

THE ASSOCIATIONS OF LITTLE BLUE HERON PREY AND VEGETATION
COMMUNITIES IN TWO SUBTROPICAL COASTAL ECOSYSTEMS

by

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Dale E. Gawlik, Department of Biological Sciences, and has been approved by the members of her 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.

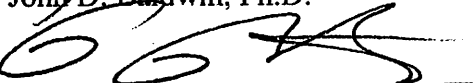
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ABSTRACT

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Shallow water availability coupled with anthropogenic degradation of seagrass beds limits wading bird food resources in dynamic coastal ecosystems. Identifying prey species critical to wading bird reproductive success and the environmental drivers of key prey species abundance is important for understanding how environmental stressors influence prey and change the quality of foraging patches. Little Blue Herons (*Egretta caerulea*) are reportedly generalists eating insects, crustaceans, and fish; however, the proportions of prey items in the diet may shift spatially and temporally from freshwater to marine systems during breeding and non-breeding periods. I investigated prey selection by Little Blue Herons in Florida at the Great White Heron National Wildlife Refuge and the western Florida Bay, during 2016 and 2017 breeding seasons by investigating prey availability at low-tide locations along mudflats compared to stomach regurgitate samples collected from Little Blue Heron chicks 1 to 4 weeks old. Little Blue Herons selected Gulf toadfish (*Opsanus beta*) and prawns (*Farfantepenaeus spp.*) from the estuarine

environment, but also consumed terrestrial prey (e.g. tree crabs) suggesting Little Blue Heron foraging habitat is not restricted to tidal flats. Additionally, these results support the characterization of Little Blue Herons as a generalist. After identifying important prey species, I modeled the associations of selected prey species with submerged aquatic vegetation density and abiotic variables to better understand habitat preferences and important habitat characteristics that drive prey density. Models support total seagrass density and algal density as having the greatest effect on prey selected by Little Blue Herons. Prawn density has a strong positive association with seagrass density. Gulf toadfish (*Opsanus beta*) and prawns (*Farfantepenaeus spp.*) had strong positive association with algae while pipefish (*Syngnathidae*) had a strong negative association with algae suggesting algae density in seagrass meadows should be considered when assessing the quality of seagrass meadows for Little Blue Heron prey and habitat suitability. My results varied from previous studies where prawns and gulf toadfish were associated with specific seagrass species. Therefore, some Little Blue Heron prey species in south Florida may not be affected by changes in submerged aquatic vegetation community composition if submerged aquatic vegetation densities remain constant. Studies are needed that clarify the complex interactions between prey and specific habitat metrics to validate the strength of landscape scale drivers of wading bird prey densities in dynamic coastal ecosystems and to determine how these communities will respond to anthropogenic environmental change.

DEDICATION

This thesis is dedicated to my parents Peter and Julia, who fostered my curiosity in the natural world and always encouraged me to pursue my passions.

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1 INTRODUCTION

Coastal ecosystems are declining due to coastal development, overfishing, increased nutrient loading, climate change and other anthropogenic causes or human-induced rapid environmental change (HIREC) (Wyda et al. 2002, Fabry et al. 2008, Sih et al. 2011, Janousek et al. 2016, Wang et al. 2016). Nutrient over-enrichment and physical disturbance (Orth and Moore 1983, Cambridge and McComb 1984, Wyda et al. 2002, Connell et al. 2017) are rapidly altering or eliminating seagrass ecosystems globally (Short and Wyllie-Echeverria 1996, Orth et al. 2006, Waycott et al. 2009). Seagrass disturbance can lead to fragmentation, a reduction in coverage, and permanent loss of habitat (McCloskey and Unsworth 2015).

Changing the submerged aquatic vegetation (SAV) species composition and structural characteristics of marine habitats alters their habitat quality for dependent fish and invertebrates (Wyda et al. 2002, Micheli et al. 2008). Stark differences in macrofaunal assemblage metrics (e.g., abundance, biomass, species diversity) occur at the boundary between vegetated and unvegetated areas, even between slightly vegetated areas and bare patches (Barnes and Hamylton 2016). Some invertebrates and fish exhibit a species-specific response to SAV community composition (Heck and Wetstone 1977, Grenouillet et al. 2002, Micheli et al. 2008) and SAV density (McCloskey Unsworth 2015). Prey species may have a quadratic relationship with SAV density (i.e., higher density at moderate SAV density; McCloskey and Unsworth 2015) or may exhibit no

response to SAV density (Lefcheck et al. 2016). Other studies have demonstrated few significant differences in abundance, growth or survival of fauna when comparing seagrass meadows to other structured habitats, such as oyster or cobble reefs, or macroalgal beds, suggesting the type of cover is not important (Heck et al. 2003).

Faunal species richness of coral reefs was successfully predicted using the topographic variables bathymetric variance and habitat rugosity along with water depth and presence of seagrass (Pittman et al. 2007). Like coral reef habitats, it may be possible to use habitat characteristics like SAV cover to predict the faunal community assemblages. Establishing the strength of SAV metrics as indicators for fauna can assist with evaluating faunal density in an area and how it may change with environmental variation like the kind caused by anthropogenic stressors.

Degraded intertidal vegetation communities alter coastal fish populations, reducing faunal diversity and abundance (McCloskey and Unsworth 2015, Iacarella et al. 2018, Santos et al. 2018), and affecting predators (i.e. wading birds) dependent on the prey productivity of seagrass beds (USACE 1999). This is the case in South Florida, where anthropogenic causes have altered natural coastal habitats including mangroves, seagrass beds, and other native wetland habitats. Seagrass beds in Florida Bay and Florida Keys are threatened by anthropogenic sources of eutrophication (USACE 1999) as well as hypersaline conditions due to the obstruction of freshwater by water control structures built by the Central & Southern Florida (C&SF) Project (USACE 1999). As a result, submerged aquatic vegetation (SAV) of the mangrove estuary have experienced massive die-offs stemming from hypersalinity levels as high as 70 ppt and high water temperatures (USACE 1999). These changed vegetation patterns have altered coastal fish

communities, reducing wading bird food resources resulting in their abandonment of historic colonies (USACE 1999). Determining the strength of SAV metrics as predictors of aquatic faunal communities will assist with assessing the spatial distribution of these species in estuaries like Florida Bay.

Quantifying the specific relationships between fauna and their associated habitat is an important preliminary step for linking wading birds to lower trophic levels and establishing effective parameters to predict how the ecosystem overall may respond to environmental variation. Wading birds are connected to an ecosystem's condition through their diet and are quickly impacted when habitats are degraded (Stolen et al. 2005). When modeling the ability of wading birds to find suitable habitat in different ecological scenarios, landscape features such as distance to deep water (Lawrie et al. 1999, Gibson 2003, Pittman et al 2004), substrate (Pittman et al. 2004) and distance to islands (Pittman et al 2004, Ellis and Bell 2008) have been used as proxies for prey density (abundance or biomass); however these proxies are not universally effective or prey-species-specific. Presence of SAV is used as a proxy for prey abundance (Matsunaga 2000), but specific SAV metrics (i.e. density) could be a more accurate method of estimating prey species density because prey species may prefer specific SAV species (Carss and Elston 2003). Landscape variables like distance to island may only be important to faunal densities because seagrass species like *Thalassia testudinum* and *Halodule wrightii* are positively correlated with proximity to island (Green et al. 2015), therefore examining the effect of SAV metrics on prey density separately from correlated landscape variables could clarify which landscape parameters are most influential to prey density.

Wading birds in tidal environments are restricted in their ability to find suitable foraging habitat by the availability of shallow water (Calle et al. 2018). Because birds are restricted to foraging in shallow water, there is a need to assess the prey quality of those areas. Due to varying nutritional values of prey species (Razeng and Watson 2015), diet composition affects wading bird productivity (Xavier et al. 2003, Wanless et al. 2005, Gingras and Paszkowski 2006, Boyle et al. 2014). Prey generalists may have preferred prey species (Jaworski et al. 2013, Terraube et al. 2014), but have a broad diet and can switch among prey species to sustain breeding. However, dietary shifts may not be possible if several nutritionally important prey species decline simultaneously (Rutz et al. 2006). Generalists choosing alternative prey can experience declines in productivity if the quality (i.e. biomass, abundance, availability, or nutritional value) of alternative prey differs from preferred prey (Suryan et al. 2002, Zarybnicka et al. 2009, Rota et al. 2015, Lamb et al. 2017).

Little Blue Herons (hereafter herons) are considered to be generalists that eat insects, crustaceans, and fish (Smith 1997, Olmos et al. 2001, Martinez 2010), but heron diet studies have shown specialization in one or a few food resources (Kushlan & Hancock, 2010). For example, some heron diets in coastal Brazil are dominated by newly molted crustaceans (Miranda and Collazo 1997, Olmos et al. 2001, Olmos and Silva 2003), whereas other populations consume mostly fish (Miranda 2010). Other coastal heron diet studies have not compared the proportion of prey items in the diet to the abundance of prey items in the foraging areas, so it is unknown if the apparent specialization is due to the nutritional superiority of the prey species or if birds are simply using the most abundant prey species. In Florida Bay and Florida Keys, it is unknown if

certain prey species are important for heron nest success. Herons are a threatened wading bird in the state of Florida (FWCC 2017) and is a species of High Concern in the North American Waterbird Conservation Plan (Kushlan et al. 2002). Despite their designation as a generalist, the decline of herons could be related to food limitation. Testing whether heron specialize on key prey species is an important step in determining whether food resources could affect reproductive success (Taylor and Schultz 2008, Dorn et al. 2011, Trexler and Goss 2009). This information can be used to examine key prey densities in foraging areas and the environmental variables that drive them.

The Comprehensive Everglades Restoration Plan (CERP) aims to restore much of the historical patterns of freshwater flow in south Florida. Sea level rise and increasing freshwater to Florida Bay will change the depth and salinity, thus changing the spatial distribution of SAV (Fourqurean et al. 2003, Herbert et al. 2011, Green et al. 2015) and potentially altering the distribution of aquatic fauna (Moore and Duffy 2016). Evaluating the effect of SAV on wading bird foraging habitat quality will assist in identifying and conserving important foraging sites.

Here, I investigate the regional diet trends of herons to more clearly understand the how these predators are linked to lower trophic levels in coastal ecosystems. In Chapter 2, I identify heron diet and prey selectivity in the Florida Keys and Florida Bay. In Chapter 3, I investigate the relationship between heron prey and different SAV metrics including SAV species type and SAV density. Finally, I explore potential improvements to how the quality of habitat can be assessed and the management implications for herons in coastal areas.

2 BREEDING SEASON DIET AND PREY SELECTIVITY OF THE LITTLE BLUE HERON IN COASTAL SOUTH FLORIDA

2.1 INTRODUCTION

2.1.1 Diet and Reproductive Performance of Predatory Birds

The reproductive performance of many avian species is directly affected by food availability and distribution (Staggenborg et al. 2017), but the consequences to reproductive performance when prey availability decreases differs between food generalist and food specialist. Prey specialists, species with a narrow ecological niche, specialize on a few prey species and may skip breeding in seasons when key prey abundance is low (Korpimäki and Hakkariainen 2012). Alternatively, prey generalists may have preferred prey species (Jaworski et al. 2013, Terraube et al. 2014), but have a broad diet and can switch among prey species to sustain breeding. However, dietary shifts may not be possible if several profitable prey species decline simultaneously (Rutz et al. 2006). Generalists choosing alternative prey can experience declines in productivity if the prey quality (i.e. biomass, abundance, availability, or nutritional value) of alternative prey differs from preferred prey (Suryan et al. 2002, Zárbynická et al. 2009, Rota et al. 2015, Lamb et al. 2017).

For colonial nesting birds, breeding colonies are maintained if food resources (hereafter used interchangeably with “prey”) are adequate to meet the birds’ dietary requirements (Lindsell et al. 2011, Djerdali et al. 2016, Ainley et al. 2018). For wading birds, differences in nesting success during the breeding season are influenced by prey

availability across the landscape and by species-specific foraging strategies (Herring 2008; Herring et al. 2010a, b). Foraging behaviors, foraging-site selection, water-depth selection, and diet may shift in response to changes in prey availability (Beerens et al. 2011). Hydrological conditions affect wading bird prey availability. Seasonal hydrological cycles in seasonally-pulsed wetlands cause prey to concentrate in the dry season and become more available to wading birds (Botson et al. 2016); however, tidal fluctuations in coastal systems change prey availability daily. The density of many aquatic prey species in marine ecosystems are disrupted by coastal development, overfishing, increased nutrient loading, and climate change (Wyda et al. 2002); adding to the difficulty of foraging in coastal areas. Generalist species are considered better adapted to withstand changes in food resources (Devictor et al. 2008, Clavel et al. 2011); however, some generalist wading birds like the Little Blue Heron (hereafter heron) in coastal South Florida are declining (Kushlan et al. 2002, FWCC 2017).

