m apart) perpendicular to the length of each slough. On each transect, I measured depth at 13-16 points (1.5 m apart), including two points on the adjacent ridges. Altogether I made a total of 51-61 measurements in each slough and 24 measurements in each of the adjacent ridges.

Crayfish Densities

To quantify crayfish densities in the slough over time, throw-trap sampling was conducted three times between 8 February and 7 April 2017, in each of the four wetland sloughs. The throw trap I used consisted of a 1-m² area (90 cm deep), with a copper frame covered in 1.5-mm nylon mesh, which was open on the top and bottom. The trap was thrown into the slough from 1-2 m away, enclosing the fish and slough crayfish (for methods see Dorn et al. 2005, Dorn and Cook 2015). All aquatic animals (mostly fish, slough crayfish, and grass shrimp) were removed with bar seines and dip nets, euthanized, preserved and returned to the lab. Throw trap samples were taken from seven random locations in the sloughs during each session. Sampling dates were spaced out roughly evenly and chosen in order to capture predator-prey dynamics at fundamentally different depths. From 8 – 10 February, depths should have been too deep for foraging (February, (mean \pm SD) 49 ± 0.7 cm), and slough crayfish were not expected to be moving off of the ridge (Cook et al. 2014). From 13-17 March and 3 – 7 April, ridges should have been very shallow or dry, with slough depths either too deep (March, 33 ± 1.8 cm) or approaching what was considered an ideal foraging depth range (April, 20 ± 1.8 cm), respectively. Based on results in Cook et al. (2014), I expected crayfish to move to the slough in early to mid-March (second sampling session). Average crayfish biomass density (g dry mass / m²) was used to examine the temporal variability in slough crayfish

biomass in the four sloughs. The total biomass of crayfish was calculated for each 1-m² trap using crayfish carapace lengths and length-dry mass regressions (Dorn et al. 2011, unpublished data).

White Ibis Foraging Activity

To quantify White Ibis foraging responses to high-density crayfish fluxes in each slough, I calculated average daily White Ibis densities and their distribution over 0.13-0.14 ha of the slough in three of the four wetlands (M1- M3) with game cameras (Reconyx PC800 Hyperfire) using time-lapse imagery (position in Fig.1). White Ibis density data were only available for three wetlands (M1, M2, M3) because the camera in the fourth wetland (M4) shifted during a windy day and more than a week of important images became unavailable. Photos were taken every three minutes over an eight-hour period from 06:00 hr. to 14:00 hr. (160 images per day). A pre-study suggested the eight-hour period typically captured 90% or more of all daily wading bird activity (N.J.D, unpublished study from 2015). The cameras were started on 27 February (mean depth \pm SD, 40 ± 1.2 cm) when wading birds were still inactive and took images for a 61-day period (i.e., until 28 April). Other wading bird species were recorded as well, but I focused on the White Ibis counts related to my hypotheses in this paper.

The images were individually inspected, and birds were counted out to 80 m from the camera, giving an observation area of 0.13- 0.14 ha in each of the three wetlands. White Ibis were only counted in the sloughs. The edges of the sloughs were visually identifiable by vegetation shifts from slough to ridge. White Ibis counts in the sloughs were recorded to calculate the daily average density in each slough and determine the distribution within each slough over time. Overall, only 7% of the birds could not be identified. Frames (an average of 20 – 22 each day) that were too dark, foggy or rainy to

distinguish birds were discarded. Each day I used 78-160 frames (averaging 138-140) per day to calculate a daily average density. I assumed that White Ibis that stayed in the camera area were most likely foraging. Many ibis' heads or bills were fully submerged and showed other postures indicative of foraging, most appearing to stay for at least 5 – 30 frames. Therefore, I considered density as an index for foraging activity and have used the terms interchangeably throughout the paper.

Statistical Methods

I expected crayfish biomass in the sloughs to increase as water receded off the ridges (Cook et al. 2014). To statistically examine variation in slough crayfish biomass dynamics through time I analyzed mean slough crayfish biomass using time factors (sampling session, within-subjects effects) with repeated measures ANOVA (linear mixed-effects model in R, v.3.4.0) and graphical interpretation. The specific temporal dynamics were then interpreted graphically.

White Ibis density dynamics in each wetland were graphically inspected through time to display the variability in foraging activity. To test my alternate hypotheses about foraging depths used by White Ibis, I used all observations to calculate the weighted mean slough depth (cm) in each slough, when the average ibis was foraging. I also examined and report the depth conditions and percent of total foraging activity on each of the five highest days of White Ibis foraging activity in each wetland. The five highest days were chosen because the foraging was highly variable between days, and $\geq 80\%$ of White Ibis activity per wetland was concentrated in these highest 5 days. The remaining 20% of activity in each wetland was spread out somewhat evenly between the other 56 days with relatively low average activity. I reported the mean slough depth and used the spatial depth variation in the sloughs (ground-measured with transects) to estimate the

percent of the slough at a depth of ≤ 19 cm for each of the five days of peak foraging in each wetland. To illustrate the time course of observed slough crayfish dynamics and White Ibis foraging dynamics together, I plotted an accumulation curve of the daily foraging activity throughout the 61-day observation period with crayfish biomass densities (g dry mass /m²) from each of the three sampling sessions, for each of the three wetlands.

