

DRY SEASON PREY TROPHIC CONCENTRATIONS

Deliverable 2.2: Annual Report 2017

Cooperative Agreement Number: W912HZ-15-2-0006, U.S. Army Engineer Research and Development Center

Principal Investigator: Dale E. Gawlik
Research Coordinator: Michelle L. Petersen
Research Assistant: Camille Herteux
Environmental Science Program
Florida Atlantic University
777 Glades Road, Sanson Life Science
Boca Raton, FL 33431
dgawlik@fau.edu
Office (561) 297-3333, fax (561) 297-2749



Table of Contents

Executive Summary	3
Introduction	4-5
Methods	5-11
Sampling design.....	5
Field methods	9
Lab methods	11
Results	13-18
Hydrology and Wading bird nesting.....	13
Sample size	13
Prey species composition.....	13
Habitat availability.....	16
Discussion	20-21
Prey composition.....	20
Habitat availability	20
Wading birds	20
Acknowledgments	21
Literature Cited	21-22

Executive Summary

This annual report contains data and analyses for the 2017 dry season, as well as comparisons of this period to the previous years starting in 2005. The objectives are to provide spatial patterns of aquatic fauna densities, provide data on inter-annual variation, and correlate fauna densities with local site characteristics, and hydrology. From 14 February 2017 to 01 June 2017, we collected 169 random throw-trap samples at 88 random sites, distributed among 10 Landscape Sampling Units (LSU) (Table 1; Fig. 1). All 10 LSUs were sampled completely (5 Primary Sampling Units). Additionally, we characterized random sites along 88 transects.

We collected 5,505 aquatic animals identified to 42 taxonomic groups. Mean prey density was 35.16 prey/m² with a maximum prey density of 207 prey/m². Greater than average water levels experienced in 2016 allowed us to sample two infrequently sampled LSUs within Everglades National Park (LSU 3536 and 39), these LSUs historically dry very early in the season and contain lower than average prey densities. The inclusion of these LSUs in the data along with lower than average recession rates likely contributed to mean prey density for 2016 being 32% lower than in 2014 (the last year sampled) and 49% lower than all years sampled. Total biomass of all specimens was 763 g with fish species contributing about 62% of the total biomass. Mean prey biomass at random sites was 4.5 g/m², which is 15% less than 2016, and 57% lower than all years sampled. The most abundant species were grass shrimp (*Palaemonetes paludosus*), mosquito fish (*Gambusia holbrooki*), and bluefin killifish (*Lucania goodei*) encompassing 68% of all individuals captured.

Although prey densities we measured were low, the amount of foraging habitat (81% of landscape; Fig. 6, Fig. 7) that became available to wading birds was almost certainly responsible for the high wading bird nesting. There were 174% more nests than in 2016, and 61% more nests than the 10-year average for all wading bird species. The high nest abundance is indicative of the moderate water levels at the start of the breeding season coupled with steady water recession experienced in the Everglades during the nesting season, which likely increased availability of suitable foraging habitat and significantly increased nest effort timing to much earlier in the season. Wood Storks, which require more than 3 months of drying conditions to nest successfully, initiated the earliest egg laying dates (early January) in recent decades and is considerably earlier than in 2016 (late March).

Introduction

One of the key sets of hypotheses underlying the Everglades restoration is collectively termed the trophic hypothesis. It states that the collapse of wading bird nesting colonies in the southern Everglades is attributed to declines in population densities and seasonal concentrations of marsh fishes and other aquatic prey organisms (RECOVER 2006, Trexler and Goss 2009). Restoration of natural hydrologic conditions is predicted to re-establish distributions of prey densities and concentrations across the landscape that in turn will support the return of large, successful wading bird nesting colonies to the southern Everglades.

The trophic hypothesis rests on the premise that (1) hydrology controls the production and availability of aquatic prey animals, and (2) food is limiting nesting populations of wading birds. This premise has been articulated as the prey availability hypothesis (Gawlik 2002, Frederick et al. 2009). The evidence for hydrologic control on aquatic prey production is strong (Loftus and Eklund 1994, Trexler et al. 2002, DeAngelis et al. 2005, Ruetz III et al. 2005, Trexler and Goss 2009). Populations of different prey fish species tend to peak after 1-8 years of continually flooded marsh (Trexler et al. 2002, Trexler et al. 2005), with the fish and macroinvertebrate community showing at least three different periods of responses that correspond to life-history strategy (Trexler and Goss 2009). Hydrologic patterns also affect the populations of aquatic predators, which influence the density of small fishes (Kushlan 1976, Chick et al. 2004) as well as affecting competitive interactions (DeAngelis et al. 2005). Increased nutrient levels increase fish production (Turner et al. 1999), but increased nutrients also increase plant density, which can reduce prey availability (Crozier and Gawlik 2002). There is a poor understanding of how wet season production of aquatic prey species is related to small-scale concentrations of prey a few months later during the dry season. This is a critical uncertainty in our knowledge because it is the concentrations of prey on which wading birds are feeding and that are likely linked to nesting measures in the Monitoring and Assessment Plan (MAP) of the Comprehensive Everglades Restoration Plan (CERP).

There is considerable indirect evidence to suggest that nesting wading bird populations in the Everglades are limited by food (Kahl 1964, Kushlan et al. 1975, Kushlan 1986, Frederick and Collopy 1989, Bancroft et al. 1990, Frederick and Spalding 1994, Frederick and Ogden 2001). These studies did not measure prey availability directly, but rather examined correlations between a wading bird nesting parameter and a hydrologic pattern, assuming that hydrologic patterns control either prey production or availability (Herring et al. 2010). The strongest relationships are that birds often fail to nest or abandon nests following a reversal in the seasonal drying trend, and that birds fail to nest if water levels are extremely high (Frederick 1995). Frederick and Ogden (2001) found a correlation between wading bird nest effort and hydrologic patterns, which they also interpreted as being controlled by food availability. However, the hydrologic pattern that produced the highest nest numbers was a drought, which reduces fish populations to their lowest levels (Loftus and Eklund 1994, Trexler et al. 2002) with most individuals being at their smallest body size. This kind of uncertainty makes predictions of wading bird responses for CERP highly uncertain. If hydrologic patterns, fish population size, and wading birds are indeed linked, then the relationship is clearly not linear and other factors must mediate it under certain conditions.

Gawlik (2002) proposed a conceptual model with a list of factors that could modify the effect of prey populations on wading birds. The model clearly depicts how factors that affect regional prey populations might only partly affect the *availability of prey* for wading birds, which is the variable to which birds respond. Although the terms food or prey “availability” and “density” are often used interchangeably, the terms are quite different (Morrison et al. 1992). It is possible that factors affecting the concentration of prey could swamp factors that produce large prey population sizes (Gawlik 2002) thus producing a periodic disconnect between wading bird nesting and prey population size.

This project avoids the disconnect between prey population sizes and wading bird nesting by directly measuring the variable (prey concentrations) to which wading birds are responding. The work is described in the MAP (Section 3.1.3.11). This project builds on 10 years of data from the previous MAP Fauna Concentration Study (Botson and Gawlik 2010), which provided the first quantitative support for the link between prey concentrations and wading bird nesting (Gawlik et al. 2009, Herring et al. 2010).