2.1.2 Using Heron Diet to Evaluate Habitat Suitability

Food limitation could be a cause of heron population decline if preferred prey are not available in adequate quantities despite herons exhibiting regional diet plasticity. Diet composition affects wading bird productivity (Xavier et al. 2003, Wanless et al. 2005, Gingras and Paszkowski 2006, Boyle et al. 2014) due to the varying nutritional values of prey species (Razeng and Watson 2015). Herons are reportedly generalist (Smith 1997, Olmos et al. 2001, Martinez 2010), but may specialize in one or a few food resources regionally (Kushlan & Hancock, 2010). The presence and proportions of taxa in coastal heron diet differs across their range. Herons mainly eat semi-terrestrial crabs in the mangrove estuaries of the Caribbean and south eastern Brazil (Miranda and Collazo

1997, Olmos et al. 2001), while other heron populations in north eastern Brazil eat mainly shrimp (Gianuca et al. 2012) or fish (Martínez 2010). Herons in Tampa Bay, FL consume mostly fish and blue crabs (Kent 1986), which also occurs in coastal Brazil (Olmos et al. 2001, Gianuca et al. 2012). However, no previous coastal heron diet study has concurrently quantified the available prey community to determine if prey selection is occurring. Quantifying prey use without accounting for prey availability can misrepresent key prey species. Identifying key prey species is an important step in understanding how the availability of these species may be influenced by environmental variation, thus affecting heron foraging success (Taylor and Schultz 2008, Frederick et al. 2009, Trexler and Goss 2009).

Hérons are sensitive to changes in water levels but little is known about other environmental factors influencing their distribution. Calle et al. (2018) developed a species distribution model to determine environmental factors affecting heron foraging locations and found that heron foraging site selection is influenced by resource availability over time. Herons feed at locations where water levels are lowest for the longest period of time. Their model also examined the effects of tidal fluctuations on wading bird prey density indirectly using literature support from experimental studies in terrestrial wetlands (Gawlik 2002) as well as observational studies of indirect associations in coastal wetlands. Examining heron diet directly could be used to develop a more robust model. For example, if herons have preferred prey, environmental variables known to influence those prey densities can be included in the model to evaluate the quality of the food resources (Rota et al. 2015). Determining the quality of available food resources can be difficult because herons exhibit an ‘exploiter’ foraging

strategy and forage in patches after prey densities decline (Gawlik 2002; Gawlik and Crozier 2007), thus the presence of herons in an area may not reflect the quality of available food resources. Additionally, examining heron diet could offer clues regarding prey density in foraging areas. In areas with high prey density, some wading bird species exercise a higher degree of prey specialization (Beerens et al. 2011); therefore, if prey density is high, herons would appear to be specializing on one or a few prey species.

This study quantifies heron diet and prey selectivity. Because variation in key prey species has been observed among heron colonies occurring ~ 3 km apart (Olmos et al. 2001), I examined the biotic and abiotic features influencing diet preferences for two populations within the same geographic region. I compare two ecologically different areas of coastal South Florida, Great White Heron National Wildlife Refuge (hereafter GWH) and Florida Bay in Everglades National Park, Florida, USA due to differences in landscape features, salinity, and nutrient inputs (Handley et al. 2007). I hypothesized herons would select one or a few prey species. If herons are selecting key prey species, I hypothesized those species would not differ between GWH and Florida Bay because the same common prey species are available to herons at both sites (personal observation).

2.2 METHODS

2.2.1 Study Site Selection

The study occurred during the 2016 and 2017 heron breeding season from February-July. This study took place in the coastal regions GWH and Florida Bay, Florida, USA (Appendix A, Fig. 1A). Prominent features of both regions are mangrove (*Rhizophoraceae*) islands, which serve as wading bird nesting habitat, and vast open mud, sand and seagrass flats, which serve as wading bird foraging habitat. Mangrove islands

were not sampled for terrestrial prey. Florida Bay (hereafter the Bay) is a shallow lagoon, with large spatial differences in water temperature, nutrients, turbidity, and salinity within the region due to separation of basins by mudflats (Handley et al. 2007). The system is driven in part by freshwater inputs, but the historic freshwater flow into the Bay has been altered by the Central and Southern Florida Project, causing hypersaline conditions (> 40 ppt, Sullivan 2018) which greatly influences the distribution and abundances of estuarine organisms (Handley et al. 2007). Mangrove tree islands provide nesting substrate and mudflats provide foraging habitat. Unlike Florida Bay, GWH is not influenced by freshwater. The mudflats differ in landscape features known to influence prey abundance such as distance to islands (Pittman et al 2004, Ellis and Bell 2008), distance to deep water (Lawrie et al. 1999, Gibson 2003, Pittman et al. 2004), seagrass (Carss and Elston 2003, Pittman et al. 2004, Moore and Hovel 2010), and substrate (Pittman et al. 2004). The Florida Keys including GWH are subjected to nutrient loading from nearshore septic systems, Florida Bay and even far away sources like the Mississippi river (Hu et al. 2005).

2.2.2 Study Species

The Little Blue Heron (*Egretta caerulea*; hereafter heron) is a threatened wading bird in the state of Florida (FWCC 2017) and is a species of High Concern in the North American Waterbird Conservation Plan (Kushlan et al. 2002). Herons may be a good indicator of an ecosystem's condition for many coastal environments because they have a widespread range, utilize both fresh and saltwater systems and respond to changes in water level due to their restrictively short leg length (Gawlik 2002, Calle et al. 2016, Calle et al. 2018).

2.2.3 Prey Species Abundance

To determine prey availability, I first identified possible foraging locations for herons using foraging distribution surveys (FDS). The FDS transects were selected within 30 km from each colony as small herons are known to forage up to 30 km from a colony (Strong et al. 1997). I conducted surveys by boat along a ~10 km transect from Upper Harbor Key (24.80851, -81.44166) to Howe Key (24.73063, -81.43104) at GWH, a 4.3 km transect at Snake Bight (25.14055, -80.89736), a 2.2 km transect at Frank Key (25.10604, -80.91135) and Murray Key (25.10759, -80.93946), and at three survey points at Sandy Key (25.03431, -81.01465) in the Bay. In such open landscapes, detectability of wading birds using the double-observer method (Nichols et al. 2000) is near 100 percent up to 600 m from the observer location (Calle et al. 2016). Therefore, a 600-m buffer around surveys transects and survey points represented the survey area. Surveys began up to two hours before low tide and the cardinal direction of the survey alternated with each subsequent survey. Heron foraging location and abundance were recorded every 500 m. Locations were recorded using a bearing and distance to the bird or middle of the flock from a GPS-referenced observer location (GPSMAP 78sc; Garmin International, Olathe, Kansas, USA). Birds in flight or perched in trees were not counted. Distance was measured with a rangefinder.

I sampled aquatic fauna and SAV at non-random or ‘used’ locations 1-2 days after initially observing a foraging heron as well as ‘available’, random locations within suitable foraging depths for herons (<0.3 m; Lantz et al. 2010). In 2017, to improve the sampling coverage of the survey area, a stratified random method of hexagonal tessellation (Birch et al. 2007) delineated random sampling locations (EMAP program,

U.S. EPA) within the survey area. Several random sampling points were generated by ArcGIS within each hexagon and one point was selected based on the water depth (<0.3 m). I sampled prey within heron foraging habitat using a 1-m² throw trap (Jordan et al. 1997) with a mesh netting frame. Prey capture, handling, and euthanasia techniques adhered to protocols approved by the Institutional Animal Care and Use Committee at Florida Atlantic University (permit number A15-37), Everglades National Park (EVER-2015-SCI-0067), U.S. Fish and Wildlife Service (FY17-03) and National Oceanic and Atmospheric Administration (FKNMS-2015-15). Aquatic animals of 0.1 – 10 cm in length were removed from the throw-trap by passing a 100 cm by 40 cm bar seine through the water column until three consecutive sweeps yield no prey. Prey ≤10 cm in total length were transferred immediately from the bar seine to jars containing a solution of source water and Tricainemethane Sulfonate (MS 222), a rapid euthanizing agent. Larger prey (>10 cm) was identified, measured, and released.

2.2.4 Prey Use

I collected regurgitated food boluses from 1-4 week old heron nestlings at located in GWH (n = 38 nests) and the Bay (n = 10 nests) during the 2016 and 2017 nesting seasons (June – July) collectively. Third Island in GWH was sampled in both 2016 and 2017 and Sandy Key in the Bay was sampled in 2017. Heron capture, handling, and bolus collection techniques adhered to protocols approved by the Institutional Animal Care and Use Committee at Florida Atlantic University (permit number A15-38), Everglades National Park (EVER-2016-SCI-002), U.S. Fish and Wildlife Service (FY17-03), and Florida Fish and Wildlife Conservation Commission (LSSC-12-00012C). To collect regurgitates from Third Island, I visited the colony 1-2 times per week or biweekly

during the breeding season (Klassen et al. 2016) after a rising tide when water levels became too deep for herons to forage on the tidal flats. Nestlings often voluntarily regurgitate in the presence of humans, making bolus content readily available. I used a through-fall method (Nell and Fredrick 2015) to opportunistically capture bolus from chicks old enough to move to the nest edge (3–5 weeks old) in Florida Bay because I could not reach nests by ladder. Tarps were installed below the nest, > 1 m above the ground and checked for bolus contents twice per week. Fresh bolus was collected from the tarps and the ground during colony visits.

I identified each prey item to the lowest taxonomic group possible; this was often to species for fish and crab, genus for shrimp, and order for other arthropods. I grouped rare prey items, comprising less than 1% of the bolus biomass to the next highest taxonomic level. I classified unidentifiable prey items (e.g., too digested) as “unknown”. Additionally, I weighed each animal to 0.01 g (Klassen et al. 2016).

2.2.5 Statistical Analysis

2.2.5.1 Regional Diet Differences

I performed multivariate analyses (Clarke and Warwick 2001) to compare prey species in heron diet between heron colonies using a Bray-Curtis similarity matrix of square-root transformed abundance data for prey species within bolus samples. The transformation down-weights the influence of dominant prey species (Clarke and Warwick 2001). I tested for differences among colony diet samples using an ANOSIM, which is a non-parametric permutation procedure to test differences based on the ranks of pairwise similarities in the Bray-Curtis matrix. The resulting R statistic value is between zero and one, with zero indicating samples are similar and values close to one are

dissimilar. To visually represent the ANOSIM, I generated a non-metric Multi-Dimensional Scaling (nMDS) ordination plot. If colony diets were significantly different in the ANOSIM (p-value ≤ 0.05), I used the similarities percentage (SIMPER) analyses to determine which prey species are driving those differences. A SIMPER analysis uses the dissimilarity to demonstrate the degree to which prey items contribute to the difference of diet among sites and indicates the percentage each prey item contributed to any differences that may exist among colonies. All techniques were performed using PRIMER v7 (Clarke and Gorley 2015).

2.2.5.2 Prey-specific Abundance and Selection

Because chicks are fed by two parents, bolus samples volunteered by chicks in a nest were summed and considered one diet sample per day. To investigate the diet and feeding strategy of herons, I analyzed the prey-specific abundance of the prey items and their occurrence in the nests using the Costello method (modified by Amundsen et al., 1996). In the diagram (Fig. 2.2), prey-specific abundance (% P_i) is on the y axis and the frequency of occurrence (range 0-1) on the x axis. Prey-specific abundance is represented as the average percent (Swanson et al. 1974) a prey taxon comprises of all prey taxon only in nests where the actual prey occurs:

$$P_i = (\sum S_i / \sum S_{ii}) \times 100$$

where P_i is the prey-specific abundance of prey i , S_i the bolus weight (g) of prey i , and S_{ii} the total bolus weight (g) in only those nests with prey i in their bolus (Amundsen et al. 1996). The prey item's location on the plot shows whether the feeding strategy is specialized or generalized and the importance of the prey item. (Amundsen et al. 1996). I used Chesson's index of selectivity (CSI; Chesson 1983) to quantify avoidance, random

feeding, or selection by comparing prey proportions and distribution found in the environment to those found in the diet. This approach assumes prey abundance is large compared to the amount of prey consumed and that each prey item has an equal probability of consumption (Chesson 1983). The diet data for each colony is represented as (1) the average percent of weight and (2) the percent occurrence in the nests or how many nests contained a particular prey item from that particular area (Prevett et al. 1979). Using an aggregate percentage approach accurately represents the relative importance of prey items and avoids the diet of a few birds dominating a sample (Swanson et al. 1974). The average percent of weight is defined as $\sum W_i/N$, where W_i is the wet weight (g) of the i th prey item expressed as a percentage of all prey items in the sample and N is the total number of nest samples for a particular site (Callaghan and Gawlik 2016). The percent occurrence of prey items is defined as $\sum F_i/\sum F_s$ and the percent occurrence in the nests is defined as $\sum F_i/N$; where F_i = occurrence of prey item i in a sample, and F_s = number of prey items in a sample.

The Chesson's index of selectivity is calculated by using the formula:

$$\alpha_i = \frac{r_i/p_i}{\sum r_i/p_i}, \quad i = 1, \dots, m$$

where α_i is the selectivity index for prey type i ; r_i is the relative abundance of prey type i consumed by the nest; p_i is the percent of prey type i in the environment calculated from the throw trapping surveys; and m is the number of prey types available in the environment. In order to interpret Chesson's index, values of α_i are related to $1/m$. Random feeding occurs when $\alpha_i = 1/m$. Preferential selection of a prey type occurs when $\alpha_i > 1/m$, and avoidance of a prey type occurs when $\alpha_i < 1/m$. The alpha value for the Chesson's selectivity index is slightly different because the the Bay site has 11 different

prey types ($1/m = 0.091$) while GWH has 12 ($1/m = 0.083$). The α_i was calculated at the individual level and then the mean indices of all individuals were taken, providing a mean selectivity index (Rudershausen et al. 2005). I excluded non-marine prey species from the analysis because only marine species were sampled for availability.