Adult slough crayfish hourly movements (night and day) are typically 0-1 m/h (van der Heiden 2012) so that slough crayfish might be expected to spend a couple hours or longer on the slough edge as they migrate downgradient. If White Ibis were capturing slough crayfish as they migrated off of the drying ridges, I predicted that they might also have a non-random distribution in the sloughs, with birds congregated along the slough edges (near the slough-ridge habitat boundary). To address this prediction, I quantified the spatial distribution of White Ibis within each slough for the five highest days of foraging activity. Using average adult White Ibis sizes to help visually scale distances, I arbitrarily defined the edge as a 1.65 m strip (five ibis body lengths) of wetland adjacent to the ridge boundary on both sides of the 80-m long observation area. I used the median body length of an adult White Ibis (approximately 33.1 cm, excluding average neck and bill length (Babbitt and Frederick 2007)) as a measurement to identify the distance from where ibis were standing to the ridge edge. The edge habitat made up 10-12% of the total slough observation area in each wetland. Average water depths along the slough edge and throughout the rest of the slough were similar in two of the three wetlands (0.4 – 0.5 cm difference), but in M3, the edge was 4 cm shallower on average. White Ibis positions (slough edge vs. center slough) were categorized for each image, and a habitat selection index was calculated with a random expectation based on the fractional distribution of

ibis observations vs. the availability of each habitat. I calculated Chesson's α index (Chesson 1983) for each date such that indices > 0.5 signified preference for the slough edge. If edges were more important on deep days because crayfish were moving or because the water was significantly shallower on the edges, then I expected there to be a positive correlation between water depth in the slough and selection for the edge. I tested this with Pearson's correlation.

RESULTS

Crayfish Densities

Slough crayfish biomass varied through time ($F_{2,6} = 9.64$, $p = 0.01$), rising to a peak in all four wetlands during the second sampling session (13-17 March) when there was an average of (mean \pm SD) 10 ± 1.6 cm of water on the ridges (Fig. 3). On average, biomass more than doubled in the sloughs (0.41 to $0.87 \text{ g} \cdot \text{m}^{-2}$) as ridge water depths declined from 26 to 7 cm. Once the ridges were dry, average biomass in the sloughs declined as the water depths receded from the second sampling session (33 ± 1.8 cm in sloughs) to the third (20 ± 1.8 cm) (Fig. 3).

White Ibis Foraging Activity

White Ibis daily average densities varied from 0-25/ha over the three wetlands during the 61 days of observation (Fig. 4). The average White Ibis foraged in water depths of 26 – 32 cm across the sloughs (i.e., density-weighted means, Table 1), with corresponding average ridge depths between 2-10.4 cm. The five highest foraging activity days in each of the three wetlands contained 80 – 89% of total White Ibis activity (Table 2), and 54-89% of foraging activity per slough occurred when the sloughs averaged ≥ 29 cm deep (Table 2). Only 0-14% of White Ibis observations occurred in

sloughs with average water depths between 9 and 19 cm. For nine of the 15 days of high foraging activity, including the top day of foraging in each wetland, 0-2% of the sloughs were ≤ 19 cm deep. Only three of the 15 days of high foraging activity (across all three wetlands) had depths ≤ 19 cm across the majority of the slough area ($> 50\%$), and those days had relatively lower White Ibis activity (≤ 2.5 / ha), later in the season (Table 2). Over time, the greatest cumulative increases in White Ibis foraging activity for each slough occurred in early March when slough depths were ≥ 29 cm and crayfish were abundant in sloughs (Fig. 5).

White Ibis favored the slough edge (10-12% of a given slough observation area) on the highest day of foraging in each wetland with 60 – 95% of all foraging birds in the slough edge. When water was still on the ridges (depth > 0 cm), ibis exhibited selection for edges in 9 of the 10 days ($\alpha = 0.55 - 0.99$, Fig. 6). Selection was more variable at lower water depths, but daily selection for edges was positively correlated with ridge water depth ($r = 0.58$, $p = 0.02$, Fig. 6).

DISCUSSION

Foraging observations in my study support the hypothesis that the activity of White Ibis was primarily driven by a high-density flux of crayfish off of the ridges, rather than a narrow range of shallow, optimal foraging depths. For many carnivorous waterbirds feeding in hydrologically dynamic wetlands, prey density needs to be assessed in relation to prevailing water depths because depth relates to both the spatial concentration of the prey and the physiological capacity of the bird to access the prey (Gawlik 2002, Ma et al. 2010, Lantz et al. 2010). The observations of relatively deep water foraging requires both a reconsideration of the costs of foraging at different water

depths and the utility of reporting simple foraging depth limits or ideal ranges (e.g., Kushlan 1979, Heath et al. 2009, Lantz et al. 2010). My results indicate that crayfish biomass mainly influences prey availability for White Ibis, and sustaining high crayfish biomass by increasing productivity and preserving the heterogenous landscape of the Everglades may further support White Ibis nesting populations.

The crayfish movement dynamics and ibis foraging distributions along the edges of the ridges point to a heretofore undescribed mechanism by which a high-density inter-habitat crayfish flux may facilitate prey availability for White Ibis. The crayfish depth-biomass dynamics observed in my study are consistent with previous literature, observing that densities of crayfish in sloughs peaked after the ridges dried (van der Heiden and Dorn 2017, Cook et al. 2014). Kushlan (1979) reported that the crayfish biomass in Everglades sloughs peaked at 25 cm, depths that correspond well to my observations at the second sampling event (Fig. 3) and measurements reported in experimental work conducted by Cook et al. (2014). More importantly, the top two days of White Ibis foraging in each wetland corresponded to ridge depths between 2 and 10.4 cm (Table 2), which is comparable to the ridge depth range described in Cook et al. (2014) (1-11 cm) that promoted crayfish to move off of ridges. Wetland M3 had notably lower crayfish biomass overall and a muted temporal biomass dynamic. The muted dynamic could be explained by an early peak of White Ibis foraging activity in the days prior to prey sampling (see Figs. 4 and 5), such that 53% of all ibis foraging activity in that wetland had occurred prior to the crayfish biomass estimate. In the other two wetlands, the first days of high White Ibis foraging came just after the crayfish sampling (Figs. 4 and 5). The observations suggest that the crayfish flux and subsequent White Ibis foraging are

timed to a restricted range of shallow conditions on the ridges rather than a range of shallow depths in the sloughs.