The goals of this project are to monitor seasonal prey concentrations and to more clearly define the linkage among hydrologic patterns, fish populations, and wading birds. The terms “maximum prey density” or “prey concentrations” represent the fish and macroinvertebrate (i.e., the crayfish, apple snail, and grass shrimp) concentrations in isolated patches of water during the seasonal dry down. The term “Fish Population Studies” refers to the “Aquatic Fauna Regional Population” monitoring project conducted by Joel Trexler (FIU) under MAP

This project is designed to meet the following objectives:

- 1) Evaluate the spatial patterns of maximum aquatic fauna densities in the landscape.
- 2) Evaluate inter-annual variation in maximum aquatic fauna densities.
- 3) Evaluate correlates between maximum aquatic fauna densities and local site characteristics, hydrological patterns, and regional aquatic fauna population size.
- 4) Evaluate correlates between maximum aquatic fauna densities and wading bird foraging and nesting patterns.
- 5) Provide summary analysis of wading bird foraging and nesting patterns in response to aquatic fauna densities and hydrologic changes.

Methods

Sampling Design

The project design is based on sampling theory, the purpose of which is to make sampling more efficient (Cochran 1977). The basis for the design is described in detail in Gawlik et al. (2005). Maximizing efficiency with complex designs requires careful attention to the estimation of means and variances, the formulas for which are a primary focus of sampling theory (Cochran 1977, Eberhardt and Thomas 1991). Estimates of variability in fauna concentrations came from the 2004 pilot study and are reported in the Final Pilot Project Report (Gawlik et al. 2005).

As in previous years, we used a multi-stage sampling design (Cochran 1977) with landscape units (LSU), primary sampling units (PSU), sites, and throw-trap subsamples (TT; Table 1). When separate estimates of maximum prey density were calculated for each LSU the data was analyzed in a 3-stage structure with PSU, sites, and TT as first, second, and third stages, respectively. When a pooled estimate of maximum prey density was calculated for the set of predetermined LSUs, data were analyzed in a 4-stage structure with the addition of a LSU stratum as the first stage. Sampling in a predetermined set of LSUs rather than from a randomly drawn set focused the sampling effort on those LSUs where the information was needed most but it does not allow us to calculate the variance for a single estimate of maximum prey density for the entire Everglades landscape. If at a later date it is necessary to make inferences to the entire Everglades landscape, it will simply require that sampling take place in a random set of LSUs drawn from the total set that define the study area. The existing design and variance formulas will still apply.



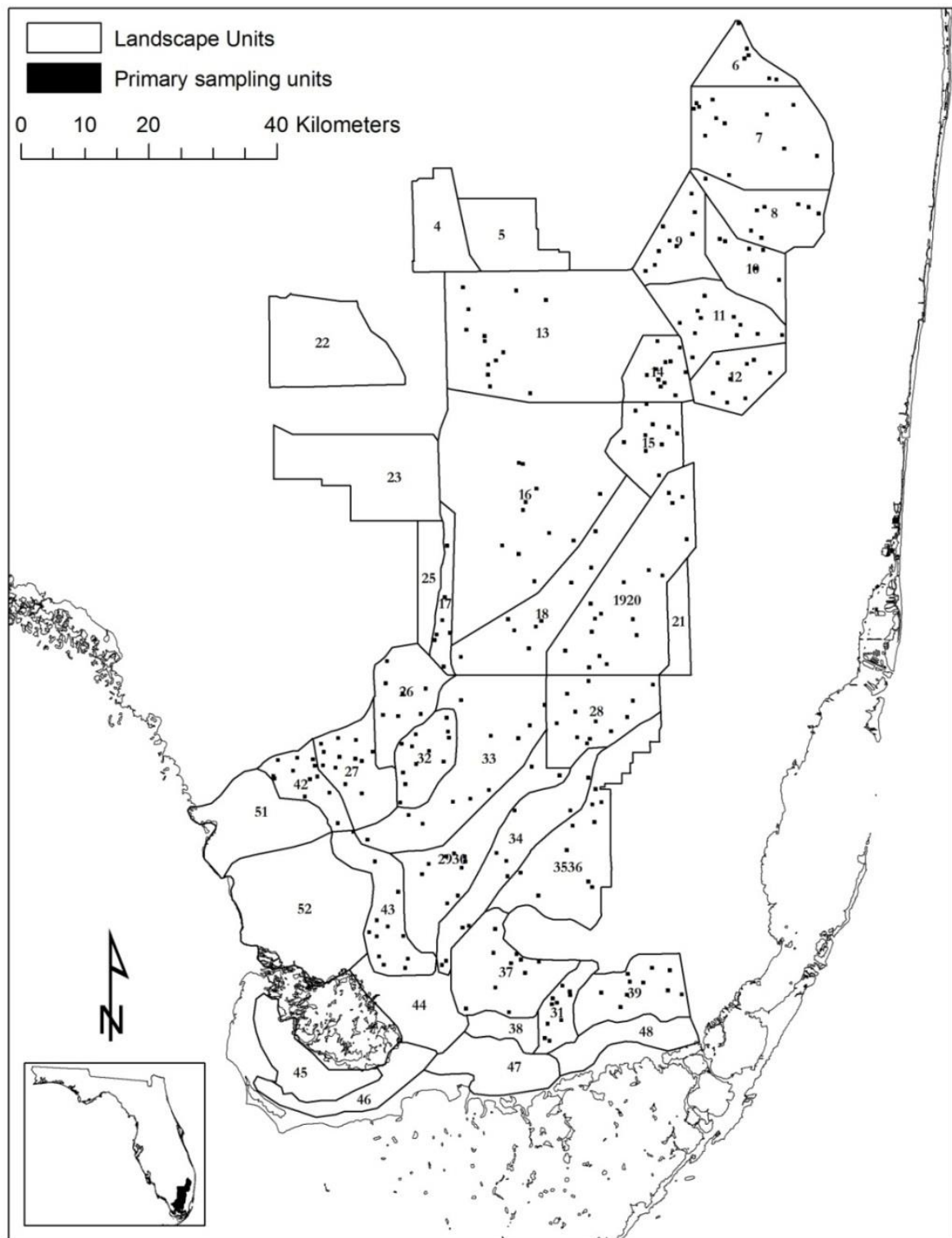


Figure 1. Full set of landscape units from which random units were drawn.

Table 1. Target sample sizes and design structure

	Number of units per strata (total 500 potential TT/year)	Unit size	Repeated measures or single random sampling
Landscape Subunits	25	Multiple km	Repeated
Primary Sampling Units	5	500 m ²	Repeated
Sites	2	2 m to 100 m ²	Single random
Throw-trap Subsamples	2	1 m ²	Single random

The spatial extent of this study includes Everglades National Park (ENP), Big Cypress National Preserve, the Water Conservation Areas (WCA) and the C-111 basin, a total of 9759 km² (ArcGIS 10.2). Landscape Units were delineated by RECOVER personnel based primarily on hydroperiod and vegetation, which approximate a physiographic region. Nine of these LSUs (Fig. 1) are in ENP. LSU 19 and 20, 29 and 30, and LSU 35 and 36 were combined based on comments from RECOVER personnel and other scientists familiar with the areas. Since the onset of the study, the original pool of LSUs was reevaluated, which resulted in the removal of LSUs 6, 8, 10, 12, 14, 17, and 37 from our sampling pool because they were not sampled regularly in the past. By focusing our resources and sampling effort we can collect more complete data that is of higher value than in the past. The current pool of 18 LSUs (4694 km²) are 7, 9, 11, 13, 15, 16, 18, 19, 20, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, and 39. Within each LSU, at least seven PSUs 500 m x 500 m in size were established at random locations using ArcGIS 10.2. Criteria for establishing the PSUs were that all points capable of comprising a 500 m² plot had an equal probability of being selected, PSUs could be adjacent but cannot overlap, and no portion of a PSU could be outside its respective LSU. Although only 5 PSUs were sampled within an LSU, the location of at least two additional PSUs were needed in the event one was found to be unsuitable habitat, such as a tree island, when it was visited in the field.