2.3 RESULTS

2.3.1 Foraging Distribution Survey

I performed a total of 21 foraging distribution surveys in GWH during which I recorded 526 detections of herons at GWH. I performed 13 foraging distribution surveys at the Bay during which I recorded 807 detections of herons.

2.3.2 Prey Species Abundance

I collected 7741 individuals of aquatic prey from 129 throw-traps within GWH. I summed the biomass for each species across all throw-traps in each site. Over 80% of the biomass was comprised of three taxonomic groups. Marine crabs (*Decapoda*) made up 43% of the prey species biomass followed by pistol shrimp 28%, and gulf toadfish 10% (Appendix A, Table A2). I collected 4048 individuals in the Bay from 67 throw traps. Over 70% of the biomass was comprised of three taxonomic groups. Pistol shrimp made up 29% of the prey species biomass followed by prawns (22%; *Farfantepenaeus spp*), and marine crabs (22%; *Decapoda*; (Appendix A, Table A2).

2.3.3 Regional Diet Differences

The contents of heron boluses were not significantly different between colonies (ANOSIM R-value = 0.03, p-value = 0.54), therefore a SIMPER analysis was not performed.

2.3.4 Prey-specific Abundance and Selection

I collected 87 bolus samples from 38 heron nests on Third Island in GWH. The total biomass of the bolus samples was 1216.1 g. Herons exhibited stronger selection for mojarra (*Eucinostomus havana*), pipefish and seahorses (*Syngnathidae spp.*), and weaker selection for prawns (*Farfantepenaeus spp.*) and gulf toadfish (*Opsanus beta*) (Table 2.1, Fig. 2.4). Prawns occurred in 89% of the bolus samples, closely followed by gulf toadfish (74%) and pipefish and seahorses (68%; Table 2.2.), respectively. In nests where the prey items occurred, prawns comprised 40% of the diet by weight, followed by gulf toadfish, which made up 31% of the diet (Table 2.2). Pipefish comprised 10% of the average bolus biomass. Prey biomass was mostly comprised of aquatic species; however, terrestrial species occurred in 61% of bolus samples. The most abundant terrestrial arthropods found in bolus samples were isopods (*Libia spp.*; 18%) and terrestrial crabs (*Aratus pisonii* and *Uca spp.*; 14%) Reptiles occurred in one bolus sample and contributed to 14% of the sample's biomass. The modified Costello graph results suggest herons in this colony are primarily generalists, but prawns and gulf toadfish are important food items (Figure 2.2 and 2.3). The colony has a high within-phenotype component (WPC) with most individuals utilizing many prey types simultaneously.

I collected 29 bolus samples from 10 heron nests on Sandy Key in the Bay. The cumulative biomass of the bolus samples was 421.41g. Herons exhibited strong selection for gulf toadfish (Table 2.1, Fig. 2.4) which occurred in 100% of nests, followed by prawns (90%) and Mangrove tree crabs (40%; Table 2.2). In nests where gulf toadfish occurred, they comprised 61% of the bolus biomass whereas prawns contributed 31% and

mangrove tree crabs 15%. The selection results suggest herons in the Bay colony are primarily generalists but exhibit slight specialization for gulf toadfish (Fig. 2.4). Gulf toadfish density was 15x higher in the foraging areas closest to the Sandy Key colony than the other foraging areas (10-20 km away) combined. The colony has a high WPC with most individuals utilizing many prey types simultaneously.

2.4 DISCUSSION

2.4.1 Heron Diet Patterns

Coastal South Florida heron diet is most similar to the diet of herons in northeast Brazil, which are mostly piscivorous, eating livebearers (*Poeciliidae*; Martínez 2010) and prawns (*Farfantepenaeus paulensis*; Gianuca et al. 2012). Heron diet studies closer in proximity including Tampa Bay, FL occurred in similar intertidal habitat, but found fish and blue crabs are the most important prey items by biomass (Kent 1986). Surprisingly, marine crabs were largely absent from heron diet in my study, ~ 340 km from that of Kent (1986). I initially considered whether the absence of marine crabs could be due to the intolerance of young chicks to salty prey in the absence of fresh water, as has been observed in White Ibis (*Eudocimus alba*; Johnston & Bildstein 1990). However, shrimp, which also have high salt content, were readily consumed by herons in my study. More likely, the difference was due to the digestibility of mud crabs which have thicker exoskeletons than blue crabs and prawns (personal observation). The blue crabs found in the bolus collected by Gianuca et al. (2012) and Olmos et al. (2001) were recently molted, supporting this hypothesis.

Semi-terrestrial/arboreal crabs were present in heron diet in my study, but not to the degree found in the diets of herons in nearby study sites. Herons in Puerto Rico feed

almost exclusively on abundant fiddler crabs (*Uca* spp.) (Miranda and Collazo 1997) and Olmos et al. (2001) found herons are scarcer on the mudflats during the breeding season, foraging in the mangrove forest and consuming mainly arboreal grapsid crabs. However, herons do not appear to consume crabs only when they are present in high numbers (Martínez 2010). Fiddler crabs are found in high densities on the nearby São Paulo coast (Olmos et al. 2001) and Cajual Island (Martínez 2004), but are almost absent from heron diets in those areas (Martínez 2010). Without quantitatively examining the available prey, the drivers of regional diet differences are not clearly understood.

Hérons in coastal South Florida specialized on two prey species, gulf toadfish and prawns; however, there was a difference in selectivity between colonies. Herons at Sandy Key colony in the Bay specialized on gulf toadfish, a slow moving and benthic predatory fish. Sandy Key was the only heron colony in the Bay despite nearby islands hosting colonies of conspecifics. Sandy Key was closest to foraging areas with highest densities of gulf toadfish, therefore herons may select colony locations near high densities of a preferred prey species.

Hérons at Third Island in the Keys specialized on gulf toadfish and prawns. They also exhibited a strong selection for mojarra, pipefish and seahorse (Fig. 2.4), but these species were not prevalent in the diet (Fig. 2.2). The strong selection for these species may be mostly a function of their rarity in the environment. Alternately, their presence could simply be a result of herons' foraging strategy. Heron diet could reflect the expanding specialist diet strategy (Heller 1980; Holt and Kotler 1987) where foragers select their preferred food until it is depleted to a critical level in a foraging patch and the bird expands its selection to opportunistically include less desirable food (Brown &

Mitchell 1989). This would explain why herons use semi terrestrial crabs in some areas and not others, regardless of their occurrence.

Hérons mitigate the restrictions of shallow water availability by supplementing terrestrial prey in their diet when the tide is too high to forage on the mudflats. The presence of reptiles, insects, fiddler and mangrove tree crabs in the bolus samples at both sites suggest heron forage in the interior of mangrove islands in addition to mudflats. It is also possible heron chicks may opportunistically capture terrestrial prey like insects around the nest. Diet samples in this study were collected just after the rising tide made the foraging habitat adjacent to the colony unavailable; therefore, the importance of terrestrial prey could be underrepresented by our study. The timing of diet sampling could partially explain the high abundance of arboreal crabs in other diet studies. For this reason, foraging habitat studies should consider the availability of island habitats not just for roosting and nesting, but also for supplemental terrestrial prey use. Mangrove island foraging habitat may become more important as shallow water available decreases with sea level rise.

Sea level rise will reduce the area and time shallow water is available for foraging further limiting heron prey availability (Calle et al. 2018). The quality of a foraging area may change even within the water level range of herons' foraging ability. Herons in coastal South Florida capture slow-moving, bottom-dwelling fish like gulf toadfish (Bohlke & Chaplin 1993), similar to diet observations by Kent (1986). If herons specialize on prey at the bottom of the water column, ideal water levels may be lower than the maximum water level herons can forage.

2.4.2 Conclusion

Some wading bird species exhibit a higher degree of prey specialization when prey density is high (Beerens et al. 2011). The variation in heron diet studies across their range could be explained by herons adjusting their prey preferences in response to prey density. This also emphasizes the importance of assessing prey density when evaluating habitat quality if foraging site selection is primarily driven by long time-integrated habitat availability (Calle et al. 2018). If herons appear to be selecting one or a few prey species like they were in GWH and the Bay, this could indicate prey density is high. If herons exhibit a strictly generalist diet, it could indicate prey densities are not optimal. The specialization of heron diet observed in GWH suggests the Calle et al. (2018) study was conducted at a time of high prey density. Herons employ an ‘exploiter’ foraging strategy, utilizing areas where shallow water is available the longest even after prey densities decline. Therefore, the quality of prey in the foraging area may not be reflected by the presence of herons, which could be problematic when trying to predict how birds will respond to environmental variation. Quantitatively evaluating available prey gives an ecosystem context to wading bird diet, which can be used to assess causes of change in wading bird productivity and direct management decisions.

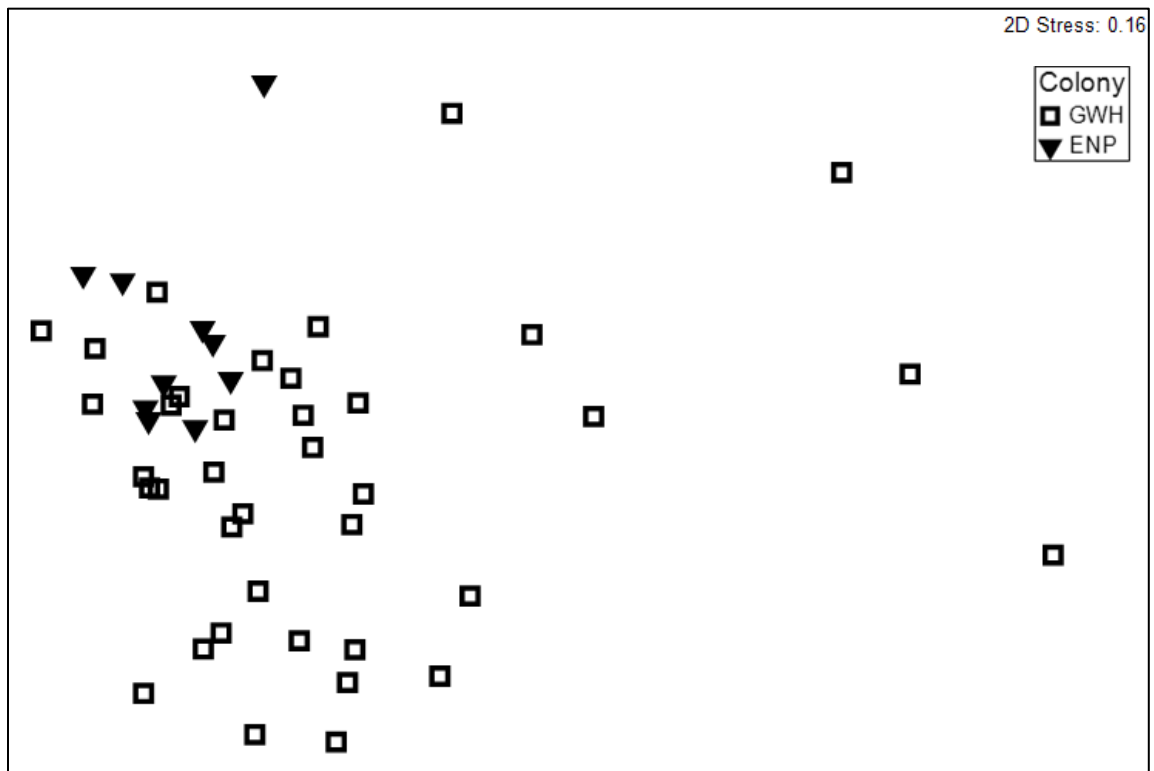


Figure 2.1 nMDS ordination of prey weight composition in nestling heron boluses in Great White Heron National Wildlife Refuge (GWH) (n = 38) and Florida Bay (ENP) (n = 10). Each point represents a nest.

Table 2.1 Mean food-type selectivity (Chesson's index, ai ; 95% CI) across all 48 nests from Great White Heron National Wildlife Refuge and Florida Bay. Both values for gulf toadfish are greater than 1/m, which indicates selection of this prey type in both colonies. Refer to the methods for a further explanation of how to interpret Chesson's index.