The spatial distributions of White Ibis within the sloughs suggested birds favored the edges of the sloughs rather than the center of the sloughs, especially early in the season when sloughs were deeper and ibis densities were high. This may correspond with observations by Kushlan (1979), where he noted that Landsat imagery showed White Ibis distributed along the edges of flooded marsh areas during the dry season recession (22 March 1973). White Ibis might have been using edges to forage in somewhat shallower conditions if edges provided better foraging depths, but M3 was the only wetland with notably shallower depths on the slough edges (avg. 4 cm shallower). Foraging activity in M3 on 2 and 11 March occurred in extremely deep water (41 and 35 cm: Table 2), and almost exclusively on slough edges, so that the ibis were probably foraging in water depths closer to 37 and 31 cm respectively. In the other two wetlands the depths were not shallower on the edges of the respective sloughs (averages = 0.4 - 0.5 cm), and therefore shallower depths along the slough edges cannot generally explain the preference for the edge. Rather, I interpret the use of the edge as a strategy employed by White Ibis to capture slough crayfish as they move downgradient from the ridge to the slough.

The profitability of waterbird foraging habitat is determined by prey density and the costs of foraging at different water depths (Ma et al. 2010). With deeper water, foraging birds become constrained by morphological limits or incur high foraging costs such that giving up densities (GUDs) – the density of prey remaining in a patch after the predator stops feeding - are generally higher in deeper water (Gawlik 2002, Nolet et al. 2006). In an experimental study of wading birds foraging on fish in 0.2 ha ponds, Gawlik

(2002) reported the highest GUD for White Ibis in the treatment with the deepest water (28 cm) and higher densities of ibis foraging at 10 cm and 19 cm treatments. He suggested that a foraging depth threshold existed somewhere between 19 and 28 cm. Lantz et al. (2010) used single species fish-stocked wetland corrals and found little ibis foraging in 25 cm, while observing most ibis foraging in a treatment 10 cm deep. Kushlan (1979) considered ideal foraging depths for White Ibis to be 5-10 cm. Powell (1987) based his foraging depth threshold for ibis solely off of leg length (16 ± 1.0 cm). Several landscape-scale studies also support that White Ibis shallowest water depth limitations (Bancroft 2002, Beerens et al. 2011, Beerens et al. 2015). In a more recent landscape study using a landscape modeling framework and aerial counts of ibis to determine optimal water depth estimates, the highest abundances of White Ibis occurred in 16 ha grid cells with a $13.40 \text{ cm} \pm 0.09$ modeled water depth (Beerens et al. 2015). In contrast to these determinations of ideal foraging depths, most of the White Ibis foraging observations in my study were in water deeper than 28 cm (54-89% of foraging activity at depths ≥ 29 cm, (Table 2) and only 0-14% of ibis foraging at 9 - 19 cm depths).

With average leg lengths between 16 cm (Powell 1987) and 22 cm (Kushlan and Bildstein 1992), images of ibises taken early in the season when they were foraging in deep water should show their undersides at least partially submerged. Review of the images show that many birds were standing in water up to their lower chest with their heads and shoulders submerged while probing. Nevertheless, some had their undersides out of the water both in the middle and the edges of the sloughs, appearing to be intermittently standing on trampled plant stems and root/rhizome systems as they move through the deep water. In order to successfully forage, tactile-foraging White Ibis also need to be able to probe the sediment. With estimated average neck and bill lengths of 27

– 32 cm (Babbitt and Frederick 2007), it is possible for them to reach the sediment in water 29-31 cm deep with most of their body still out of the water.

The depth discrepancy between my observations and those of previous mesocosm studies of White Ibis foraging limitations can be partly explained by the focal prey. Past experimental studies have examined White Ibis foraging with fish prey (Gawlik 2002, Lantz et al. 2010). While fish are consumed by many wading birds including White Ibis, they are not typically a large component of White Ibis diets during the spring nesting season unless water depths reach extremely low levels in the Everglades (Dorn et al. 2011, Boyle et al. 2012, Boyle et al. 2014). Thus, I suggest crayfish were the primary prey of the ibis in the wetlands I studied. Additionally, crayfish biomass in my wetlands responded significantly to water depth changes through time ($p < 0.05$), but biomass of prey fishes (> 2 cm SL) did not follow the same trend (see Appendix C). Finally, based on previous experimental work, it is highly unlikely White Ibis were foraging on fish in such deep water (Gawlik 2002, Heath et al. 2007, Lantz et al. 2010).

White Ibis are tactile probing foragers when feeding on invertebrates and crayfish are bottom-dwelling/crawling macroinvertebrates. Ibis may be able to perceive and capture crayfish almost as easily in 30 cm of water as in 15 cm because the crayfish inhabit a small volume of water near the sediment surface in either case. In contrast, discovering fish in 30 cm instead of 15 cm of water means sweeping and feeling through twice the volume, because fish inhabit the entire water column and can escape in additional dimensions with active, strongly directed swimming. I suggest that within a large range of practical depths (perhaps up to 35-37 cm), the success and willingness of White Ibis to forage on crayfish probably depends mainly on crayfish biomass.