Figure 2. Photos of two sloughs in WCA 2A. The left photo depicts shallow water in sloughs and no water on ridges. Prey are not yet concentrated in refuges. The center photo shows a small (roughly 4 m diameter) refuge created by alligator movements. Less than one-third of the slough contained surface water. Prey density in the refuge was 1695 prey/m². Right photo shows a foraging flock of foraging utilizing a site meeting target conditions.



Within each PSU, the locations of 2 random points were generated. The closest suitable habitat to the random point marked the TT site. Suitable habitat is loosely defined as an area with sparse to moderate vegetation with less than one-third of its surface covered with water. These areas are represented by sloughs in the ridge-and-slough portion of the landscape (Fig. 2). Within each site, fauna were sampled from two random TTs. To characterize the physical features of sites, ancillary environmental data were measured along two 50-m transects which ran perpendicular to the direction of flow (Fig. 3).

Field Methods

Over time we have optimized our ability to detect when sites reach target sampling conditions by using the Everglades Depth Estimation Network (EDEN), field depth measurements from previous years, and aerial photos of PSUs. We calculated the difference between EDEN real-time daily stage readings on a given date from the stage reading on the dates a PSU was sampled in previous years. We also consulted the aerial photos and depth data taken at the same PSU on that date. Using this method, we were able to track from the lab, the conditions on the ground at all of our previously sampled PSUs. This approach drastically reduced our use of helicopter time. We also developed a hydroperiod map using EDEN which enabled us to identify the sequence in which LSUs dry down.

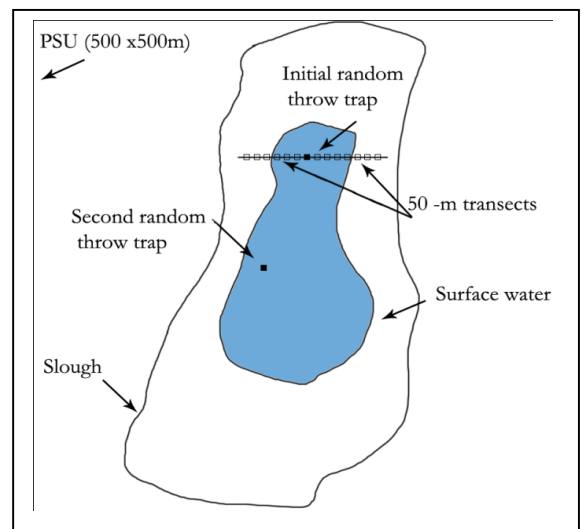
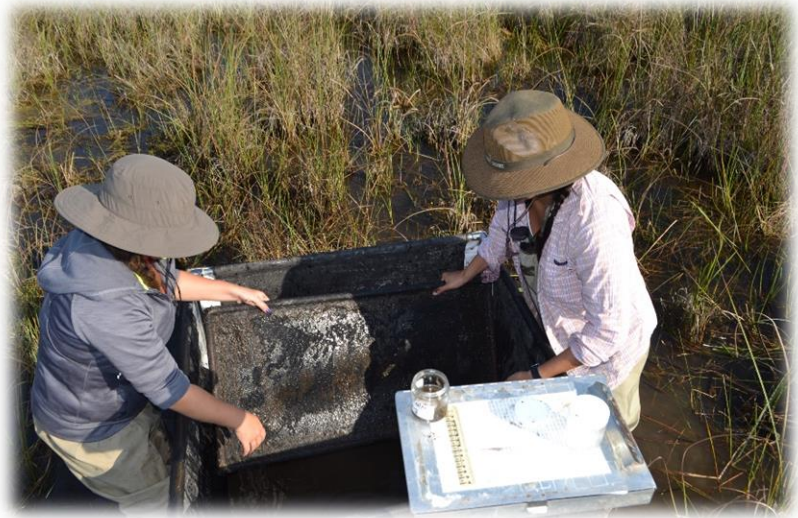


Figure 3. A schematic of the sampling components within a PSU.

During each prey sampling event (approximately weekly), we verified the suitability of habitat (shallow water and sparse vegetation) at a PSU thought to be at target water levels. We also noted areas with large flocks of foraging wading birds. Upon confirmation that the PSU was at target water levels, we visited two random points within the PSU in sequence. We flew 2-3 east - west transects across the PSU to identify the closest suitable habitat to each point. We recorded the percentage of suitable vegetation (i.e., vegetation that is sparse enough to be sampled with a throw-trap) and the percentage of suitable vegetation that has water present (collectively referred to as suitable habitat). Through repeated visits to sites we will eventually establish a relationship between the EDEN data and target depths which will allow us to optimize the sequence of visitation to sampling sites and maximize the number of sites sampled.

During the first 3 years of the project we did not sample in LSUs that we knew had already dried down within the season even if they were rewetted to an appropriate depth following a reversal. Our reasoning was that these areas were probably depleted of prey and were not reflective of the foraging habitat used by birds. Casual observations suggested that wading birds simply switched to neighboring LSUs that had not yet dried down. However, we realized in 2008 that in some instances previously dried regions that have been rewetted are all that is available within the foraging range of many colonies, and are thus reflective of what is available to wading birds. Therefore, we now sample these areas but we account for the difference in drying conditions with a new variable which specifies whether samples were collected before or after a site had dried down.

The boundaries of the PSU and the real-time location of the helicopter are displayed simultaneously with the Archer 2 Field PC mobile GIS system equipped with ESRI's ArcPad mobile mapping software. We recorded the location of the closest suitable habitat to each random point and were dropped off by helicopter just downstream from that point to avoid disturbing the sampling site. We selected a random TT within the suitable habitat by



standing at the location and estimating the minimum and maximum bearing and distance that encompassed the suitable habitat. Using a random number table, we selected a random bearing and distance that was in the predetermined range. Once at the TT location, we tossed the throw trap to the N (standardized direction). If the N direction is outside the range of suitable habitat, then we toss the trap to the east or west. We determined the location of the second random TT by selecting a random direction and random distance (≥ 10 m) from the first TT site, with the restriction that it must occur within the suitable habitat.

After tossing the throw-trap, we measured enclosed vegetation and then removed it from the trap to facilitate collection of aquatic fauna. We removed all aquatic fauna from the throw-trap by passing a 100 cm x 40 cm bar seine through the water column within the trap until we had five consecutive sweeps with no fish or invertebrates. We transferred captured fauna <15 cm in length directly from the bar seine to jars containing a solution of water and MS 222, a rapid euthanizing agent. Larger fauna we identified, measured, and released. Once the trap was cleared, we stored all samples on ice until we arrived back at the lab and transferred them to a solution of Prefer fixative to preserve sample tissues. Once the samples were fixed (approximately 1 week), we transferred them to a 70% ethanol solution for storage until they could be identified, measured, and weighed. We conducted all sampling in accordance with the FAU Institutional Animal Care and Use Committee (Protocol #A16-45).



In previous years, we characterized the physical features of a site by measuring a suite of variables (including total water depth, flocculent layer thickness, and emergent/submerged vegetation structure) in 0.5 m x 0.5 m quadrants every 5 meters along a 100 m transect. Due to budget cuts in 2012, we restricted our measurements to total water depth taken every 1 m. All 100 m transects were centered on the first TT at each site and upon reaching a ridge, we discontinued the transect after three measurements (15 m), or upon reaching a tree island, discontinued the transect after one measurement (5 m). Thus, some transects were less than 100 meters. The orientation of transects is perpendicular to the direction of water flow if it is apparent, otherwise it is east and west if north of Tamiami Trail, and northwest and southeast if south of Tamiami Trail.