		Colony location	
Food item		Great White Heron National Wildlife Refuge	Florida Bay (n=10)
		(n=38)	
Species	Common Name	Mean (95% CI) (1/m = 0.083)	Mean (95% CI) (1/m = 0.100)
<i>Opsanus beta</i>	Gulf toadfish	0.103 (0.054-0.15)	0.829 (-0.028-0.028)
<i>Eucinostomus</i>	Mojara	0.236 (0.106-0.366)	0.030 (-0.092-0.153)
<i>Syngnathidae</i>	Seahorses & pipefishes	0.198 (0.167-0.228)	0.002 (0.001-0.005)
<i>Penaeus spp.</i>	Prawns	0.159 (0.109-0.210)	0.086 (0.049-0.123)
<i>Pleuronectiformes</i>	Flatfish	0.063 (0.061-0.064)	0.008 (0.00-0.00)
<i>Actinopterygii</i>	Ray-finned fishes	0.057 (-0.003-0.116)	0.013 (0.00-0.00)
<i>Cyprinodontiformes</i>	Live bearers	0.055 (-0.044-0.154)	0.001 (0.000-0.003)
23 <i>Gobiidae</i>	Goby	0.018 (0.003-0.032)	0.001 (0.001-0.001)
<i>Percoidei</i>	Percoidei	0.007 (-0.002-0.009)	0.028 (-0.033-0.087)
<i>Alpheus spp.</i>	Pistol shrimp	0.002 (0.000-0.004)	0.005 (-0.003-0.012)
<i>Decapoda</i>	Marine Crab	0.001 (-0.002-0.005)	-
<i>Anguilliformes</i>	Eels	0.065 (0.037-0.092)	-

Table 2.2 Results comparing diet differences between colonies. Biomass estimates of food items in heron stomachs from GWH (n = 38) and Bay (n =10) in south Florida June to July 2016-2017. The numbers in parentheses indicate the sample size for the corresponding area. The percent occurrence in the nests (i.e., the number of nests that consumed a particular item from that colony). + indicates that the item was present but comprised less than 1.0% of the mass.

		Colony location			
Food item		Great White Heron National Wildlife Refuge (n=38)		Florida Bay (n=10)	
Species	Common Name	Mean (95% CI)	% Occurrence of food item	Mean (95% CI)	% Occurrence of food item
<i>Opsanus beta</i>	Gulf toadfish	31 (0.2-0.4)	74	61 (0.5-0.7)	100
<i>Penaeus spp.</i>	Prawns	40 (0.3-0.5)	89	31 (0.2-0.4)	90
<i>Aratus pisonii</i>	Mangrove treecrab	14 (0.1-0.2)	37	15 (-0.1-0.4)	40
<i>Cyprinodontiformes</i>	Live bearers	10 (0.0-0.2)	34	+	50
<i>Syngnathidae</i>	Seahorses & pipefishes	10 (0.1-0.1)	68	+	20
<i>Eucinostomus</i>	Mojara	8 (0.0-0.1)	50	3 (0.0-0.1)	20
<i>Arthropoda</i>	Terrestrial invertebrate	8 (0.0-0.2)	42	+	20
<i>Decapoda</i>	Marine Crab	7 (-0.1-1.3)	21	+	10
<i>Pleuronectiformes</i>	Flatfish	5 (0.0-0.1)	37	1	10
<i>Anguilliformes</i>	Eels	4 (-0.3-0.4)	19	-	-
<i>Alpheus spp.</i>	Pistol shrimp	3 (-0.2-0.2)	39	4 (0.0-0.1)	40
<i>Gobiidae</i>	Goby	2 (0.0-0.0)	32	+	20
<i>Actinopterygii</i>	Ray-finned fishes	2 (0.0-0.0)	29	3	10
<i>Percoidei</i>	Percoidei	1 (0.0-0.0)	11	5 (0.0-0.1)	20
<i>Anolis spp.</i>	Anole	14	3	5	10

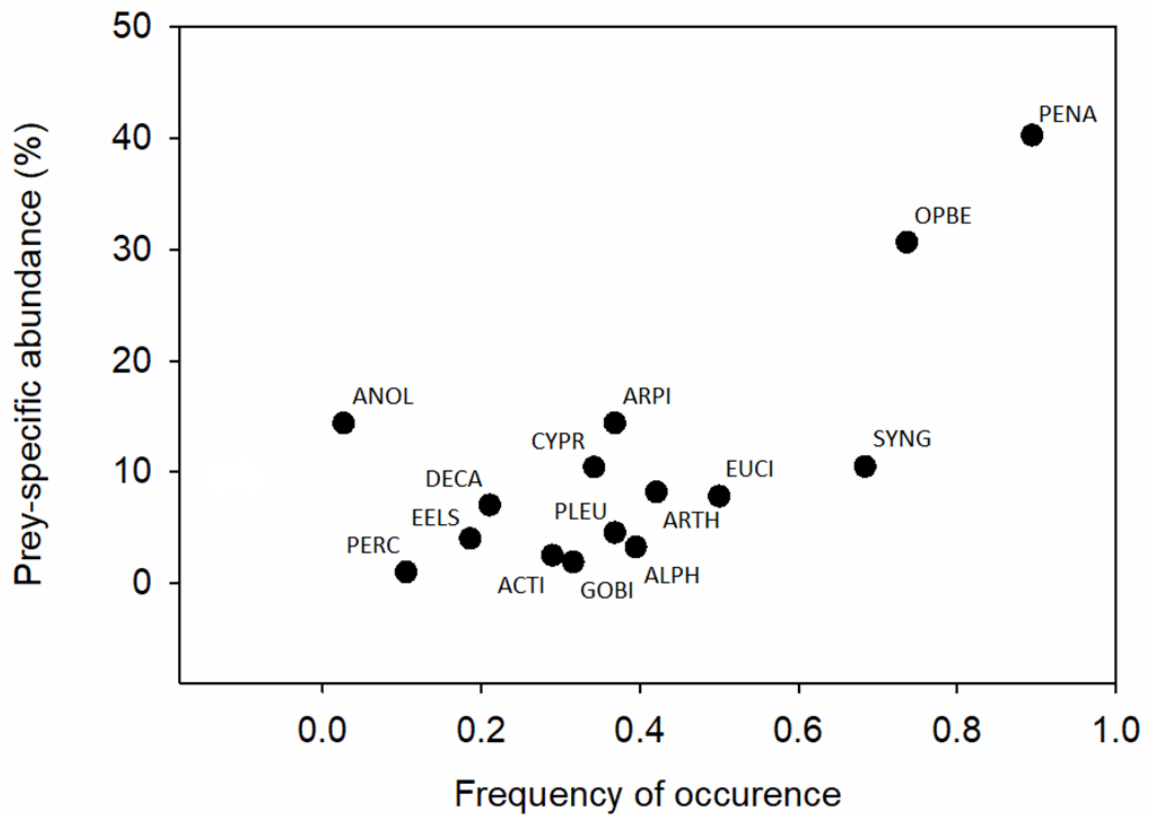


Figure 2.2 Modified Costello graphs (Amundsen et al. 1996) of diet samples from 38 nests in GWH. Prey species names are abbreviated scientific names (Appendix 1A, Table A1). Refer to Methods for a further explanation of how to interpret graphs.

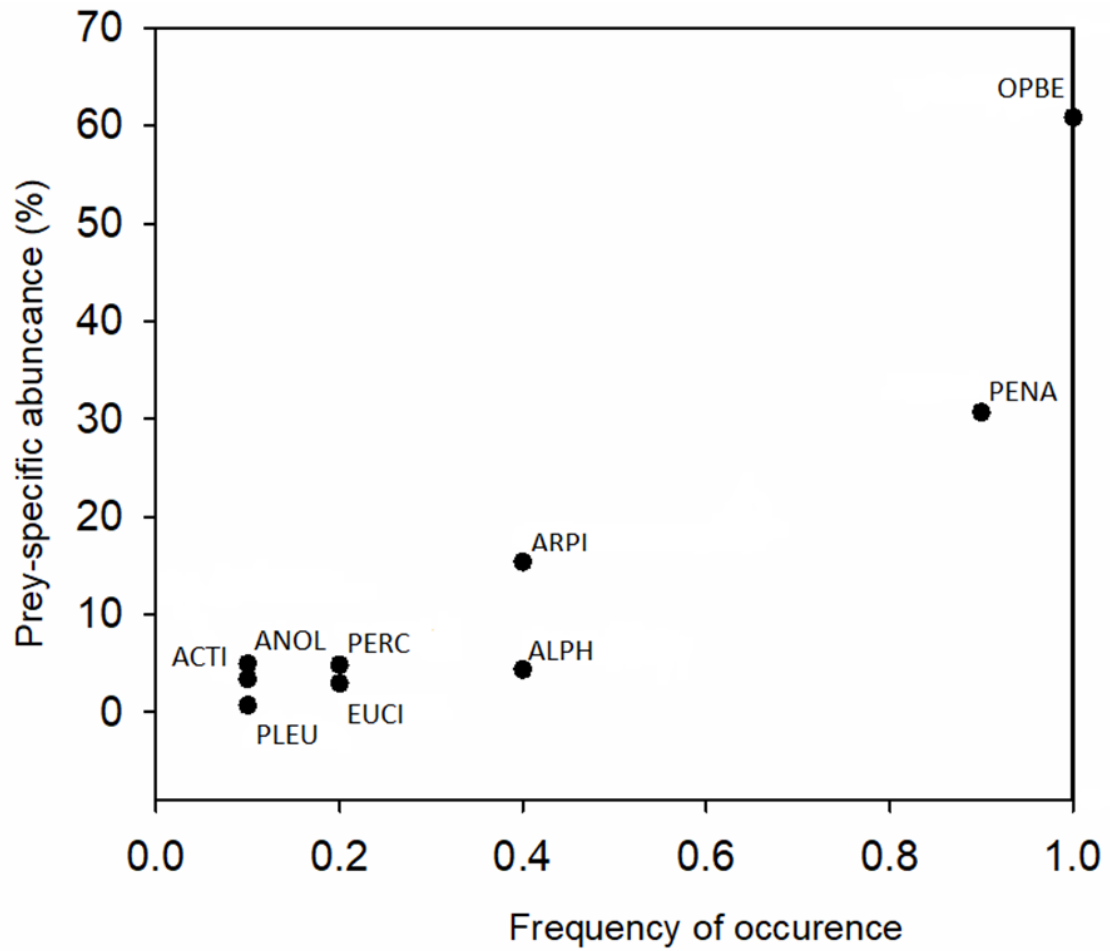


Figure 2.3 Modified Costello graphs (Amundsen et al. 1996) of nestling diet from 10 Little Blue Heron nests in Florida Bay. Prey species names are abbreviated scientific names (Appendix 1A, Table A1). Refer to Methods for a further explanation of how to interpret graphs.

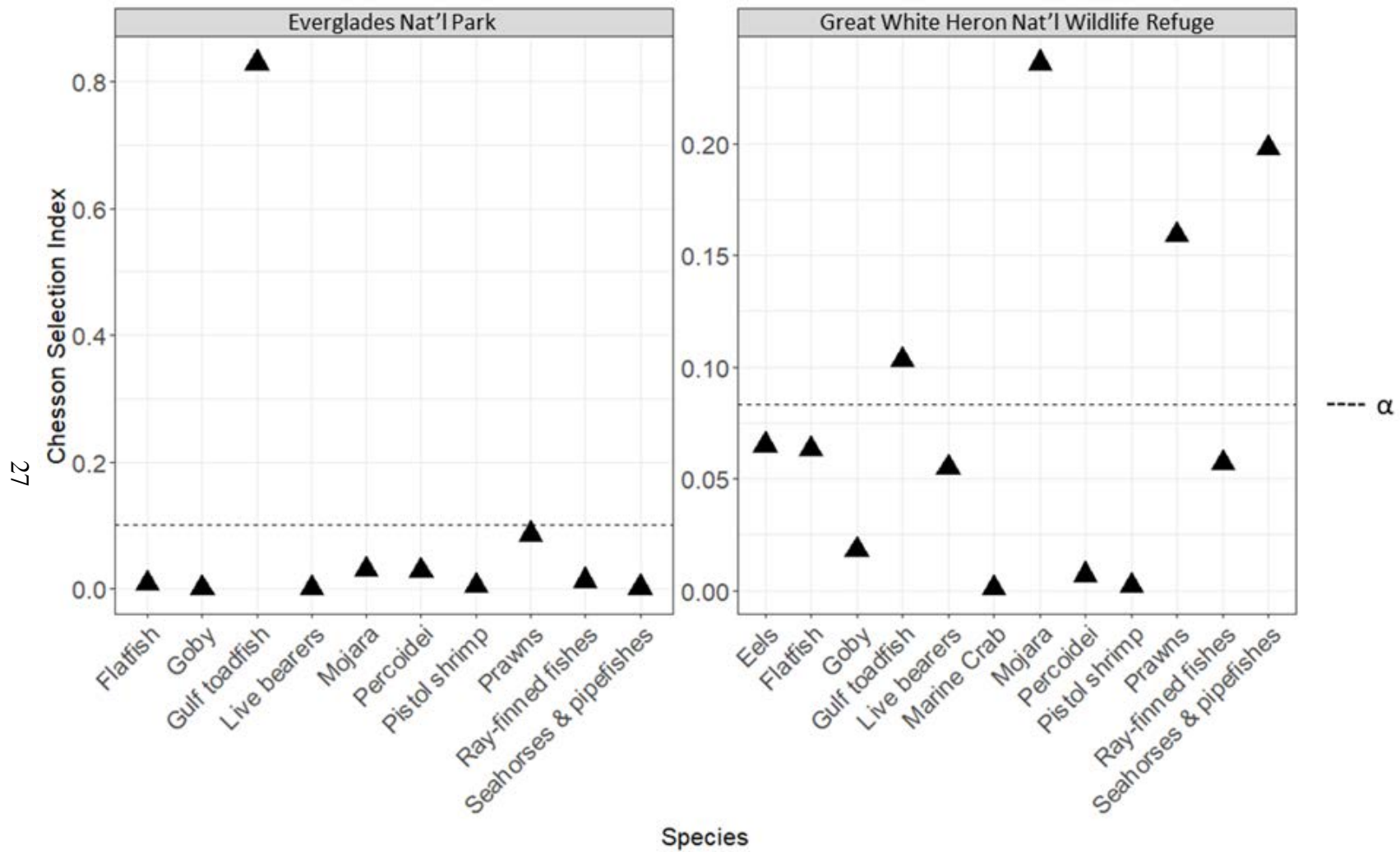


Figure 2.4 Prey species selection using Chesson's Selectivity Index, of the Little Blue Heron from nests in Great White Heron National Wildlife Refuge and Florida Bay (n=48) in Everglades National Park.