The difference in White Ibis foraging depths between this study and those of previous landscape-scale investigations of White Ibis foraging limitations may be due to the difference between ridge elevations in the current natural Everglades landscape and my study site (LILA), and the illustrated inclination to forage along the edge of elevation shifts immediately following inter-habitat crayfish fluxes. The current Everglades landscape contains smaller elevation differences between ridge and slough (15 – 20 cm; Givnish et al. 2008, Harvey et al. 2009), than the 20-26 cm difference in LILA, so that if White Ibis respond to a crayfish flux as ridges dry to 1-11 cm, they may not be foraging in > 25 cm slough depths in the natural Everglades. Further, crayfish may move downgradient between microtopographic shifts inside of sloughs, making the phenomenon general to all elevational shifts; both within and adjacent to sloughs. It is likely that White Ibis forage within the sloughs at several different landscape-level water depths depending on the microtopographic relief within sloughs.

If the landscape-scale, inter-habitat flux of crayfish biomass is more important than particularly low slough water depths for foraging White Ibis, then the ecological conditions that improve crayfish production in the wetland landscape should be of primary importance for promoting this predator-prey interaction. Slough crayfish dominate invertebrate biomass in densely vegetated cattail (phosphorus enriched) habitats (King and Richardson 2007, Hagerthey et al. 2014). However, White Ibis typically forage in less-vegetated areas, and most foraging wading birds tend to avoid cattail areas (Beerens et al. 2011). Cattail removal via active management or fires may provide substantial sources of slough crayfish prey for ibis (Hagerthey et al. 2014). The heterogenous landscape of the ridge-slough system also creates high crayfish biomass, but the ridge and slough may have distinctive costs and benefits for crayfish in differing

hydrological conditions. van der Heiden and Dorn (2017) conducted repeated sampling in adjacent ridge and slough habitats (each 50% of the landscape in the study) and found similar densities of crayfish in both habitats during flooded periods. The higher elevation ridge provided protection against predatory fish, but growth rates of juvenile crayfish were greater in the sloughs (van der Heiden and Dorn 2017). In unpolluted ridge-slough settings, crayfish biomass positively responds to short-term drying (i.e., hydrological disturbances). This is because predatory fish are diminished by the same disturbances, which releases crayfish populations from aquatic predators (Dorn and Trexler 2007, Dorn and Cook 2015). In fact, any hydrological phenomena that produce spatially extensive low-fish or fishless wetland habitat can be important mechanisms for crayfish production in the Everglades and potentially in other wetlands. The current study and the work by Cook et al. (2014) emphasize dry season concentration and suggest that high densities of slough crayfish in the ridge and slough landscape may occur via inter-habitat prey flux promoted by the ridge drying. The functional connection between the ridges producing prey concentrations for wading birds in sloughs had not been explored explicitly until this study and that of Cook et al. (2014).

Maintenance and restoration of the ridge and slough landscape may be important for White Ibis populations nesting in the central Everglades because it increases crayfish prey availability. Anthropogenic changes to the Everglades' hydrology through compartmentalization and manipulated drainage have curtailed the water flow, lengthened or shortened periods of inundation, and created extensive ponding in some regions. Collectively the changes have encouraged a flattening of the Everglades landscape (Fleming et al. 1994, Ogden 1994, Larsen et al. 2007, Frederick et al. 2009), and at least 25% of the ridge-slough landscape in the Everglades has been lost since pre-

drainage times (Ogden 2005). I encourage further exploration of this mechanism at a landscape scale and expect that if the mechanism is broadly important, then groups of foraging White Ibis in the ridge-slough landscape will be found predominantly along micro-topographic elevation/vegetation gradients, including, but not limited to the ridge-slough boundaries.

I found that foraging activity by a predator in a dynamic heterogeneous landscape was mainly driven by a prey flux across habitat boundaries (Allen and Wesner 2016). This inter-habitat prey flux presumably allowed for increased prey availability first along the ridge-slough boundaries and then throughout the entire slough as crayfish followed receding water levels. Over hundreds of km² of ridge-slough wetland landscape, seasonal crayfish prey fluxes may contribute greatly to energy demands for the tens of thousands of nesting White Ibis during the breeding season in southern Florida (Martin 1987, Herring et al. 2010). At a broader scale, my results suggest a potentially important role for habitat heterogeneity, which promotes the maintenance of elevational gradients in wetland ecosystems so that resources can continue to move downgradient with water flows, supplementing lower elevation habitats or ecosystems (Leroux and Loreau 2008). Predator and prey characteristics, as well as environmental drivers (i.e., water depth and habitat variation in wetlands), must be carefully evaluated when considering where and how predators access their prey (Sutherland 1996, Gawlik 2002). Though much of the prey flux work in ecology relates to movement over ecosystem boundaries (Leroux and Loreau 2008, Allen and Wesner 2016) I suggest more work can be done to address prey availability in the context of large-scale inter-habitat prey fluxes, a little studied but important ecological process that has been disrupted by anthropogenic activity in many systems (Nakano and Murakami 2001). As human populations grow and more habitats

are simplified or eliminated, important inter-habitat prey fluxes that support biodiversity and food webs may be lost before they are found.

Table 3.1. The weighted mean White Ibis foraging depths in sloughs over 61 days of observation (28 February – 28 April 2017) in three replicate wetlands at the Loxahatchee Impoundment Landscape Assessment (Palm Beach County, Florida, U.S.A.). Each wetland progressively dried and the depth ranges over the entire observation period are listed in the last columns. The standard deviation reported is for the measured spatial variation within each slough from the depth measurements taken in each slough.

Wetland	Weighted Mean Slough Depth (cm)	STDEV	Depth Range Over 61 Days (cm)
M1	28.6	5.1	7.0 – 40.9
M2	26.4	3.6	5.0 – 37.6
M3	32.5	5.0	10.2 – 44.1

Table 3.2. White Ibis densities and depth conditions for the five days of most active foraging in each wetland (80- 89% of all White Ibis activity per wetland) from all 61 days of observation (27 February – 28 April 2017). The mean water depths and fraction of the slough ≤ 19 cm were calculated from the ground-measured depths and spatial variation in each wetland. Depth measurements in the slough were calculated using n=59, n=61, n=51 points (M1, M2 and M3 respectively), and using n=24 points on ridges in every wetland.