Lab Methods

In 2004, 2005, and 2006 we identified, weighed to the nearest 0.01 g, and measured total length (tip of snout to tip of tail) in millimeters for each individual prey item (fish or invertebrate). Starting with prey data collected during the 2007 dry season, we also measured standard length (snout to posterior end of the last vertebra). Beginning in 2010 we measured only standard length for the most common species for which we had an adequate sample size to formulate a regression between standard and total length. We now have how 21 species with an adequate sample size ($N > 30$) to estimate total length from standard length. Invertebrates with irregular body shapes (e.g., shrimp) were measured from the tip of the mandibles to the tip of the tail. Each animal was identified using a variety of keys, field guides, and online databases. Animals that could not be positively identified were preserved and labeled as unknown with a unique identifying number for each species. Unknowns were subsequently sent to experts at Florida International University or U.S. Geological Survey to confirm identification.

Statistical Methods

We used an Information Theoretic Approach to investigate competing models (Burnhan and Anderson 2002). We developed an *a priori* set of candidate models based on maximum prey

abundance of large fish, crayfish, and shrimp (≥ 2 cm; Klassen et al. 2017), habitat availability, timing of prey availability and interactions (Table X). To identify which of our *a priori* models were most parsimonious, we used Akaike's Information Criteria for small sample sizes (AICc). We computed ΔAICc values to determine the separation between the best model and candidate model set within 4 AICc units of the best model. We calculated model probabilities (w_i) to gather additional support for the models. We calculated a likelihood version of the correlation coefficient for each candidate model to assess model fit (Anderson 2007).

We quantified the relationship between wading bird prey abundance and hypothesized

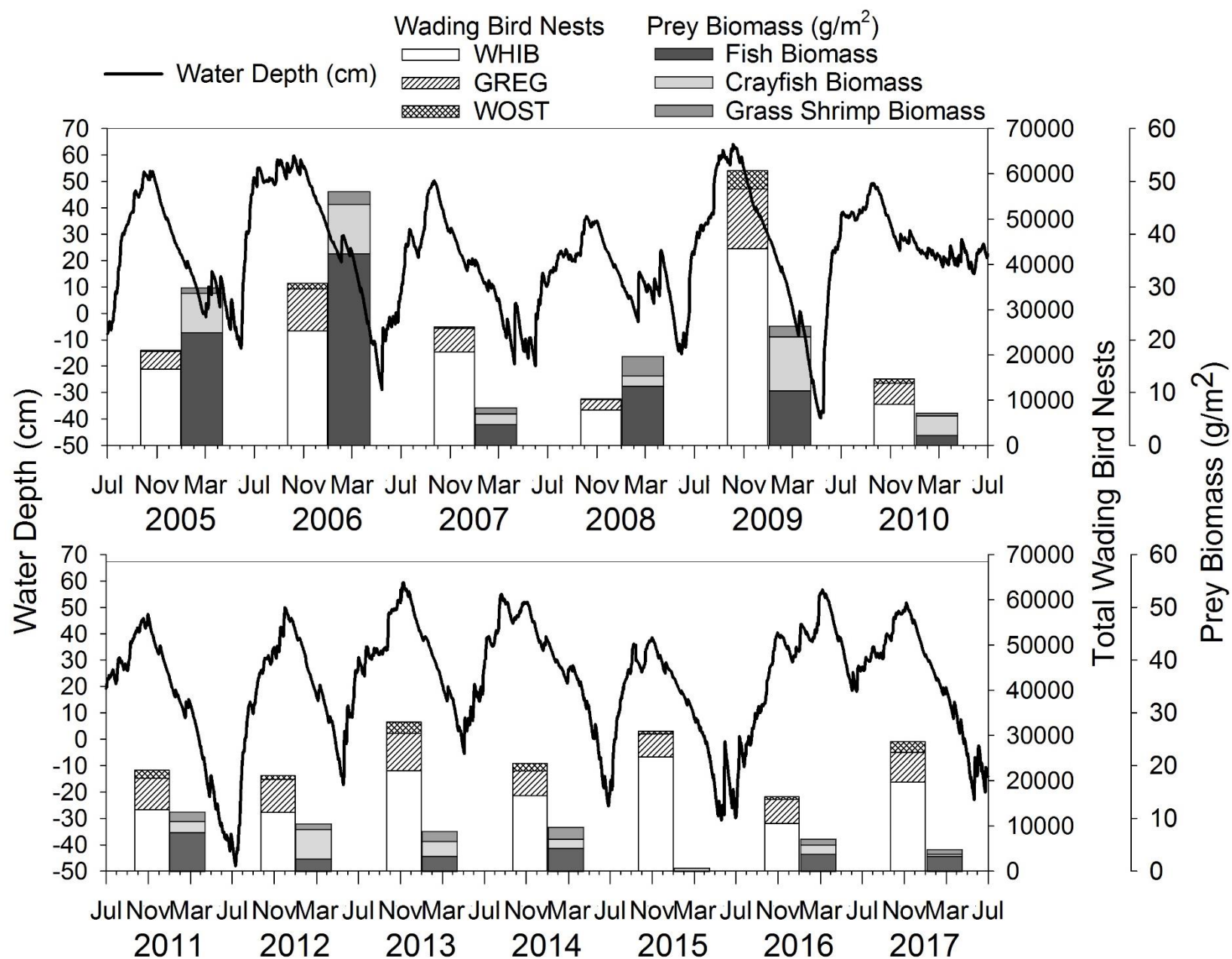


Figure 4. Mean water depth, number of wading bird nests and dry season prey biomass throughout the Florida Everglades from June 2005 to July 2017. Depth values represent the mean of 42,415 EDEN grid cells throughout most of the freshwater portion of the Everglades. (Note: 2015 prey biomass reflects only one day of data collection)

Results

Hydrology and Wading Bird Nesting

Hydrologic conditions and wading bird nesting effort differed considerably among years during 2005-2017 (Fig. 4, Table 2).

Water levels were exceptionally high during the 2016 dry season. Record breaking amounts of rainfall was experienced from November through April averaging nearly 1-foot above average over the entire Everglades system. (Fig. 4, Fig. 6). Only 36% of the landscape became available for wading bird foraging, and the timing of habitat availability was earlier than in past years, but was halted by heavy rainfall in January (Fig. 6, Fig. 7). Nest effort in 2016 was relatively poor as compared to the 12-year average, and the lowest effort since 2010 (Fig. 4, Table 2). White Ibis nest efforts decreased by 58% since 2015, while nest effort for small herons increased by 35% in WCAs and ENP combined (Cook 2017).

Table 2. Nesting effort for 2005-2016 WCAs and ENP combined. Species are: Great Egret (GREG), White Ibis (WHIB), Wood Stork (WOST), and small herons and egrets (species include Snowy Egret, Little Blue Heron, and Tricolored Heron) (SMHE).

Year	GREG	WHIB	WOST	SMHE	Total
2005	3,893	16,845	273	3,003	24,014
2006	9,265	25,277	1,314	10,453	46,309
2007	5,193	20,661	340	464	26,658
2008	2,308	3,731	145	1,560	7,744
2009	13,211	43,415	4,063	5,092	65,781
2010	4,627	9,047	1,000	2,323	16,997
2011	6,971	13,599	1,727	1,618	23,879
2012	7,290	13,022	820	2,032	22,819
2013	8,208	22,226	2,511	684	33,629
2014	5,391	16,725	1,735	819	24,670
2015	5,069	25,256	648	812	31,472
2016	5,291	10,545	580	1,247	17,663
2017	6,607	19,677	2,359	925	28,643

Sample Size

In 2017, we sampled 10 LSUs from our pool of 18 LSUs (Fig. 1). We collected 169 random throw-trap (TT) samples (Table 3). Random samples were collected at 45 PSUs and 88 sites. Additionally, microtopography of each of the 88 sites was characterized by depth transects.

Table 3. Number of throw-trap samples and distribution among LSUs and PSUs.