3 LITTLE BLUE HERON PREY ASSOCIATIONS WITH AQUATIC VEGETATION METRICS IN COASTAL SOUTH FLORIDA

3.1 INTRODUCTION

Coastal ecosystems are declining due to a number of anthropogenic causes, including coastal development, overfishing, increased nutrient loading, and climate change (Wyda et al. 2002, Fabry et al. 2008, Sih et al. 2011, Janousek et al. 2016, Wang et al. 2016). Many of the consequences of these disturbances drastically affect key marine species such as submerged aquatic vegetation (SAV). Ocean warming and acidification reduce the abundance of canopy forming algae (Schiel et al. 2004) and inhibit calcification of calcareous algae (Feely et al. 2004, Hoegh-Guldberg et al. 2007), which provide habitat for marine fauna like crabs (Stachowicz and Hay 1996). Nutrient over-enrichment and associated physical disturbance leads to seagrass meadow fragmentation and reduction, rapidly altering or eliminating seagrass ecosystems globally (Orth et al. 2006, Waycott et al. 2009). SAV provides carbon sequestration (Trevathan-Tackett et al. 2018), nutrient cycling (Delgado et al. 2017), sediment stabilization (van Katwijk et al. 2010), and is crucial habitat for marine fauna (Kingsford & Choat 1985, Nordlund et al. 2018). Changing the SAV species composition and structural characteristics of vegetated marine habitats may reduce their value for higher trophic levels (Wyda et al. 2002, Micheli et al. 2008, Sweatman et al. 2017).

Coastal ecosystems in South Florida have experienced increased salinity levels and extensive seagrass mortality due to a disruption of natural freshwater flow through

water control structures and anthropogenic nutrient enrichment (USACE 1999). A recent episodic seagrass mortality event in Florida Bay killed over 8,777 ha of *Thalassia testudinum* (Hall et al. 2016). Degraded intertidal vegetation communities alter coastal fish populations, reducing faunal diversity and abundance (McCloskey and Unsworth 2015, Iacarella et al. 2018, Santos et al. 2018), and affecting predators like wading birds dependent on the prey productivity of seagrass beds (USACE 1999).

Wading bird prey densities in freshwater ecosystems are higher in vegetated than non-vegetated areas (Ntiamoa-Baidu et al. 1998, Laubhan and Gammonley 2000, Safran et al. 2000). Likewise, in marine systems, stark differences in macrofaunal assemblage metrics (e.g., abundance, biomass, and species diversity) occur at the boundary between vegetated and unvegetated areas, even between slightly vegetated areas and bare patches (Barnes and Hamylton 2016). Some invertebrates and fish exhibit a species-specific response to SAV community composition (Heck and Wetstone 1977, Grenouillet et al. 2002, Micheli et al. 2008) and SAV density (McCloskey Unsworth 2015). Prey species may have a quadratic relationship with SAV density (i.e., higher density at moderate SAV density; McCloskey and Unsworth 2015) or may exhibit no response to SAV density (Lefcheck et al. 2016). Alternatively, some studies have demonstrated few significant differences in abundance, growth or survival of fauna when comparing seagrass meadows to other structured habitats, such as oyster or cobble reefs, or macroalgal beds, suggesting the type of cover is not important (Heck et al. 2003). Quantifying the specific relationships between fauna and their associated habitat is an important preliminary step for linking wading birds to lower trophic levels and

establishing effective parameters to predict how the ecosystem overall could respond to environmental variation.

Wading birds are connected to an ecosystem's condition through their diet and are quickly impacted when habitats are degraded (Stolen et al. 2005). When modeling the ability of wading birds to find suitability habitat in different ecological scenarios, landscape features such as distance to deep water (Lawrie et al. 1999, Gibson 2003, Pittman et al. 2004), substrate (Pittman et al. 2004) and distance to islands (Pittman et al. 2004, Ellis and Bell 2008) have been used as proxies for prey density (abundance or biomass); however these proxies are not universally effective or prey-species-specific. Presence of SAV is also used as a predictor of prey abundance (Matsunaga 2000), but specific SAV metrics (i.e. density) could be a more effective and accurate method of estimating prey species density because of prey preferences. For example, Carss and Elston (2003) showed that prey abundance was higher in SAV areas dominated by *Ascophyllum sp.* than an area dominated by *Fucus sp.* in the same loch. Consequently, more Gray Herons foraged in the area with higher prey abundance. Thus, relative prey density can be predicted using the dominance of only the preferred SAV species (Grenouillet et al. 2002, McCloskey and Unsworth 2015). Landscape variables like distance to island are also important for determining the distribution of the seagrass species like *T. testudinum* and *H. wrightii* (Green et al. 2015), therefore examining the effect of SAV metrics on prey density separately from correlated landscape variables could clarify which landscape parameters are most influential to prey density. Additionally, SAV maps are regularly generated by state agencies and remote sensing technologies can be used to gather seagrass species density values for sites (Eugenio et al.

2017) making access to SAV data cost effective and less invasive to gather than conventional sampling methods (Comas Gonzalez 2015).

I investigated whether SAV density is associated with densities of three key wading bird prey species, namely gulf toadfish (*Opsanus beta*), prawns (*Farfantepenaeus spp.*), and pipefish (*Syngnathidae spp.*). In Florida, gulf toadfish are reportedly associated with *T. testudinum* (Serafy et al. 1997), prawns with *H. wrightii* (Costello et al. 1986; Robblee et al. 1991, Pérez-Castañeda et al. 2010), and pipefish with mixed seagrass beds with low algae cover (Masonjones et al. 2010). The objectives of this study were to determine the associations of wading bird prey (prawn, gulf toadfish, and pipefish) abundance and biomass with specific SAV densities, or if abiotic variables of salinity and seasonality are stronger indicators when SAV is present. Prey abundance is a useful measure for prey available to wading birds (Lorenz 2014); however, biomass can be a better approximation of productive capacity (Stoneman and Jones 2000). I predicted the vegetation community composition in tidal flats would be different between locations. I predict gulf toadfish will be positively associated with *T. testudinum* density and prawns will be positively associated with moderate densities of *H. wrightii* while pipefish will be positively associated with mixed seagrass beds with low algae density. Understanding the relationship between specific SAV metrics and wading bird prey will further elucidate influential parameters of prey density.

3.2 METHODS

3.2.1 Study Site Selection

This study took place in Great White Heron National Wildlife Refuge (GWH) and Florida Bay (hereafter Bay) in Everglades National Park. The Bay is a shallow lagoon,

with large spatial differences in water temperature, nutrients, turbidity, and salinity due to the separation of basins by mudflats (Handley et al. 2007). The Bay's ecosystem processes are driven in part by freshwater inputs, but alteration of the historic freshwater flow into the Bay, causes hypersaline conditions (>40 ppt, Sullivan et al. 2018) which greatly influence the distribution and abundances of estuarine organisms depending on their salinity tolerance (Hall et al. 2006). Unlike the Bay, GWH is less influenced by freshwater inputs, but more affected by nutrient loading which originates from nearshore septic systems, Florida Bay, and farther sources like the Mississippi river (Hu et al. 2005). Additionally, both areas have dissimilar landscape features known to influence prey abundance such as distance to deep water (Lawrie et al. 1999, Gibson 2003, Pittman et al 2004), substrate (Pittman et al. 2004), and seagrass (Carss and Elston 2003, Pittman et al. 2004, Moore and Hovel 2010).

3.2.2 Study Species

The Little Blue Heron (*Egretta caerulea*; hereafter heron) is a threatened wading bird in the state of Florida (FWCC 2017) and is a species of High Concern in the North American Waterbird Conservation Plan (Kushlan et al. 2002). Herons may be a good indicator of ecosystem health across their range because they utilize both fresh and saltwater systems and respond to changes in water level due to their restrictively short leg length (Gawlik 2002, Calle et al. 2016, Calle et al. 2018).

In Florida Bay and Florida Keys, heron diets are dominated by three species: prawns (*Farfantepenaeus spp.*), gulf toadfish (*Opsanus beta*), and pipefish (*Syngnathidae spp.*) (see heron diet chapter). High densities of early settlement prawns like (*Farfantepenaeus duorarum*), are often observed in shoal grass (*Halodule wrightii*) beds

suggesting a preference for this SAV species (Costello et al. 1986; Robblee et al. 1991, Pérez-Castañeda et al. 2010); however, Sheridan et al. (1997) did not find prawns to associate with one species of seagrass. Additionally, seagrass density preferences of prawns have not been investigated. Other estuarine shrimp species (*Pandalus latirostris*) exhibit a preference for high seagrass density over seagrass species richness/diversity (Yusa et al. 2018). Perez-Castaneda et al. (2010) found a negative relationship with prawn abundance and algae density, although in some estuaries it has been reported that algal beds support densities of juvenile shrimp (*Penaeus semisulcatus*) equal to those found in seagrass beds (Haywood et al. 1995). As algae may provide additional shelter to prawns, the influence of algae on prawn abundance and biomass has not been studied in the Bay. The distribution and abundance of gulf toadfish in the Bay are correlated with presence of *T. testudinum* (Serafy et al. 1997). In Florida, high pipefish abundances and larger body sizes are correlated with low microalgal cover and mixed seagrass species assemblages that provide camouflage for a range of pipefish body types (Masonjones et al. 2010).

3.2.3 Heron Abundance Surveys

To identify heron foraging locations I conducted surveys along a ~10 km transect from Upper Harbor Key (24.80851, -81.44166) to Howe Key (24.73063, -81.43104) at GWH, a 4.3 km transect at Snake Bight (25.14055, -80.89736), a 2.2 km transect at Frank Key (25.10604, -80.91135) and Murray Key (25.10759, -80.93946), and at three survey points at Sandy Key (25.03431, -81.01465) in the Bay. In such open landscapes, detectability of wading birds using the double-observer method (Nichols et al. 2000) is near one hundred percent up to 600 m from the observer location (Calle et al. 2016).

Therefore, a 600 m buffer around surveys transects and survey points represented the survey area. I performed surveys from February to July 2017 to coincide with the heron breeding season. Surveys began up to two hours before low tide and the direction of transect surveys alternated by 180 degrees with each subsequent survey. I recorded locations and abundance of foraging herons every 500 m along transects by recording a bearing and distance to the bird or center of the flock from a GPS-referenced observer location (GPSMAP 78sc; Garmin International, Olathe, Kansas, USA). I did not count birds in flight or perched in trees. I used a rangefinder or visual estimation to measure distance.

3.2.4 Quantification of Prey Species Abundance and Biomass

From February to July 2017 I assessed prey community at 122 sampling points which were comprised of non-random (i.e., used) and random (i.e., available) locations. To establish non-random locations, I randomly chose one heron foraging location from the foraging distribution survey, estimated the water depth in relation to the nearest tidal gauge, calculated the time that the water depth would be within 3 cm of the observed depth on the sampling date, then used ArcGIS to plot the foraging location, and sampled within 3 m of the location. To delineate random locations, I applied a stratified random method of hexagonal tessellation to the survey area (Birch et al. 2007). Several random sampling points were generated by ArcGIS within each hexagon and one point was selected based on suitable water depth for herons (<0.3 m; Kushlan et al. 1985).

I sampled prey at non-random and random locations using a 1-m² throw trap with a mesh netting frame (Jordan et al. 1997). Throw-trapping is an effective method for sampling species that show a behavioral response of diving into the seagrass bed when

disturbed (Shulman 1985). First, salinity was measured using a refractometer, then SAV measurements are taken (See section 3.2.6) before all vegetation is removed. Prey is collected from the throw-trap by passing a 100 cm by 40 cm bar seine through the water column until three consecutive sweeps yielded no prey (Chastant et al. 2018). Larger prey (>10 cm) was identified, measured, and released. The specimens were identified to species and weighed to 0.01 g. Prey capture, handling, and euthanasia techniques adhered to protocols approved by the Institutional Animal Care and Use Committee at Florida Atlantic University (permit number A15-37), Everglades National Park (EVER-2015-SCI-0067), U.S. Fish and Wildlife Service (FY17-03) and National Oceanic and Atmospheric Administration (FKNMS-2015-15).

3.2.5 Quantification of Submerged Aquatic Vegetation Community

I used a 1-m² quadrat divided into four 0.25-m² grid cells to quantify the percent cover of SAV species at 36 non-random and 86 random sampling locations. For every species present in each grid cell I assigned a Braun-Blanquet score that best represents its density (Table 3.1; Braun-Blanquet 1972, Fourqurean et al. 2002). The percent cover of each species per 1-m² quadrat was calculated as the average of the four Braun-Blanquet scores. I repeated this assessment 5m from the sampling location in each cardinal direction to acquire 5 replicates per sampling event.