Wetland	White Ibis Density (#/ha)	% of All Foraging	Slough Depth (cm)	% Slough ≤ 19 cm	Ridge Depth (cm)	Date
M1	25.0	49	31.5	0	10.4	3/16
	8.9	18	30.9	2	9.8	3/19
	2.5	5	29.9	2	8.9	3/20
	2.5	5	16.8	66	-4.3	4/8
	1.7	3	19.6	54	-1.5	4/5
M2	19.1	36	31.1	0	10.2	3/17
	15.7	30	22.8	23	2.0	3/31
	3.8	7	31.1	0	10.2	3/18
	2.5	5	16.7	75	-4.1	4/10
	1.5	3	16.7	75	-4.1	4/9
M3	18.1	29	31.3	0	4.6	3/16
	15.8	25	35.0	0	8.2	3/11
	7.3	12	22.8	25	-4.0	4/3
	7.3	12	34.7	0	7.9	3/13
	7.2	12	40.8	0	14.0	3/2

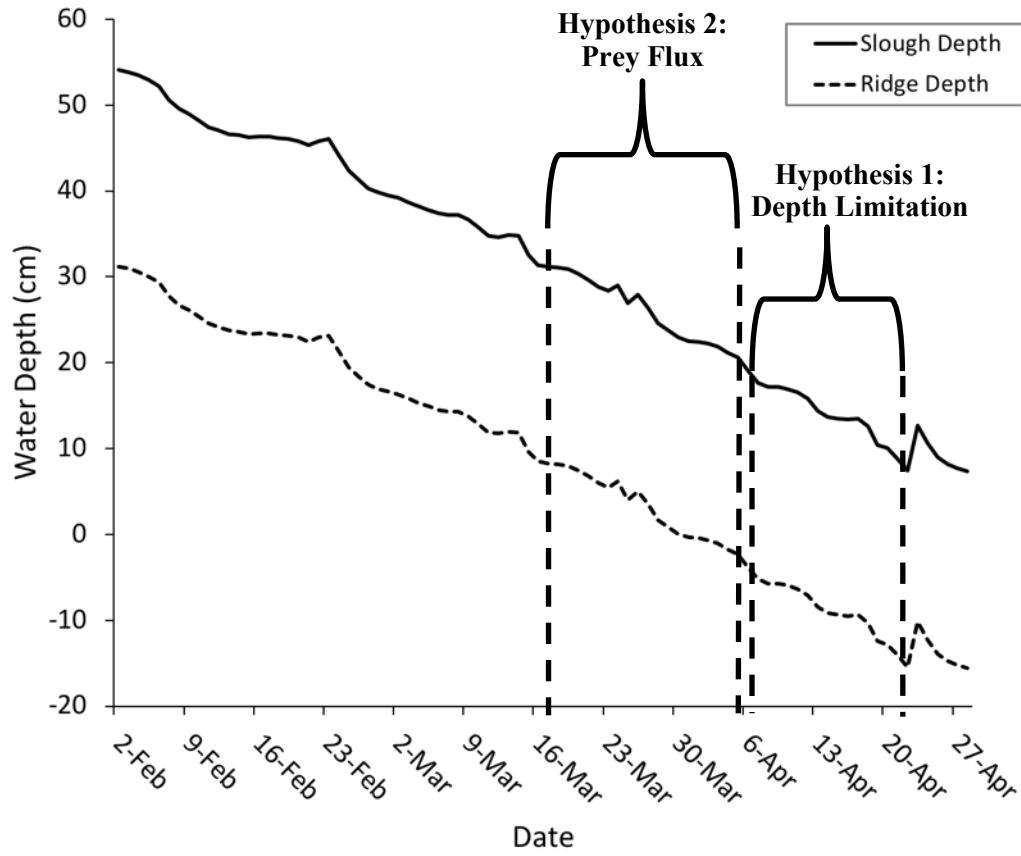


Figure 3.1. Dry season hydrographs of water depths (cm) in adjacent ridge and slough habitats and a graphical contrast of predicted White Ibis foraging depths in sloughs according to two different hypotheses. The depth limitation hypothesis was based on strict depth limits, ibis forage at energetically ideal (or typical) foraging depths (9 -19 cm slough depths) as reported by foraging observations in the literature. The prey flux prediction was based on previous observations of peak crayfish densities when crayfish prey move downgradient from ridges to sloughs (an average of 1-11 cm ridge depths and 20 - 32 cm slough depths) (Cook et al. 20014).



Figure 3.2. Aerial image of two of four 8-ha replicate wetlands at the Loxahatchee Impoundment Landscape Assessment. The camera observation areas are highlighted within the slough. Each replicated wetland contains tree islands, ridges and sloughs. The ridge elevations are 20-26 cm higher than the sloughs, depending on the wetland.