LSU	# PSUs	# Sites	# throw-traps
7	5	10	19
9	5	10	19
13	1	1	2
16	5	9	16
18	5	10	20
31	5	10	19
33	5	10	19
34	4	8	16
1920	5	10	19
2930	5	10	20

Prey Species Composition

In 2016 we collected a total of 5,436 aquatic animals from 40 different taxa (Table 4). Grass shrimp (*Palaemonetes paludosus*), bluefin killifish (*Lucania goodie*), and mosquito fish (*Gambusia holbrooki*) were the most abundant species encompassing 68% of all individuals captured. Total biomass of all specimens was 731.4 g with crayfish species contributing 24% of the total biomass. This proportion is only 6% less

than average, 4% greater than 2014, and 22% less than 2012, which had the highest percentage of crayfish biomass in the study (Fig. 4, Table 4).

Table 4. Species captured in throw-traps in 2017. N is the total number of individuals captured.

Common name	Scientific name	N	Biomass (g)
Grass shrimp	<i>Palaemonetes pauludosus</i>	2153	146.55
Bluefin killifish	<i>Lucania goodie</i>	902	96.17
Mosquito fish	<i>Gambusia holbrooki</i>	656	62.32
Alligator flea	<i>Pelocoris femoratus</i>	364	8.93
Least killifish	<i>Heterandria formosa</i>	289	12.63
Dragonfly	<i>Anisoptera</i>	213	36.03
Golden topminnow	<i>Fundulus chrysotus</i>	140	52.83
Crayfish	<i>Procambarus spp.</i>	111	67.03
Everglades pygmy sunfish	<i>Elassoma evergladei</i>	100	13.14
Bluespotted sunfish	<i>Enneacanthus gloriosus</i>	93	64.71
Flagfish	<i>Jordanellae floridae</i>	81	29.61
Sailfin molly	<i>Poecilia latipinna</i>	59	19.01
Marsh killifish	<i>Fundulus confluentus</i>	47	21.47
Predacious diving beetle	<i>Dytiscidae</i>	42	3.41
Water boatman	<i>Corixidae</i>	33	0.22
African jewelfish	<i>Hemichromis letourneauxi</i>	23	20.73
Giant water bug	<i>Belostomatidae</i>	18	5.16
Water scavenger beetle	<i>Hydrophilidae</i>	12	0.40
Redear sunfish	<i>Lepomis microlophus</i>	9	3.81
Unknown invertebrate		9	0.56
Spotted sunfish	<i>Lepomis punctatus</i>	7	14.98
Sheepshead minnow	<i>Cypripodon variegatus hubbsi</i>	6	2.42
Taillight shiner	<i>Notropis maculatus</i>	6	2.40
Unknown fish		6	0.19
Leech	<i>Hirudinae</i>	5	0.64
Tadpole	<i>Anura</i>	5	0.77
Unknown killifish		5	0.09
Beetle	<i>Coleoptera</i>	4	0.04
Coastal shiner	<i>Hoplosternum littorale</i>	4	0.31
Jaguar cichlid	<i>Odonata</i>	4	1.26
Damselfly	<i>Zygoptera</i>	4	0.09
Dollar sunfish	<i>Lepomis marginatus</i>	3	5.91
Lake chubsucker	<i>Erimyzon sucetta</i>	3	21.10
Pike killifish	<i>Belonesox belizanus</i>	3	0.61
Tadpole madtom	<i>Noturus gyrinus</i>	3	2.73
Unknown sunfish	<i>Lepomis spp.</i>	3	0.46
Brown bullhead	<i>Ameiurus nebulosus</i>	2	2.28
Chain pickerel	<i>Esox niger</i>	2	0.59
Mayan cichlid	<i>Cichlasoma urophthalmus</i>	2	6.66
Spider	<i>Arachnida</i>	2	0.04
Black acara	<i>Cichlasoma bimaculatum</i>	1	0.51
Warmouth	<i>Lepomis gulosus</i>	1	2.68
Total	-	5,436	731.41

Prey densities vary among locations across the Everglades due to topography, vegetative structure, management regimes, and hydrology. For this reason, we have broken down mean prey density for years sampled by the 7 general locations included in our sampling area (Fig. 5).

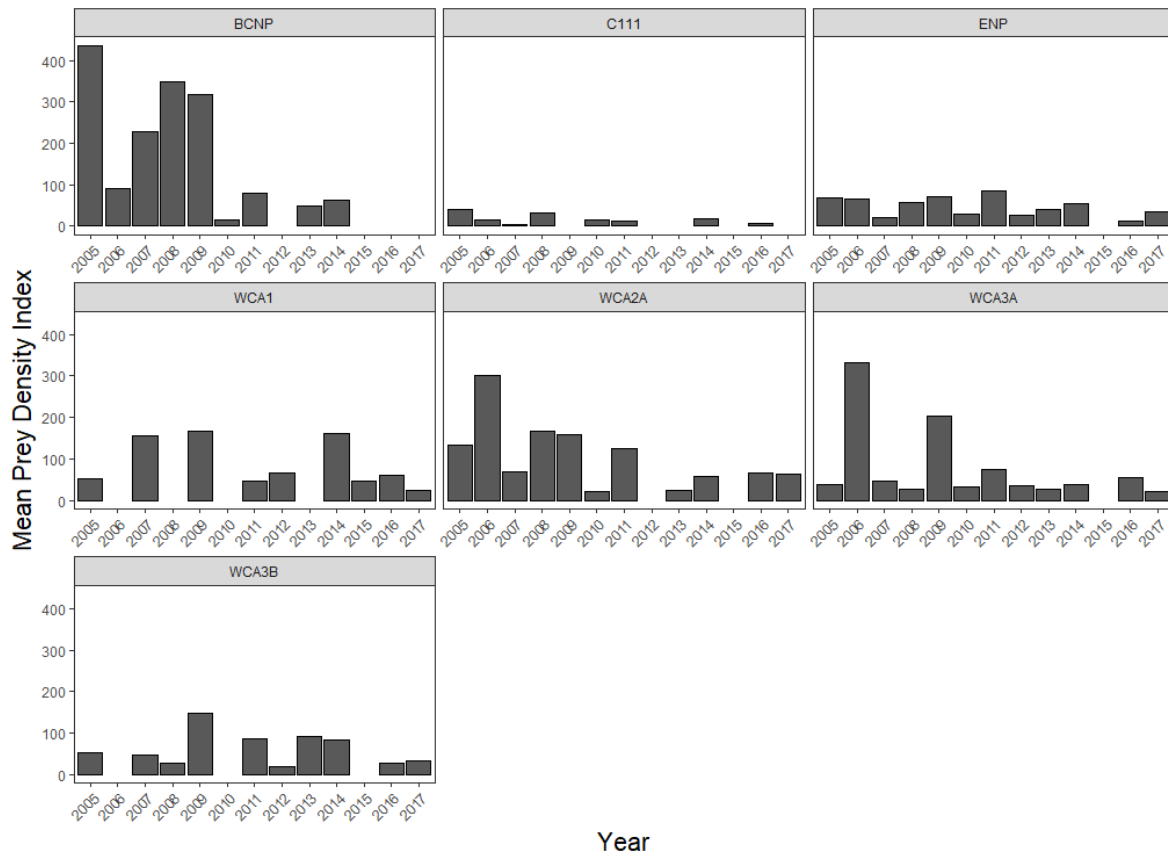


Figure 5. Mean prey density by year for each of the 7 general locations of the Everglades: Big Cypress National Preserve (BCNP), C-111, Everglades National Park (ENP), Water Conservation Area (WCA1, WCA2A, WCA3A, WCA3B). Years in which particular general locations were not sampled is expressed by the absence of a bar.