I used Braun-Blanquet scores to calculate SAV abundance (1), frequency (2) and density.

$$(1) \quad A_i = \frac{\sum_{j=1}^n s_{ij}}{N_i}$$

where N_i is the number of quadrats or replicates at a site in which taxon i was present, j = quadrat number from 1 to N , the total number of quadrats sampled at a site, and s_{ij} = the

Braun-Blanquet score for taxon i in quadrat j . For any taxon, A can range between 0 and 5, the maximum Braun-Blanquet cover class score.

$$(2) \quad F_i = \frac{N_i}{n}$$

where n is the total number of quadrats observed at a site, such that $0 < F_i < 1$

(Fourqurean et al. 2002). I calculated density of taxon (Di) as the product $A_i \times F_i$ and calculated total species density (D) as sum of all taxa (Di) values. I combined algae species into one gross taxonomic group since focal prey species do not demonstrate a preference for algae species.

3.2.6 Abiotic Variables

The seasonality parameter ‘day length (hours)’ was included in my prawn models as the literature supported seasonal trends and an influence of temperature on the abundance (Browder et al. 2002). Literature support for seasonal abundance trends was conflicting for gulf toadfish (Sarafy et al. 1997, Barimo et al. 2007) and pipefish (Barrows et al. 2009, Masonjones et al. 2010), so ‘day length (hours)’ was included in the abiotic models and global models. The effect of salinity (ppt) levels on adult abundance and biomass is unknown for gulf toadfish and pipefish (but see Lorenz 1999, Lorenz and Serafy 2006) and was initially included in models, then removed as it did not improve models.

3.2.7 Statistical Analysis

3.2.7.1 Similarity Analysis

I performed multivariate analyses as outlined by Clarke and Warwick (2001) to compare SAV species in foraging areas between GWH and the Bay. A Bray-Curtis similarity matrix was calculated on square-root transformed density data for SAV species

within samples. This analysis generates an index of similarity between pairwise samples. The transformation down-weights the influence of dominant SAV species. I tested for differences among study location SAV samples using an ANOSIM, which is a non-parametric permutation procedure to test differences based on the ranks of pairwise similarities in the Bray-Curtis matrix. I also used an NMDS plot derived from the Bray-Curtis similarity matrix to visually examine diet overlap between colonies based on prey composition. The resulting R statistic value is between zero and one, with zero indicating samples are similar and values close to one are dissimilar. If SAV communities were significantly different in the ANOSIM ($p \leq 0.05$), I used the similarities percentage (SIMPER) analyses to determine which SAV species are driving those differences. A SIMPER analysis uses dissimilarity to demonstrate the degree to which SAV species density contributes to the difference of vegetation community sites and indicates the percentage each SAV species contributed to any differences that may exist between sites. All techniques were performed using PRIMER v7 (Clarke and Gorley 2007).

3.2.7.2 Model Framework

I tested support of 4 *a priori* prey species abundance/biomass hypotheses, Single Species Association Hypothesis, Total Cover Hypothesis, Moderate Density Association Hypothesis and Abiotic Hypothesis (Table 3.2 and Table 3.3), using a model selection approach. The Single Species Association Hypothesis predicts that prey species density is associated with the species-specific SAV density (D_i). Total Cover Hypothesis predicts that prey density and biomass are associated with a combined SAV density (D) of two or more SAV species. The Moderate Density Association Hypothesis predicts prey density and abundance peaks at moderate SAV density; therefore, SAV density is modeled using

a quadratic relationship (D_i^2 , D^2). The Abiotic Hypotheses predicts prey density and abundance is influenced by season (hours of daylight) and/or salinity (ppt) rather than SAV density.

Species-specific densities models are a function of hypothesized biotic and abiotic covariates analyzed using a generalized linear mixed model. Site location was included as a random effect to account for abiotic differences between sites not included in the models (i.e. distance to islands, distance to deep water, substrate). I excluded samples where prey species were not detected. I tested for multicollinearity among parameters by examining pairwise Pearson correlation coefficients. When correlation coefficients were > 0.7 one of the correlated variables was excluded. All analyses were performed in R version 3.5.1 (R Core Team, 2013).

Competing models were compared using Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2004). I calculated Akaike evidence weights (w_i) and averaged models with ΔAIC_c values < 2 (Bolker et al. 2009, Grueber et al. 2011). I used the MuMIn (Barton and Barton 2018) package in R version 3.5.1 (R Core Team 2013) to determine conditional average parameter estimates, relative importance, and confidence intervals for parameters of interest (Barton and Barton 2018). Pseudo R^2 values were calculated for top models and averaged models to evaluate the predictive power of the models (Table 3.7).

To establish which habitat characteristics are important predictors of prawn abundance I used general linear mixed effects model with a negative binomial distribution to account for overdispersion typical of count data (GLMM, package lme4: Bates et al. 2015). I used a power transformation on prawn biomass then fit the data to a

linear mixed effects model (LMM, package lme4: Bates et al. 2015). I tested my first hypothesis that prawns would be associated with moderate densities of SAV by including quadratic terms for the SAV density variables (*H. wrightii* (D_i), density of *T. testudinum* (D_i), density of algae (D)). Models with quadratic terms did not perform better than linear models (lower AIC values) and the quadratic terms were removed. I tested my second hypothesis that prawn abundance/biomass will be associated with *H. wrightii* using 5 models including total SAV density and a model with only *H. wrightii* density. A model with salinity (ppt.) was tested as a competing hypothesis for prawn abundance/biomass (Browder et al. 2002). Seasonality (hours of daylight) was included in all models due to literature support.

To determine which habitat characteristics are important predictors of gulf toadfish abundance, I used general linear mixed effects model with a Poisson distribution (GLMM, package lme4: Bates et al. 2015). For gulf toadfish biomass, I used general linear mixed effects models with a gamma distribution (GLMM, package lme4: Bates et al. 2015) for overdispersed, continuous data. I tested my first hypothesis that gulf toadfish would be associated with moderate densities of SAV by including quadratic terms for the SAV density variables (*H. wrightii* (D_i), density of *T. testudinum* (D_i), density of algae (D)). No species of SAV exhibited a quadratic relationship with gulf toadfish, so the quadratic terms were removed and the species and were used in the habitat characteristic models as linear variables. I tested my second hypothesis that gulf toadfish will be associated with *T. testudinum* using three models including density of *T. testudinum* (D_i), and total SAV cover. I included a model representing the alternative

hypothesis that gulf toadfish abundance/biomass is seasonally driven using the variable 'hours of daylight'.

To establish which habitat characteristics are important predictors of pipefish species abundance I used general linear mixed effects models with a Poisson distribution (GLMM, package lme4: Bates et al. 2015). For pipefish biomass, I used general linear mixed effects models with a gamma distribution (GLMM, package lme4: Bates et al. 2015). Because herons do not select for a specific type of pipefish, I developed models to test pipefish relationships with SAV metrics that might be similar across many pipefish species. I tested my first hypothesis that pipefish would be associated with moderate seagrass and an alternative hypothesis that pipefish would be associated with moderate algae densities by including quadratic terms for the variables *H. wrightii* (Di) density, density of *T. testudinum* (Di), and density of algae (D). No species of SAV exhibited a quadratic relationship with pipefish, so the SAV density variables were included in the habitat characteristic models as having linear relationships. I tested my second hypothesis that pipefish abundance/biomass will be positively associated with mixed seagrass beds with low algal cover using 6 models: *H. wrightii* (Di) associated, *T. testudinum* (Di) associated, algal associated. My alternative hypothesis that pipefish abundance/biomass is seasonally influenced was tested using 'hours of daylight'. I expected the global model to perform the best.

3.3 RESULTS

3.3.1 Prey Species Abundance and Biomass

I collected 4,048 individual prey items from 67 throw traps within Florida Bay. Gulf toadfish were present in 38 samples, prawns were present in 83 and pipefish were

present in 49 samples. Prawn was the most common prey species representing 17% of individuals followed by pipefish (1%), and gulf toadfish (1%) (Appendix A, Table A3). Prawns comprised 22% of the prey biomass followed by pipefish (0.2%), and gulf toadfish (0.1%). I collected 3,021 individuals from 55 throw traps within GWH. Similarly, prawns represented 18% of individuals followed by gulf toadfish (2%), and pipefish (0.1%). Gulf toadfish comprised 10% of the prey biomass followed by prawns (7%), and pipefish (0.01%).

3.3.2 Submerged Aquatic Vegetation Community

The ANOSIM results showed that the vegetation composition differed significantly between sites (ANOSIM R value = 0.459, p-value = 0.01). The SIMPER analysis results indicated algae contributed the most to SAV density differences between groups. Seagrass was found at 93% of the locations, *H. wrightii* at 78% and *T. testudinum* at 60%. Algae spp. were found at 72% of locations. The average *H. wrightii* density was 25-50% cover ($2 < D < 3$). The average *T. testudinum* density was 5-25% cover ($1 < D < 2$). I identified three species of seagrass and 34 species of algae. The average total algae density was 5-25% cover ($1 < D < 2$). Manatee grass (*Syringodium filiforme*) was only detected at two locations and was included in the 'total seagrass density' variable, but not tested separately for SAV species preference in the models.

I recorded 53 hypersaline events (> 40 ppt, Sullivan 2018) of which 83% occurred in Florida Bay. Maximum salinity ranged from 45 ppt in GWH to 52 ppt in the Bay. Prawns were found in salinities ranging from 34-52 ppt. Pipefish were found in salinities ranging from salinity 34-52 ppt. Gulf toadfish were found in salinities ranging from 34-49 ppt.

The Combined Cover Hypothesis best represents prawn abundance and biomass (Table 3.3, Table 3.4). The top model for prawn abundance ($w_i = 0.75$) and biomass ($w_i = 0.98$) was seasonality, algae density and seagrass density and accounted for 52% and 22% (respectively) of the variation in prawn density (Table 3.5). Prawn abundance is highest when density of algae and all seagrass species increases (Table 3.6). There is a lack of support for season as the 95% confidence interval overlapped zero. Unlike prawn abundance models, prawn biomass is increased only under increased seagrass density (Table 3.6).

The Combined Cover Hypothesis best represents gulf toadfish abundance and biomass (Table 3.3, Table 3.4). The top model for gulf toadfish abundance ($w_i = 0.74$) and biomass ($w_i = 0.44$) was algae density and seagrass density and accounted for 46% and 22% (respectively) of the variation in gulf toadfish density (Table 3.5). Gulf toadfish abundance is highest when density of algae increases (Table 3.6). There is a lack of support for seagrass as the 95% confidence interval overlapped zero.

The Combined Cover Hypothesis best represents pipefish biomass (Table 3.3, Table 3.4). The top model for pipefish biomass ($w_i = 0.18$) was algae density and seagrass density and accounted for 18% (respectively) of the variation in pipefish density (Table 3.5). Pipefish biomass is highest when density of algae decreases (Table 3.6). There is a lack of support for seagrass as the 95% confidence interval overlapped zero (Table 3.6). The top model for pipefish abundance was the null model.

3.4 DISCUSSION

Total seagrass density and algae density were stronger predictors of heron prey than individual seagrass species. Contrary to other studies (Costello et al. 1986; Robblee

et al. 1991, Pérez-Castañeda et al. 2010, Browder et al. 2002), prawn density was not influenced by salinity, or associated with density of *H. wrightii* (but see Sheridan et al. 1997). Seasonality and the total density of seagrass (D) were the strongest predictors of prawn biomass. The positive association prawns in Florida Bay and the Florida Keys have with algae suggests prawns can utilize algal habitats as documented in other estuaries (Haywood et al. 1995) and may prefer more complex vegetation communities. The positive effect of algae on abundance, but not biomass may suggest algae are utilized by smaller juvenile shrimp. The lack of seagrass species preference suggests shrimp abundance and biomass may be influenced more by density of available cover than by taxonomic traits (Heck et al. 2003) that differ among seagrass species like blade width. This may also be true of gulf toadfish, which exhibited a strong positive relationship with algae cover rather than a single species of seagrass as they did in previous studies (Serafy et al. 1997, Sheridan et al. 1997). Gulf toadfish burrow in sediment for camouflage (Serafy et al. 1997) and have been documented using artificial shelters (Barimo et al. 2007); therefore, SAV may be utilized as additional cover. SAV also provides habitat for gulf toadfish prey: crustaceans, mollusks and gobies (Lopez et al. 2017) and densities of these species could influence gulf toadfish density. Crabs in particular associate with structurally complex habitats (Mateo-Ramírez et al. 2018) and macroalgae is important to some species like juvenile blue crabs (Wilson et al. 1990). Additionally, shrimp are opportunistic omnivores and consume prey which feed on algae, so high densities of algae may increase food resources for shrimp (Schwamborn & Criales 2000, Gomes et al. 2018).

As predicted, pipefish biomass had a negative relationship with algae. Some species of pipefish are associated with microalgae (Scapin et al. 2018); however, the majority of pipefish species in the Bay and GWH may not be. This suggests SAV communities with high densities of algae would be detrimental to pipefish abundance and biomass. The weak association with seagrass could also be attributed to the aggregation of five pipefish species, thus masking species-specific habitat associations. For example, seagrass density preferences can differ among pipefish species (Scapin et al. 2018). Likewise, Syngnathids in Portugal exhibited distinctly different distributions among certain macro- and microhabitats based on age, interspecific and intersexual preferences (Muller and Erzini 2017).