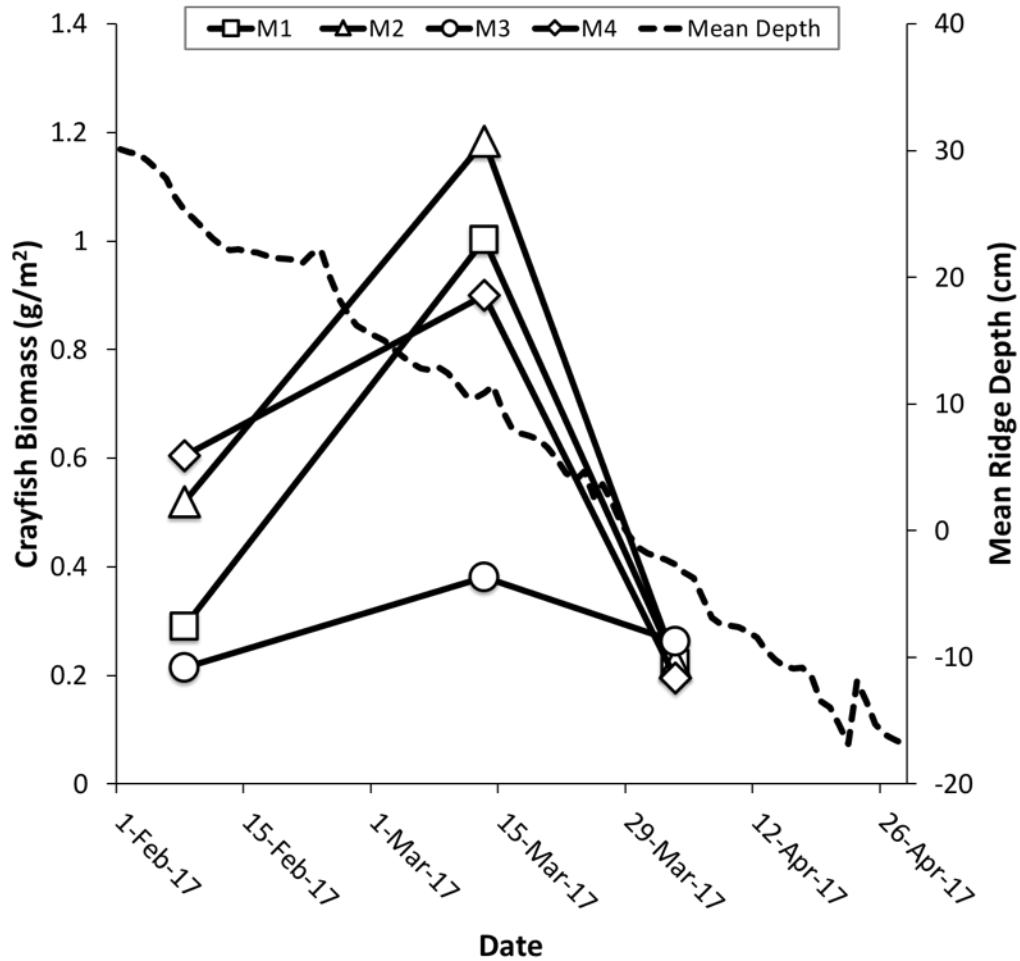


Figure 3.3. Mean crayfish biomass density (g dry mass/ m², n = 7 randomly placed throw traps each session) in sloughs over all three sampling sessions in the dry season of 2017. Mean water depth on ridges is plotted on the secondary y-axis. The ridges had an average of 8-12 cm of water throughout the second sampling session, with M3 ridges 4 cm shallower than the other wetlands due to a greater ridge elevation (4 cm higher than the other wetlands).

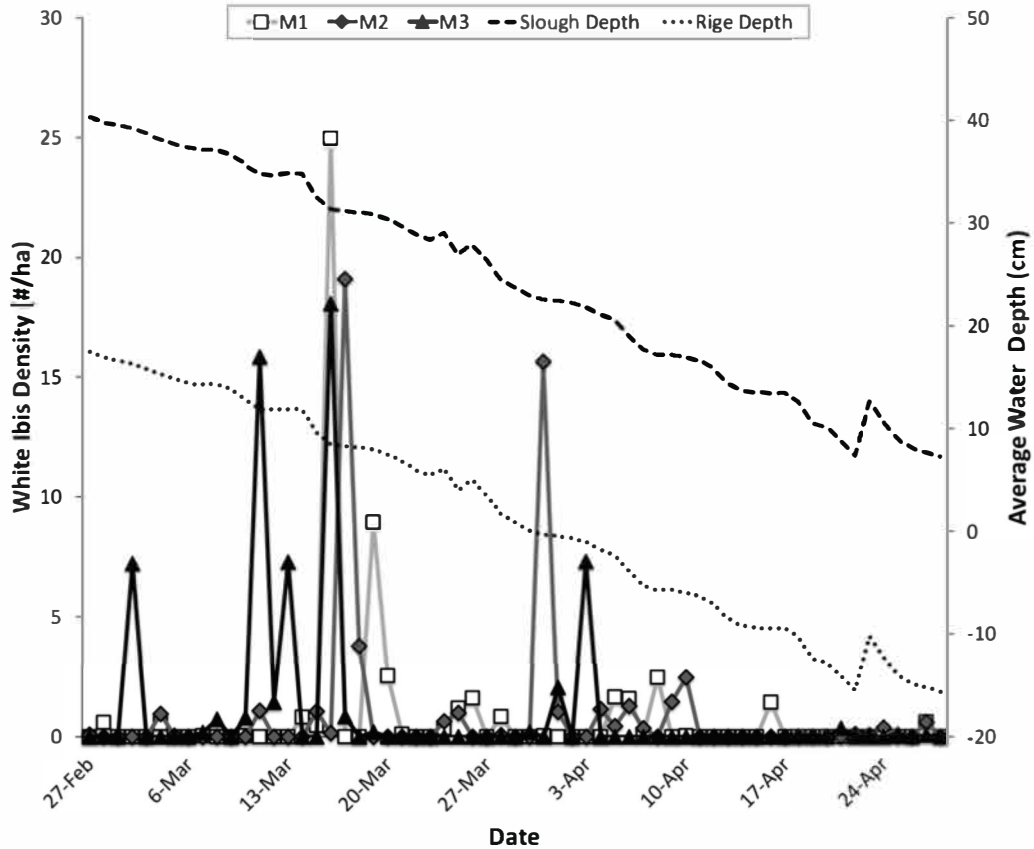


Figure 3.4. Average daily White Ibis density in shallow sloughs of the three replicate wetlands at the Loxahatchee Impoundment Landscape Assessment over a 61-day period of observation. Mean water depth in sloughs is plotted on the secondary y-axis. The adjacent ridges were completely dry (0 cm) between March 27 and April 4, with ridges in M3 drying earliest.