Habitat Availability

Available habitat for each dry season was calculated using data downloaded from EDEN, comprised of 42,415 400 m cells with daily water depth estimations (Figure 6). In 2017, 81% of the landscape became available as suitable foraging habitat. The system experienced much slower recession rates with greater than average rainfall (Figure 6). While the majority of the system never became available, areas that did become suitable were available either early in the dry season (Nov—Dec 2015) or in late March (Fig. 6, Fig. 9).

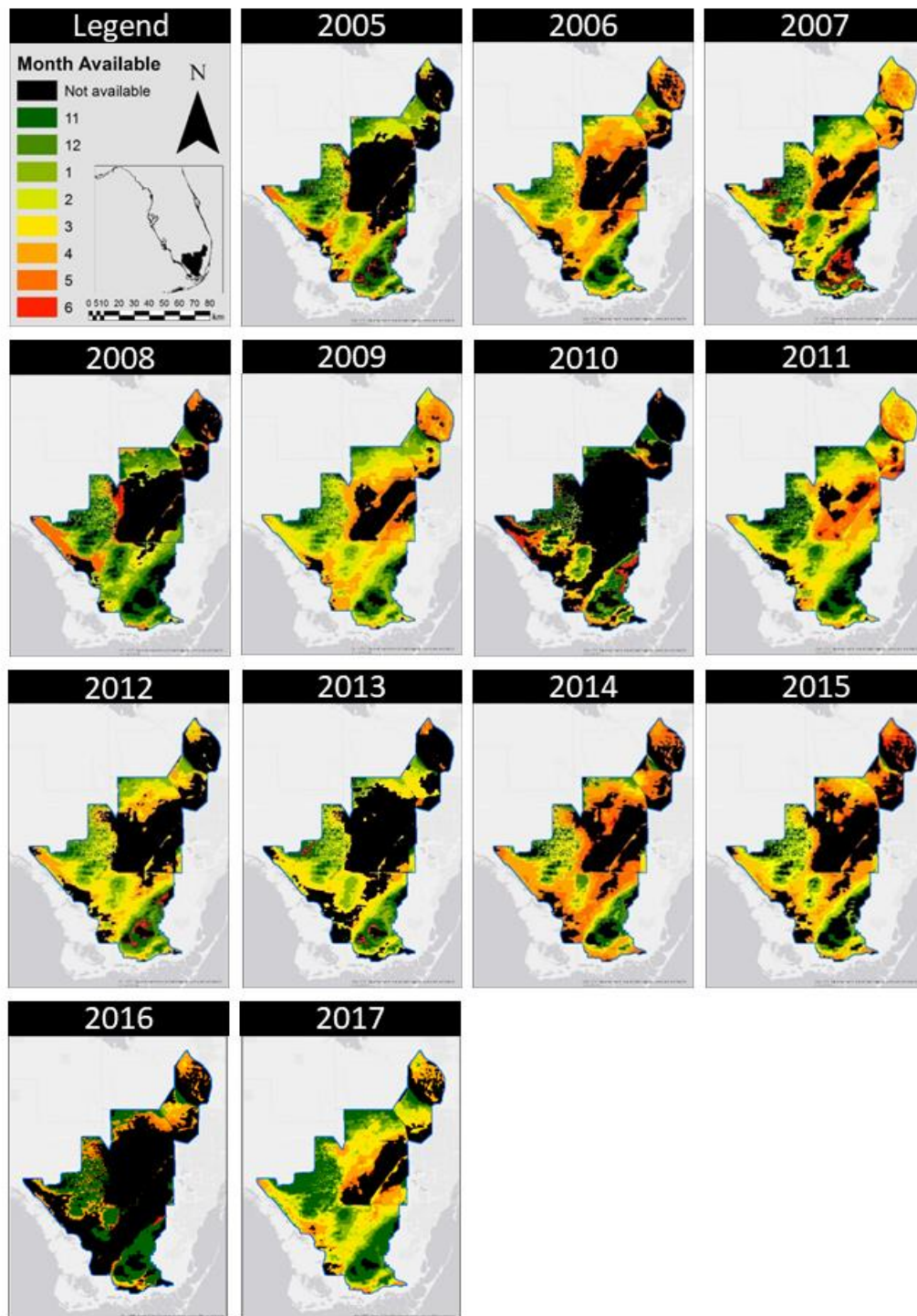


Figure 6. Monthly available habitat throughout the Everglades. Colors indicate the month at which habitat became available for wading bird foraging. Black indicates that habitat did not become available, either because it was too wet, or because it remained dry throughout the year. (Note: November and December in each map represent previous calendar year)

We estimated the proportion of suitable habitat that became available to wading birds in a given year by calculating the number of previously wet EDEN grid cells that became dry (water depth ≤ 0) (Fig. 6, Table 5). 6,037 km² or 81% became available to birds as foraging habitat in 2017, which is 19% above the 13 year average (Fig. 6, Table 5).

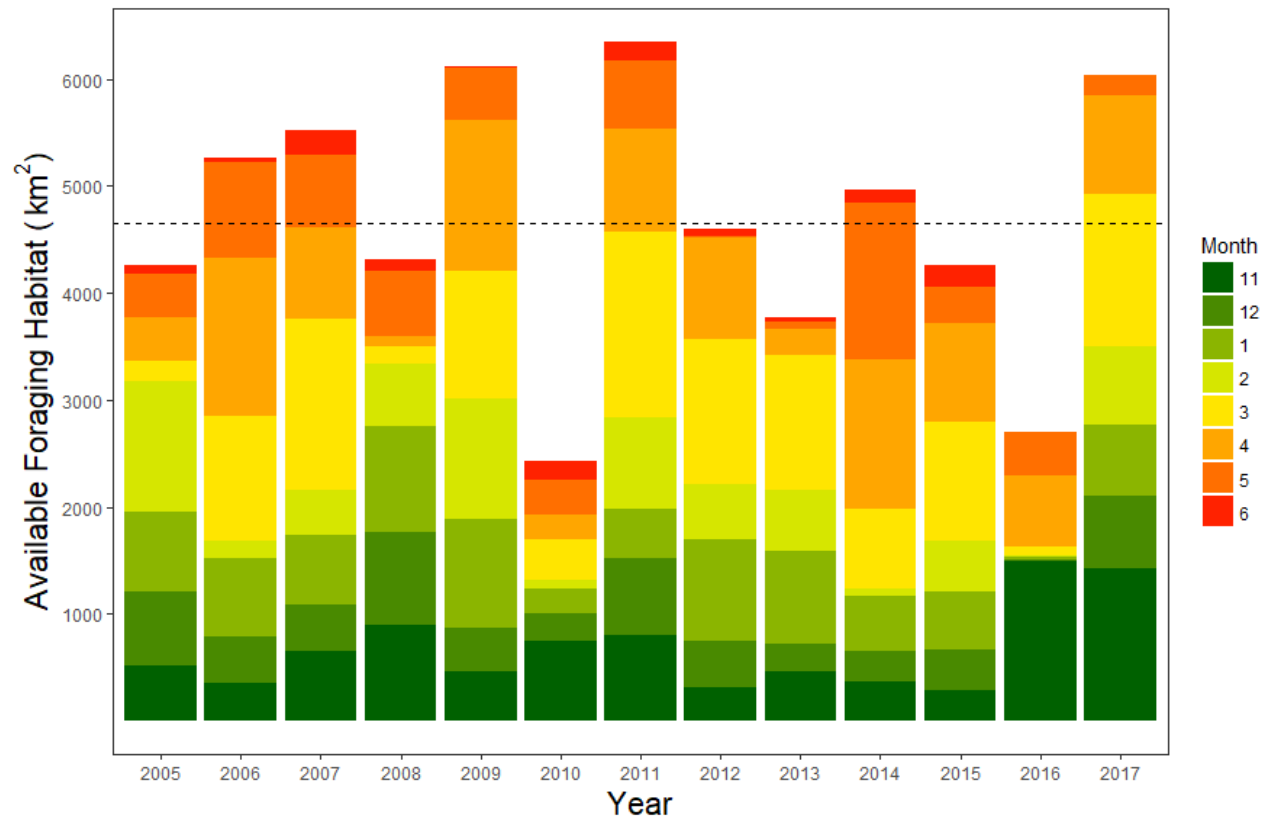


Figure 7. The amount of available wading bird foraging habitat from 2005-2017 based on the number of EDEN cells that dried down (water depth ≤ 0). Colors represent the month in which the cell became dry. Dashed line represents mean available habitat.