Top models for all prey species included seagrass and algae. Models for gulf toadfish and prawn abundance/biomass were the best fitting models. Seagrass density is an indicator for prawn biomass and abundance and was included in top models for gulf toadfish and pipefish, but it was a weak predictor. Somewhat surprisingly, algae was the strongest predictor for gulf toadfish abundance/biomass, prawn abundance, and pipefish biomass. This suggests algae should be treated as a separate variable instead of including it with seagrass as one variable for density, especially when evaluating pipefish density, which was negatively influenced by algae. Neither salinity nor seasonality (except prawn biomass) were strong indicators; however, the time frame of this study is limited to the wading bird breeding season when high densities of prey are most critical.

Determining the strength of SAV as a predictor of prey communities assists with assessing the spatial distribution of prey species with future restoration plans. Sea level rise and increasing freshwater flow to Florida Bay with CERP efforts will change water

depth and salinity, altering the distribution of benthic habitat types and changing the current spatial distribution of SAV (Fourqurean et al. 2003, Herbert et al. 2011, Green et al. 2015). Previous studies indicated a seagrass species preference for prawns and gulf toadfish; however, such associations were not detected in this study and this fauna may be impervious to structural changes like shifting proportions of SAV species if density remains constant. Changes in nutrient loads also affects SAV distribution, with algae species dominate benthic habitats at the highest nutrient input levels (Armitage et al. 2006). Based on the results of this study, prawns and gulf toadfish may be better able to adapt to an SAV species shift favoring algae than species like pipefish.

This study is one of the first to use SAV measurements sampled with the Braun-Blanquet method (Braun-Blanquet 1972) modified for Florida (Fourqurean et al. 2002) to investigate habitat preferences of fauna (Lozano-Álvarez, and Briones-Fourzán, 2009, Palomar-Abesamis et al. 2017). This method is used by state and federal agencies to generate seagrass maps. While this method uses coarse cover class measurements, it may be at an appropriate scale to be useful for predicting associated marine fauna abundance and biomass. Additionally, remote sensing technologies can be used to gather seagrass species density values for sites (Eugenio et al. 2017). Both of these tools could negate the need to directly sample sites for fauna of interest if strong predictor variables for faunal densities like SAV preferences are established. This could increase the speed at which wildlife habitat assessments can be made, especially after hurricanes or seagrass die-off events.

Table 3.1 Braun-Blanquet abundance scale used to assess seagrass density. Cover is defined as the fraction of the bottom that is obscured by the species when viewed from directly above. A ramet is an independent individual composed of the leaf bundle, a piece of rhizome, and a root bundle. For algae species, a strand or filament of algae is equivalent to a ramet.

Cover Class	Description
0	Absent
0.1	Solitary individual ramet, less than 5% cover
0.5	Few individual ramets, less than 5% cover
1	Many individual ramets, less than 5% cover
2	5-25% cover
3	25-50% cover
4	50-75% cover
5	75-100% cover

Table 3.2 A priori models testing hypotheses for different SAV metrics in GWH and the Bay and the associated model variables.

Hypothesis	Hypotheses description	Variables
Modeate Density	The biomass (g) or abundance (n) of prey has a quadratic relationship with SAV density.	Quadratic SAV density (Di^2 , D^2)
Single Species Association	The biomass (g) or abundance (n) of prey is positively associated with one type of SAV (Di).	SAV taxon density calculated as the averaged cover class vlaue of each replicate quadrat at the sample location: % <i>T. testudinum</i> (TDi), % <i>H. wrightii</i> (HDi)
Combined Cover	The biomass (g) or abundance (n) of prey is positively associated with one overall SAV density (D).	The sum of all SAV species average cover class values (D); values can be greater than 5
Abiotic model	The biomass (g) or abundance (n) of prey is associated with salinity (ppt) and/or season.	Salinity level of the water in parts per thousand (ppt), Hours of daylight to account for seasonality.

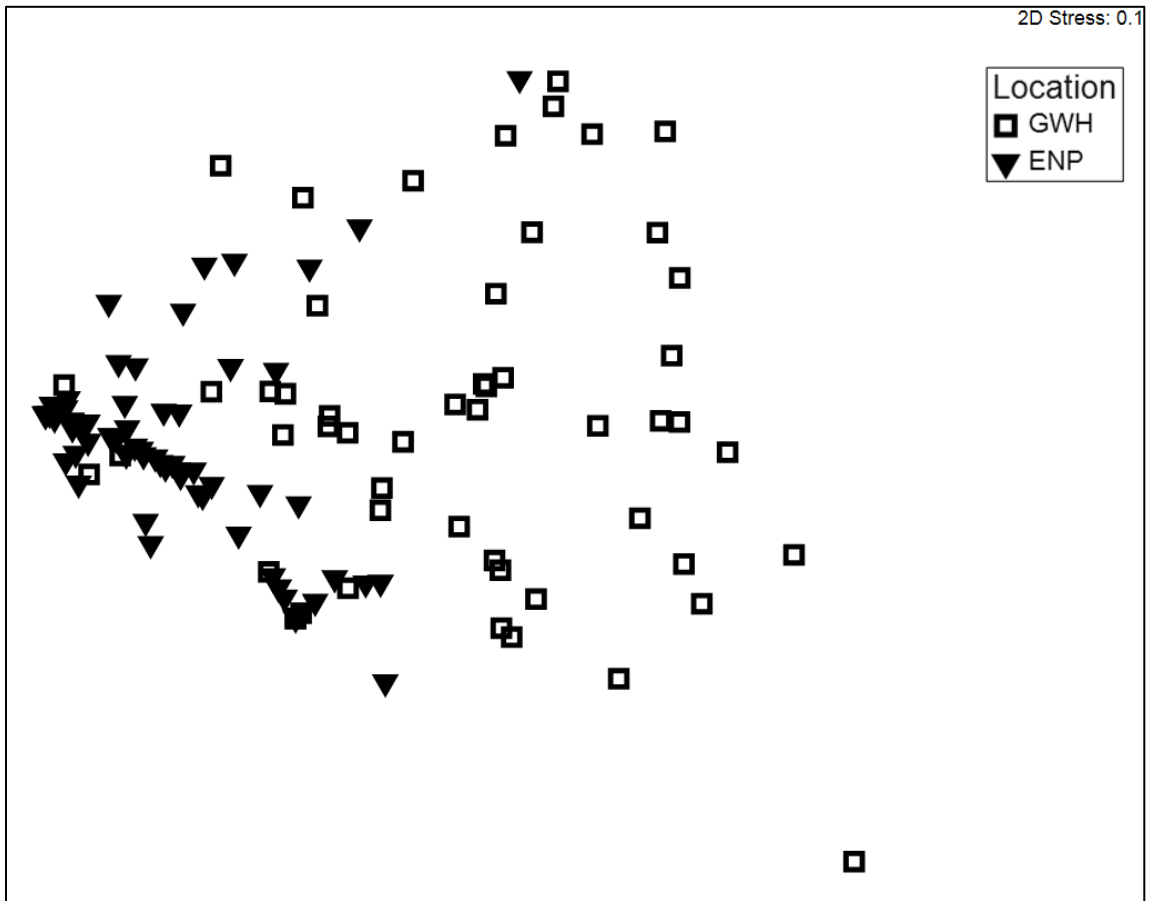


Figure 3.1 nMDS plot of differences in SAV community composition. ANOSIM and SIMPER results for differences in SAV communities between study sites Great White Heron National Wildlife Refuge (GWH) and Florida Bay.

Table 3.3 List of a priori models and modeling results from Akaike's Information Criterion model selection for biotic and abiotic factors affecting heron prey species abundance

Hypotheses	Model Framework	K	AICc	ΔAICc	Log-Lik.	wi
Prawns						
Combined Cover	Location + Seasonality + Algae (D) + Seagrass (D)	6	648.3	0	-317.725	0.752
Global	Location + Seasonality + Salinity + SAV cover (D)	7	650.5	2.22	-317.685	0.248
Null	Location	3	681	32.7	-337.386	0
Abiotic	Location + Seasonality + Salinity	5	681.5	33.18	-335.441	0
<i>H. wrightii</i> Preference	Location + Seasonality + <i>H. wrightii</i> (Di)	5	682.5	34.19	-335.947	0
Gulf toadfish						
Combined Cover	Location + Algae (D) + Seagrass (D)	4	132.2	0	-61.506	0.74
Global	Location + Seasonality + SAV cover	5	134.9	2.66	-61.505	0.195
Null	Location	2	138.4	6.17	-67.025	0.034
<i>T. testudinum</i> Preference	Location + <i>T. testudinum</i> (Di)	3	139.5	7.23	-66.373	0.02
Abiotic	Location + Seasonality	3	140.6	8.4	-66.957	0.011
Pipefish						
Null	Location	2	136.6	0	-66.175	0.286
Global	Location + Seasonality + Algae (D) + Seagrass (D)	3	137.9	1.3	-65.691	0.149
Combined Cover	Location + Algae (D) + Seagrass (D)	3	138.4	1.77	-65.926	0.118
Abiotic	Location + Seasonality	4	139.3	2.69	-65.196	0.074

Table 3.4 List of a priori models and modeling results from Akaike's Information Criterion model selection for biotic and abiotic factors affecting heron prey species biomass.

Hypotheses	Model Framework	K	AICc	ΔAICc	Log-Lik.	wi
Prawns						
Combined Cover	Location + Seasonality + Algae (D) + Seagrass (D)	6	196.7	0	-91.904	0.924
Global	Location + Seasonality + Salinity + SAV cover (D)	6	202.6	5.95	-94.879	0.047
Null	Location	3	204.4	7.69	-99.061	0.02
<i>H. wrightii</i> Preference	Location + Seasonality + <i>H. wrightii</i> (Di)	5	206	9.37	-97.717	0.009
Abiotic	Location + Seasonality + Salinity	5	210.7	14.03	-100.045	0.001
Gulf toadfish						
Combined Cover	Location + Algae (D) + Seagrass (D)	5	179.4	0	-83.779	0.444
Null	Location	3	180.5	1.03	-86.881	0.264
Global	Location + Seasonality + Total SAV cover (D)	5	181.8	2.41	-84.985	0.133
Seasonality	Location + Seasonality	4	182.8	3.4	-86.809	0.081
<i>T. testudinum</i> Preference	Location + <i>T. testudinum</i> (Di)	4	182.9	3.48	-86.849	0.078
Pipefish						
Combined Cover	Location + Algae (D) + Seagrass (D)	5	-3.4	0	7.364	0.527
Global	Location + Algae (D) + Seagrass (D) + Seasonality	6	-2.9	0.49	8.416	0.413
Null	Location	3	1.6	4.99	2.451	0.044
Abiotic	Location + Seasonality	4	3.6	6.96	2.646	0.016

Table 3.5 Pseudo R² values for top models.

Hypotheses	Model Description	Pseudo R²
<i>Prawn Abundance</i>		
Combined Cover	Location + Seasonality + Algae (D) + Seagrass (D)	0.52
<i>Gulf toadfish Abundance</i>		
Combined Cover	Location + Algae (D) + Seagrass (D)	0.46
<i>Prawn Biomass</i>		
Combined Cover	Location + Seasonality + Algae (D) + Seagrass (D)	0.22
<i>Gulf toadfish Biomass</i>		
Combined Cover	Location + Algae (D) + Seagrass (D)	0.20
<i>Pipefish Biomass</i>		
Combined Cover	Location + Algae (D) + Seagrass (D)	0.18

Table 3.6 Model parameter estimates, standard error, adjusted standard error, 95% confidence intervals, T-values and Z-values for parameters of interest in top competing models ($\Delta AIC_c < 2$).

SAV Metrics	Estimate(β)	SE	Adj. SE	t value	z value	Pr(> z)	LCL	UCL
<i>Prawn Abundance</i>								
Seagrass	0.59261	0.09657			6.14	8.42e-10	0.4037374	0.7837741
Algae	0.46447	0.09596			4.84	1.30e-06	0.2823893	0.6602259
<i>Gulf toadfish Abundance</i>								
Algae	0.28033	0.09125			3.07	0.00212	0.1021688	0.4605086
<i>Prawn Biomass</i>								
Seasonality	0.2476	0.1065		2.325			0.0431226	0.4520133
Seagrass	2.7565	0.6084		4.531			1.5881691	3.9248769
<i>Gulf toadfish Biomass</i>								
Algae	0.38	0.1715	0.1781		2.13	0.0328	0.0309919	0.7289658
<i>Pipefish Biomass</i>								
Algae	-0.5108	0.1789	0.1821		2.81	0.00503	- 0.8676808	- 0.1539382

4 SYNTHESIS

Coastal ecosystems are declining due to a number of anthropogenic causes, disrupting seagrass meadows and the productivity of prey species crucial to wading bird populations. Differences in nesting success during the breeding season are influenced by prey availability across the landscape and by species-specific foraging strategies (Herring 2008; Herring et al. 2010a, b). Foraging behaviors, foraging-site selection, water-depth selection, and diet may shift in response to changes in prey availability (Beerens et al. 2011). Identifying key prey species is the first step in understanding how wading bird populations respond to environmental changes that affect food resources. Generalists like the Little Blue Herons are thought to be more adaptable to changes in prey availability than specialist species; however, herons are a species of concern in North America. The diet of herons varies across their range and was previously unquantified in coastal South Florida.

