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Jessica Copertino
University of Central Florida

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BIRD ABUNDANCE AND DIVERSITY AND THE IMPACTS OF OYSTER REEF RESTORATION ON THE BIRD COMMUNITY IN MOSQUITO LAGOON, FLORIDA, USA

by

JESSICA COPERTINO
B.S. University of North Florida, 2006

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Sciences
at the University of Central Florida
Orlando, Florida

Spring Term
2021

Major Professor: Linda Walters

ABSTRACT

Birds are often used as indicators for biodiversity and ecosystem health. While birds have been monitored in other parts of the Indian River Lagoon (IRL), there has been little research on birds in Mosquito Lagoon (ML, the northernmost portion of the IRL). This thesis first examines the abundance and diversity of birds in ML by using two years of photographic observations to assess seasonal variations and the use of various habitat features by specific bird taxa. Abundance and species richness were highest in winter, while evenness and Simpson's diversity were highest in summer. Moreover, natural and artificial habitat features were differentially utilized by specific bird taxa. A second objective was to use monthly bird surveys for three years to assess the utilization of live, restored, and dead oyster reefs by birds and to determine how oyster reef restoration impacts the bird community in ML. Infaunal abundance was also monitored in the reef sediments, as infauna serve as prey for birds. Results indicated that while restored reefs had relatively low bird abundances, they had similar proportions of foraging birds and similar bird assemblages as live reefs. By 6 months post-restoration, infaunal abundances on restored reefs became similar to live reefs, indicating similarities in prey availability. Another goal was to explore the selection of certain dead reefs by nesting Least terns and American oystercatchers. Reefs on which nesting activity had previously been observed were characterized and compared to reefs where nesting was not previously observed. Nesting sites had taller mangroves, steeper slopes, higher elevations, more vegetative cover, and less live oyster cover than non-nesting sites. Overall, results indicate that live, restored, and dead reefs are all being utilized by birds in ML, and that a mosaic of reef types may be best for providing foraging, loafing, and nesting habitat for birds.

I dedicate this thesis to my husband and children for supporting me through this whole process, to my parents for always encouraging me to strive for excellence, and to my students for inspiring me to continue my education. With all my heart – thank you.

ACKNOWLEDGMENTS

First and foremost, I would like to thank my advisor, Dr. Linda Walters, for guiding and motivating me through this process and for her constant encouragement. I would also like to thank my committee members, Dr. Geoffrey Cook and Dr. Kristy Lewis, for their advice and support. Thank you, also, to Dr. Melinda Donnelly and Dr. Paul Sacks for always being willing to offer help and advice.

A huge thank you, also, to my lab mates Casey Craig and Becca Fillyaw. I am so lucky to have had the two of you right there with me cheering me on through everything these past 3 years. Thank you to Brice Giles, Jacob Hromyak Michelle Shaffer, Katherine Harris, Lyndsey Chute, Indirha Meulens, Sophia Vermeulen, Katherine Lowen, Katherine Guise, Dakota Lewis and many other volunteers who assisted with data collection and analyses for this project. Thank you, also, to my husband, Cole Copertino, and my father, Dan Bodoh, for stepping in to help with fieldwork during the pandemic. I would also like to thank Jean Olbert, Janell Brush, and Joeseph Marchianno from FL FWC and Matthew Anderson from FL DEP for their advice and assistance. This thesis would not have been possible without this big team of people helping me out along the way.

Finally, I would like to thank my funding sources for making my research possible. Funding for this project was provided by NSF Award #1617374, Disney Conservation Fund, Indian River Lagoon National Estuary Program, and the University of Central Florida.

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CHAPTER ONE: INTRODUCTION

The Indian River Lagoon (IRL) is widely considered to be one of the most biodiverse estuaries in North America (Gilmore 1995; Lang and Hines 2005; Provancha et al. 1992; Smith and Breininger 1995; Schmalzer 1995) and is home to over 4,000 plant and animal species, including more than 50 species that are classified as either threatened or endangered (IRLNEP 2019). The Indian River Lagoon National Estuary Program (2019) estimates that there are over 300 species of birds that utilize the IRL, some as permanent residents and some as wintering residents. The IRL is located along the 'Atlantic Flyway', so many birds, including migratory shorebirds, seabirds, and waterfowl, stop within the IRL during their spring or fall migrations (IRLNEP 2019).