Table 5. The number of Everglades Depth Estimation Network (EDEN) cells that became available, total area, and percentage of total wading bird foraging habitat available during each dry season from 2005-2016.

Year	Number of Available Cells	Available Habitat Area (km ²)	Available Habitat (%)
2005	26,604	4,257	57
2006	32,906	5,265	70
2007	34,468	5,015	74
2008	26,979	4,317	58
2009	38,248	6,120	82
2010	15,130	2,421	32
2011	39,661	6,346	85
2012	28,760	4,602	61
2013	23,579	3,773	50
2014	30,986	4,958	66
2015	26,657	4,265	57
2016	16,932	2,709	36
2017	18,717	6,037	81
Mean	27,664	4,622	62

Both wading bird nest effort, and available foraging habitat were above average in the 2017 breeding season. Figure 8 shows the relationship between these variables among years.

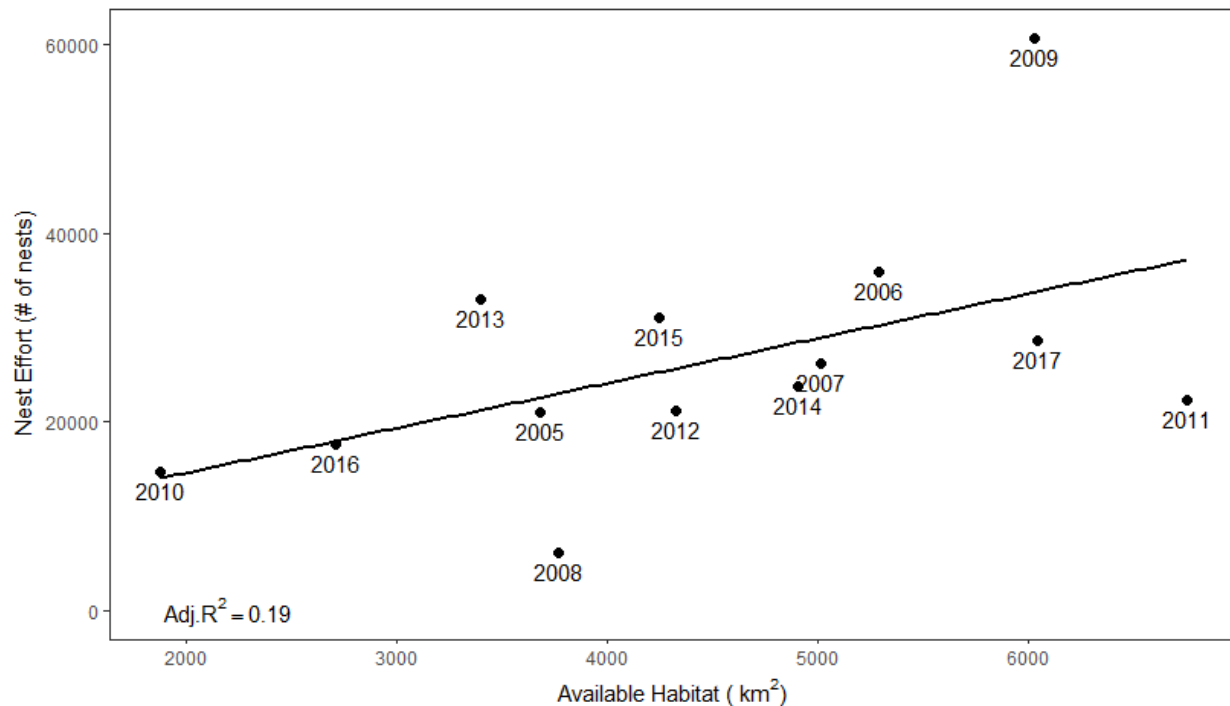


Figure 8. Amount of available habitat regressed against total wading bird nest effort (White Ibises, Wood Storks, Great Egrets combined) for 2005-2017.

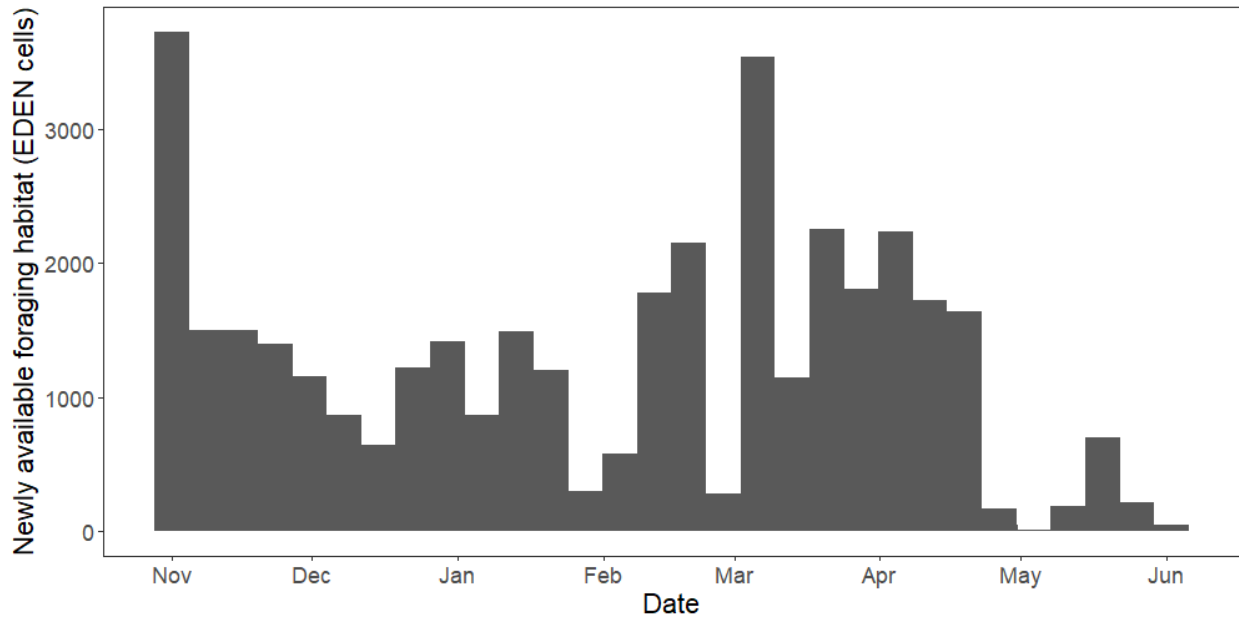


Figure 9. Timing of 2016 wading bird foraging habitat availability based on initial dry down (water depth ≤ 0) date of each EDEN grid cell.

Discussion

Prey Composition

The 2016 dry season experienced strong El Niño conditions which produced above-average rainfall, thus resulting in much slower recession rates than historic norms. As a result we were able to sample the Rocky Glades (LSU 3536), and Eastern Perrine Marl Prairie (LSU 39) (Fig. 1), unique portions of the Everglades which historically dry much earlier in the season (Fig. 6), and contain lower than average prey densities. High rainfall averages in conjunction with the inclusion of these low-prey density LSUs likely contributed to mean prey density for 2016 being 32% lower than in 2014 (the last year adequately sampled) and 52% lower than all years sampled since 2005. The lower than average prey density in 2016 was concurrent with lower than average available wading bird foraging habitat and nest effort, illustrating the connection between hydrology, prey availability and wading bird nest effort (Fig. 4).