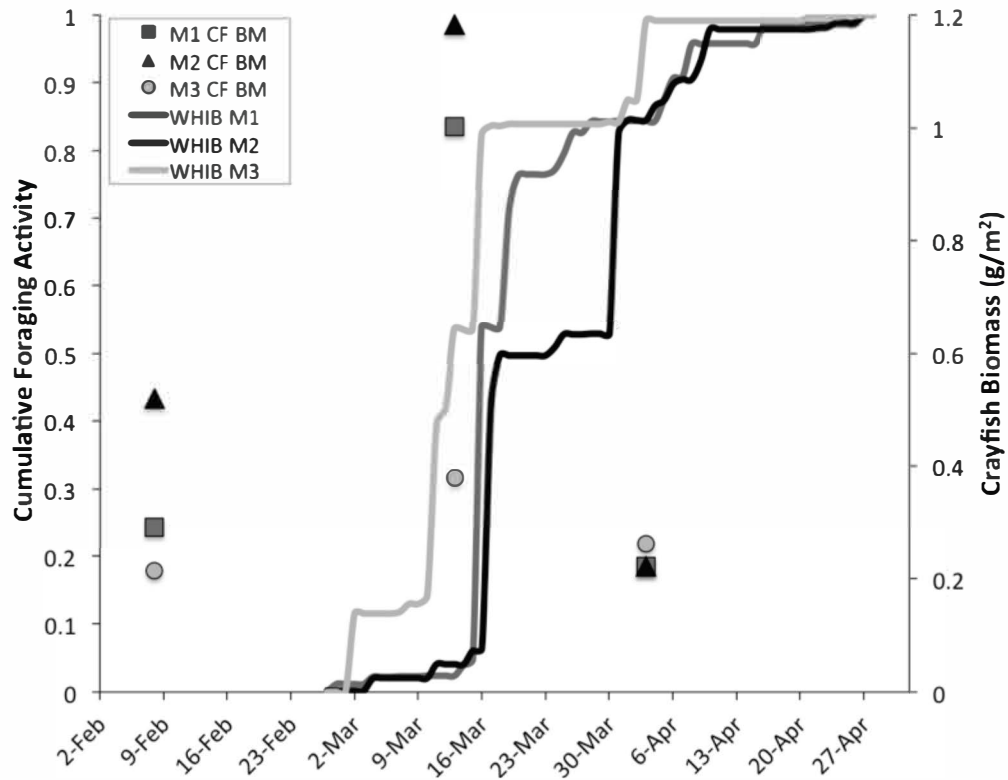


Figure 3.5. The accumulation of White Ibis foraging activity over the 61-day observation period. Mean crayfish biomass (g dry mass /m²) in the sloughs was plotted for the three wetlands (secondary y-axis).

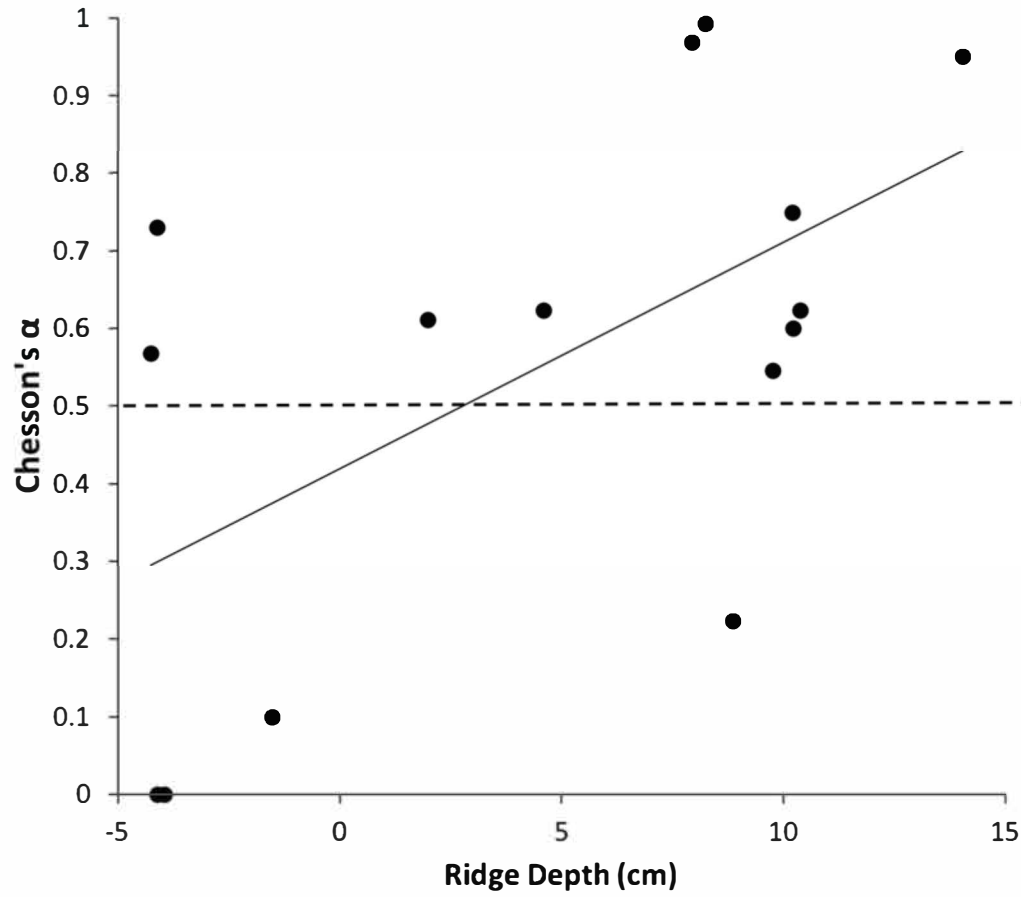


Figure 3.6. Chesson's selectivity (α) for the edge of the slough (1.65-m border along the ridges) versus ridge depth for the 15 days of highest White Ibis foraging activity. α -values > 0.5 indicate preference for the edge.