In Chapter 2, I confirmed herons in coastal South Florida select for two key prey species and utilize terrestrial prey when water levels are too high to forage on the mudflats. South Florida coastal heron diets are more similar to heron diets in Northeastern Brazil than study sites in Northwestern Florida and the Caribbean. Unlike herons populations close in proximity to South Florida (Miranda and Collazo 1997, Olmos et al. 2001), marine and terrestrial crabs were not important in the diets of herons, but shrimp were (Olmos et al. 2001). This may suggest crabs are a less preferred prey item that herons will use in the absence of preferred aquatic prey like shrimp and fish.

Future research should quantify terrestrial prey density to understand the link between herons and this food resource. This study further illustrates the diet plasticity of herons across their range; however, this is the first study to evaluate aquatic prey selection by herons.

In Chapter 3, I found that when present, prawn density has a positive relationship with seagrass density, but gulf toadfish and pipefish do not. Furthermore, I did not find support for the supposed associations of gulf toadfish and prawns with specific seagrass species (Costello et al. 1986; Robblee et al. 1991, Serafy et al. 1997, Pérez-Castañeda et al. 2010, Browder et al. 2002.) This could indicate the presence of seagrass cover is a better metric for prawn density and total combined cover is a better metric for gulf toadfish density than one specific SAV species. The lower thresholds of prey for SAV density have not been confirmed; however, no heron prey were found in areas completely void of seagrass.

Sea level rise and increasing freshwater flow to Florida Bay with CERP efforts will change water depth and salinity, altering the distribution of benthic habitat types and changing the current spatial distribution of SAV (Fourqurean et al. 2003, Herbert et al. 2011, Green et al. 2015). Abrupt and largescale changes to seagrass density occur with seagrass die-off events and hurricanes. Future studies should examine this distinction to understand the influence of structure type (i.e. SAV species type) to accurately predict changes to associated faunal density with anthropogenic changes. While seagrass meadows provide an important nursery structure, the particular type of structure (i.e. seagrass species) may not be as important to some faunal species (Heck et al. 2003) like gulf toadfish. Knowing how prey density will respond to these changes is important;

however, specific habitat preferences of key heron were previously unconfirmed. This chapter quantitatively evaluated the effect of different SAV metrics on key heron prey abundance and biomass.

Predicting how herons and other wading bird species will respond to environmental changes caused by anthropogenic stressors requires a clear understanding of how they are linked to lower trophic levels. This research is an example of how those links can vary with different food resource availability and the importance of evaluating prey selection in conjunction with diet composition. After this is accomplished, regionally effective proxies for prey density can be established for habitat suitability models. Identifying important variables will improve the ability of managers to conserve high quality foraging habitat and predicting how populations will respond to restoration efforts and anthropogenic stressors.

5 APPENDICES

Table 5.1 Appendix A: Tables not included in the chapters.

Table A1 Prey species identified from Little Blue Heron boluses collected in the 2016-2017 nesting season from Great White Heron National Wildlife Refuge (GWH), and Florida Bay, FL

Common name	Scientific Name	Taxa group
Anole	<i>Anolis spp.</i>	<i>Anolis</i>
Atlantic needlefish	<i>Strongylura marina</i>	<i>Actinopterygii</i>
Bigeye majora	<i>Eucinostomus havana</i>	<i>Eucinostomus</i>
Blue Crab	<i>Callinectes sapidus</i>	<i>Decapoda</i>
Caterpillar	<i>lepidoptera</i>	<i>Arthropoda</i>
Code goby	<i>Gobiosoma robustum</i>	<i>Gobiidae</i>
Crab spider	<i>Gasteracantha cancriformis</i>	<i>Arthropoda</i>
Cricket	<i>Orthoptera</i>	<i>Arthropoda</i>
Darter goby	<i>Ctenogobius boleosoma</i>	<i>Gobiidae</i>
Deer fly	<i>Chrysops</i>	<i>Arthropoda</i>
Dragonfly	<i>Odonata</i>	<i>Arthropoda</i>
Fiddler crab	<i>Uca</i>	<i>Decapoda</i>
Gold brutula	<i>Gunterichthys longipenis</i>	<i>Percoidei</i>
Goldspotted killifish	<i>Floridichthys carpio</i>	<i>Cyprinodontiformes</i>
Ground beetle	<i>Carabidae</i>	<i>Arthropoda</i>
Gulf toadfish	<i>Opsanus beta</i>	<i>Opsanus</i>
Isopod	<i>Libia spp</i>	<i>Arthropoda</i>
Lined seahorse	<i>Hippocampus erectus</i>	<i>Syngnathidae</i>
Mangrove tree crab	<i>Aratus pisonii</i>	<i>Arthropoda</i>
Marsh killifish	<i>Fundulus confluentus</i>	<i>Cyprinodontiformes</i>
Mud crab	<i>Panopeidae</i>	<i>Decapoda</i>
Pinfish	<i>Lagodon rhomboides</i>	<i>Percoidei</i>
Pistol Shrimp	<i>Alpheus sp.</i>	<i>Alpheus sp.</i>
Polychaeta	<i>Polychaeta</i>	<i>Annelida</i>
Porgy	<i>Porgies spp.</i>	<i>Percoidei</i>
Prawn	<i>Penaeus sp.</i>	<i>Penaeus sp.</i>
Pugnose pipefish	<i>Bryx dunckeri</i>	<i>Syngnathinae</i>
Rainwater killifish	<i>Lucania parva</i>	<i>Cyprinodontiformes</i>
Red lizardfish	<i>Synodus ulae</i>	<i>Actinopterygii</i>
Sailfin molly	<i>Poecilia latipinna</i>	<i>Cyprinodontiformes</i>
Sheepshead minnow	<i>Cypridodon variegatus hubbsi</i>	<i>Cyprinodontiformes</i>
Shortfinned pipefish	<i>Cosmocampus elucens</i>	<i>Syngnathidae</i>
Spaghetti eel	<i>Moringua edwardsi</i>	<i>Anguilliformes</i>
Speckled worm eel	<i>Myrophis punctatus</i>	<i>Anguilliformes</i>

Spider	<i>Araneae</i>	<i>Arthropoda</i>
Spider crab	<i>Lbinia emarginata</i>	<i>decapoda</i>
Spottailed tonguefish	<i>Symphurus urospilus</i>	<i>Pleuronectiformes</i>
Spotted Seatrout	<i>Cynoscion nebulosus</i>	<i>Percoidei</i>
Spotted Whiff	<i>Citharichthys macrops</i>	<i>Pleuronectiformes</i>
Tonguefish	<i>Cynoglossidae</i>	<i>Pleuronectiformes</i>

Table A2 Prey species density (total g of prey/ total trap area m²), percent of density and biomass from 48 nests in Great White Heron National Wildlife Refuge (GWH), and Florida Bay (Bay) FL.

		Colony location					
Prey item		Great White Heron National Wildlife Refuge (n= 129)			Florida Bay (n=66)		
Species	Common Name	Density (g/m ²)	% Density	% Biomass	Density (g/m ²)	% Density	% Biomass
<i>Opsanus beta</i>	Gulf toadfish	1.81	11	10	0.51	5	5
<i>Actinopterygii</i>	Ray-finned fishes	0.07	0	< 1	0.16	1	1
<i>Penaeus spp.</i>	Prawns	1.53	10	9	2.43	22	22
<i>Eucinostomus</i>	Mojara	0.06	0	< 1	0.08	1	1
<i>Pleuronectiformes</i>	Flatfish	0.13	1	1	0.07	1	1
<i>Alpheus spp.</i>	Pistol shrimp	5.12	32	28	3.27	29	29
<i>Cyprinodontiformes</i>	Live bearers	0.43	3	2	1.49	13	13
<i>Percoidei</i>	Percoidei	0.42	3	2	0.22	2	2
<i>Gobiidae</i>	Goby	0.13	1	1	0.28	3	3
<i>Decapoda</i>	Marine Crab	7.73	49	43	2.41	22	22
<i>Syngnathidae</i>	Seahorses & pipefishes	0.22	1	1	0.2	2	2
<i>Anguilliformes</i>	Eels	0.05	0	< 1		0	< 1
Total prey density	-	15.89			11.12		

Table A3 Percent composition of heron prey captured in 122 throw traps in GWH and the Bay.

Species	Common Name	Sample Location			
		Great White Heron National Wildlife Refuge (n=55)		Florida Bay (n= 67)	
		Abundance % Occurrence	Biomass % Occurrence	Abundance % Occurrence	Biomass % Occurrence
<i>Opsanus beta</i>	Gulf toadfish	2	10	1	0.1
<i>Farfantepenaeus spp.</i>	Prawns	18	7	17	22
<i>Syngnathidae</i>	Pipefishes	0.1	0.1	1	0.2

Figure 5.1 Appendix A: Figures not included in the chapters.

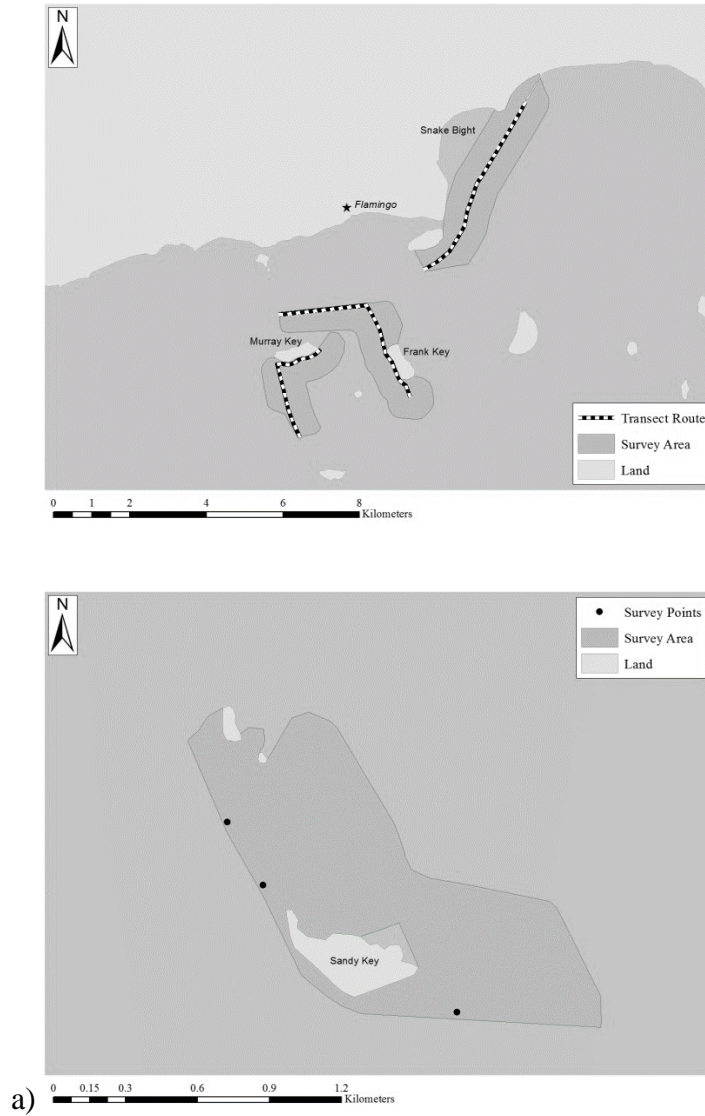


Figure A1 Survey areas for foraging distribution surveys at Snake Bight, Frank Key, and Murray Key, and Sandy Key within Florida Bay, Everglades National Park.

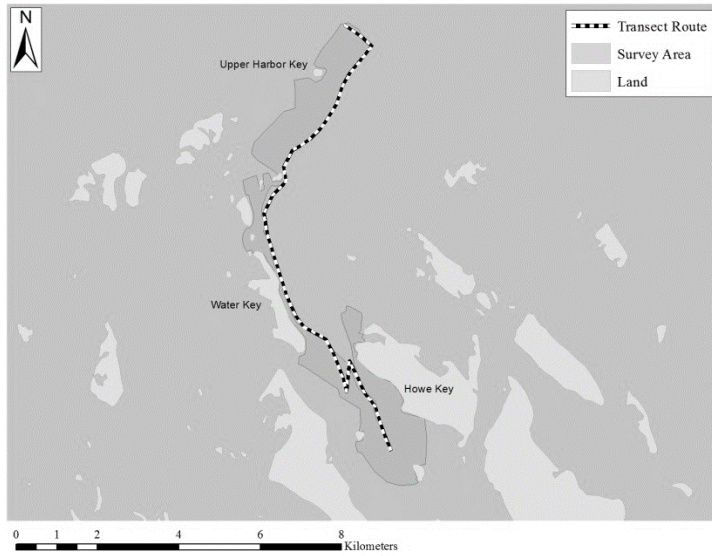


Figure A2 Survey areas for foraging distribution surveys near Big Pine Key, in Great White Heron National Wildlife Refuge

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