Habitat Availability

Due to annual fluctuations in hydrology, our “window” of sample-able habitat shifts in size and location from year to year. A lower than average amount of the landscape (2,709 km² or 36%) became available to wading birds as suitable foraging habitat in 2016. Although portions

of the Everglades became available early in the dry season (Nov—Dec), heavy rains reaching up to 300% greater than average in January abruptly halted newly available habitat until late March (Fig. 6, Fig. 7). The hydrology of 2016 was most similar to the 2010 dry season, with 36% and 32% of the landscape becoming available for foraging, respectively (Fig. 6, Table 5). These were the two lowest years over the 12-year duration of monitoring.

Wading Birds

Overall, the 2017 wading bird nesting season was high compared to the 10-year average, with most wading bird species showing an increased nest effort across South Florida (Cook 2017). Of the five indicator species included in the Comprehensive Everglades Restoration Plan (CERP), all exhibited reduced nest efforts (Great Egret, White Ibis, Wood Stork, Snowy Egret, and Tricolored Heron), while only two species (Great Egret and White Ibis) were able to meet the CERP numeric restoration targets for 2017 (Cook 2017). The Everglades Protection Area (ENP and WCAs) which supports 75-95% of all wading bird nests in the Everglades, experienced 44% fewer nests than in 2015, and 45% fewer nests than the 10-year average for all wading bird species. The poor nest effort is indicative of the extremely wet conditions experienced in the Everglades during the nesting season, which not only greatly reduced available suitable foraging habitat, but significantly delayed nest effort timing to much later in the season. This delay likely resulted in too short a window for some species such as the Wood Stork, which require more than 3 months of drying conditions to nest successfully. Bird species requiring such conditions largely left the Everglades during the 2016 nesting season to either nest at more northern locations, or forgo nesting entirely.

Acknowledgements

Funding for this project was provided by RECOVER through the U.S. Army Corps of Engineers, Engineer Research and Development Center. We thank Jenna May, April Patterson, Glenn Rhett, and Sherry Whitaker for contract support. We are grateful to the long list of students and volunteers who contributed to this project over the years.

Literature Cited

- Bancroft, G. T., S. D. Jewell, and A. M. Strong. 1990. Foraging and nesting ecology of herons in the lower Everglades relative to water conditions. National Audubon Society.
- Chick, J. H., C. R. Ruetz, and J. C. Trexler. 2004. Spatial scale and abundance patterns of large fish communities in the freshwater marshes of the Florida Everglades. *Wetlands* **24**:652-664.
- Cochran, W. G. 1977. Sampling techniques. John Wiley and Sons Inc., New York.
- Cook, M. I. 2017. South Florida Wading Bird Report. South Florida Water Management District.
- Crozier, G. E. and D. E. Gawlik. 2002. Avian response to nutrient enrichment in an oligotrophic wetland, the Florida Everglades. *Condor* **104**:631-642.
- DeAngelis, D. L., J. C. Trexler, and W. F. Loftus. 2005. Life history trade-offs and community dynamics of small fishes in a seasonally pulsed wetland. *Canadian Journal of Fisheries and Aquatic Sciences* **62**:781-790.

- Eberhardt, L. L. and J. M. Thomas. 1991. Designing environmental field studies. *Ecological Monographs* **61**:53-73.
- Frederick, P., D. E. Gawlik, J. C. Ogden, M. I. Cook, and M. Lusk. 2009. The White Ibis and Wood Stork as indicators for restoration of the everglades ecosystem. *Ecological Indicators* **9**:S83-S95.
- Frederick, P. C. 1995. Wading bird nesting success studies in the water conservation areas of the Everglades, 1992-1995. Department of Wildlife Ecology and Conservation, University of Florida.
- Frederick, P. C. and M. W. Collopy. 1989. Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. *The Auk* **106**:625-634.
- Frederick, P. C. and J. C. Ogden. 2001. Pulsed breeding of long-legged wading birds and the importance of infrequent severe drought conditions in the Florida Everglades. *Wetlands* **21**:484-491.
- Frederick, P. C. and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. Pages 659-691 in J. C. Ogden and S. M. Davis, editors. *Everglades: The ecosystem and its Restoration*. St. Lucie Press, Boca Raton, FL.
- Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* **72**:329-346.
- Gawlik, D. E., P. C. Frederick, B. Botson, G. Herring, J. M. Beerens, J. C. Trexler, and M. I. Cook. 2009. Predator-prey Interactions of Wading Birds and the Aquatic Fauna Forage Base
- Herring, G., D. E. Gawlik, M. I. Cook, and J. M. Beerens. 2010. Sensitivity of nesting great egrets (*Ardea Alba*) and white ibises (*Eudocimus Albus*) to reduced prey availability. *The Auk* **127**:660-670.
- Kahl, M. P. J. 1964. Food ecology of the wood stork (*Mycteria americana*) in Florida. *Ecological Monographs* **34**:97-117.
- Kushlan, J. A. 1976. Wading bird predation in a seasonally fluctuating pond. *The Auk* **93**:464-476.
- Kushlan, J. A. 1986. Responses of wading birds to seasonally fluctuating water levels: strategies and their limits. *Colonial Waterbirds* **9**:155-162.
- Kushlan, J. A., J. C. Ogden, and A. L. Higer. 1975. Relation of water level and fish availability to Wood Stork reproduction in the southern Everglades, Florida. USGS, Tallahassee, FL.
- Loftus, W. F. and A. M. Eklund. 1994. Long term dynamics of an Everglades small fish assemblage. Pages 461-483 in S. M. Davis and J. C. Ogden, editors. *Everglades. The Ecosystem and Its Restoration*. St. Lucie Press, Boca Raton, Florida, USA.
- Morrison, M. L., Marcot, B. G., Mannan, R. W., & Relationships, W. H. (1992). *Concepts and Applications*.
- RECOVER. 2006. RECOVER: Monitoring and Assessment Plan (MAP), Part 2: 2006 Assessment Strategy for the MAP. <http://www.evergladesplan.org>.
- Ruetz III, C. R., J. C. Trexler, F. Jordan, W. F. Loftus, and S. A. Perry. 2005. Population dynamics of wetland fishes: spatio-temporal patterns synchronized by hydrological disturbance? *Journal of Animal Ecology* **74**:322-332.
- Telis, P. A. (2006). *The Everglades Depth Estimation Network (EDEN) for support of ecological and biological assessments* (No. 2006-3087). Geological Survey (US).

- Trexler, J. C. and C. W. Goss. 2009. Aquatic fauna as indicators for Everglades restoration: applying dynamic targets in assessments. *Ecological Indicators* **443**:1-12.
- Trexler, J. C., W. F. Loftus, and S. Perry. 2005. Disturbance frequency and community structure in a twenty-five year intervention study. *Oecologia* **145**:140-152.
- Trexler, J. C., W. F. Loftus, F. Jordan, J. H. Chick, K. L. Kand, T. C. McElroy, and J. O. L. Bass. 2002. Ecological scale and its implications for freshwater fishes in the Florida Everglades. Pages 153-181 in J. W. Porter and K. G. Porter, editors. *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*. CRC Press, Boca Raton, Florida, USA.
- Turner, A. M., J. C. Trexler, C. F. Jordan, S. J. Slack, P. Geddes, J. H. Chick, and W. F. Loftus. 1999. Targeting ecosystem features for conservation: standing crops in the Florida Everglades. *Conservation Biology* **13**:898-911.