APPENDIX C

As a comparison analysis to crayfish prey dynamics, fish prey biomass in the slough were quantified using 1-m² throw trap sampling (Dorn et al. 2005, Dorn and Cook 2015), at three separate time periods during the dry-down (8 February – 10 February, 13 March -17 March, and 3 April – 7 April). I created a stratified random sampling method in QGIS 2.18 to sample seven locations within each shallow slough during each of the three sampling periods for a total of 28 throw traps per sampling period, each year. Each sampling point was at least 5 m away from the next in order to increase the independence and spatial coverage of the point estimates.

Average fish (>2 cm SL) biomass (per m²) was calculated to determine the absolute increase in fish densities and biomass in all macrocosms (Cook et al. 2014, Dorn and Cook 2015). Fish were euthanized with MS222, preserved in formalin and returned to the lab. All prey items were identified, counted and measured in the lab. The biomass of fish were calculated for each trap using lengths and length-dry mass regressions (Dorn et al. 2011, unpublished data). Total biomass per trap was quantified as g dry mass/ m². To statistically examine variation in fish biomass dynamics through time, I analyzed mean fish biomass using time factors (sampling session, within-subjects effects) with repeated measures ANOVA (linear mixed-effects model in R, v.3.4.0). The specific temporal dynamics were then interpreted graphically.

I graphed fish > 2 cm SL biomass densities over all three sampling sessions using throw trap sample data (Fig. 1). There was a visible increase in fish density in M1 and M4

from February (when depths are well above the ridge height) to March. Concentration effects in M2 and M3 were weak (February to March), and biomass in M3 increased from March to April (Fig. 1). There was no effect of time on fish > 2 cm SL biomass ($F_{2,6} = 2.88$, $p = 0.13$) in the sloughs.

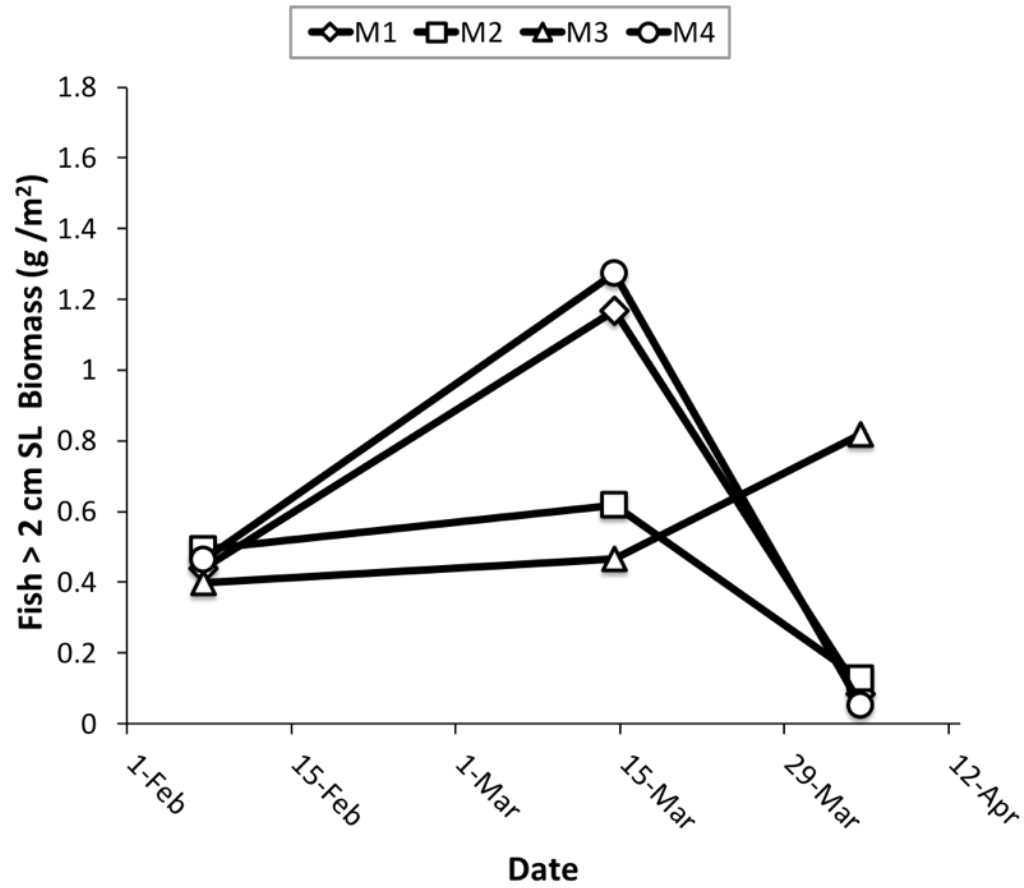


Figure 3.1.C. Mean fish biomass density ($\text{g} \cdot \text{m}^{-2}$, all fish > 2 cm SL, $n=7$ randomly placed throw traps each session) in sloughs over all three sampling sessions. The ridges dried just before the second sampling session in all macrocosms except perhaps in M3.

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