These birds provide a myriad of ecosystem services, including nutrient deposition and transport and serving as mobile links between aquatic and terrestrial ecosystems (Sekercioglu et al. 2016; Whelan et al. 2008). They also serve as an important draw for ecotourism in the area. The Space Coast Birding and Wildlife Festival, which takes place every January in Titusville, FL, has economic impacts in Brevard County of hundreds of thousands of dollars annually (Witenhafer 2020).

While birds are of ecological and economic importance in the region, little research has been conducted regarding the bird community composition in Mosquito Lagoon. Surveys in the late 1980s and early 1990s focused on Mosquito Lagoon waters associated with Merritt Island and the area surrounding Kennedy Space Center (KSC), including southern Mosquito Lagoon, but not on the entirety of Mosquito Lagoon (Breininger and Smith 1990; Schikorr and Swain 1995; Smith and Breininger 1995). A more recent study focused on shorebird abundance in wetland impoundments within the KSC and Merritt Island National Wildlife Refuge (MINWR) area, which includes the southern portion of Mosquito Lagoon, the Indian River, and the northern portion of the Banana River, but did not include any sites within Mosquito Lagoon (Epstein 2019). Additionally, these previous studies focused on specific bird groups (wading birds or shorebirds), rather than surveying all birds. Shaffer et al. (2019) surveyed all bird types in Mosquito Lagoon, but only in reference to their use of oyster reefs, so did not include bird use of other habitat features. Similarly, Litwak and Rifenberg (2021) made observations of vertebrates, including birds, but their study was limited to a recently restored living shoreline site in Mosquito Lagoon.

Birds have also been used as indicators of ecological health and biodiversity (Gregory et al. 2003; Gregory and Strien 2010; Schikorr and Swain 1995). While there is some debate in the literature as to the sensitivity of birds as bio-indicators for small-scale changes, there is general agreement that birds can serve as indicators of long-term environmental trends (Temple and Wiens 1989), and are acceptable proxies for biodiversity in ecosystems with heterogeneous landscapes (Eglington et al. 2012). Temple and Weins (1989) suggest continuous broad-scale monitoring of bird populations combined with more intensive, targeted, long-term monitoring efforts in specified study areas (specifically, National Parks or other protected areas) in order to assess community changes and potential causes. Additionally, they emphasize the importance of bird data in the preparation and review of Environmental Impact Statements by the Environmental Protection Agency in determining the impacts of specific projects (Temple and Weins 1989).

The overall aim of this thesis is to provide data on the bird community in Mosquito Lagoon, the northernmost portion of the Indian River Lagoon system, and to evaluate the impacts of oyster (*Crassostrea* virginica) reef restoration on avian taxa. The first part of this thesis assesses the abundance and diversity of avian populations in the biodiverse estuary of Mosquito Lagoon in order to better assess the impacts of future environmental changes. Oyster reefs in Mosquito Lagoon are utilized by birds for foraging, loafing, and nesting. The Coastal and Estuarine Ecology Lab at the University of Central Florida has been restoring oyster reefs in Mosquito Lagoon for over a decade, and the restored reefs have been deemed successful in terms of oyster densities, shell lengths, and reef heights. However, little research has been done regarding the success of restored reefs in provision of habitat for birds. The second part of this thesis evaluates the use of natural, restored, and dead oyster reefs in Mosquito Lagoon and to evaluate the success of oyster reef restoration in terms of bird habitat provision. The previously unavailable baseline data on the avian community in Mosquito Lagoon and assessment of the impacts of oyster reef restoration gleaned from this thesis may be used to better inform future restoration and management strategies.

CHAPTER TWO: A SURVEY OF BIRD ABUNDANCE AND DIVERSITY IN MOSQUITO LAGOON, FLORIDA

Introduction

Coastal ecosystems are experiencing declines due to anthropogenic factors and climate change (e.g., Bindoff et al. 2019). Mangrove forests, seagrass beds, and oyster reefs are important habitats for a myriad of coastal species but are in global decline, and predicted to continue to decline (e.g. Beck et al. 2011; Blomberg et al. 2018; Duke et al. 2007; Field 1995; Polidoro et al. 2010; Ward et al. 2016). Species that rely on these coastal habitats, such as crustaceans, fish, and coastal birds, will likely be negatively impacted by the alterations and losses of these habitats. As these habitats continue to change due to anthropogenic factors and climate change, it is important to have baseline data on ecologically and economically valuable taxa in order to assess the impacts of these changes over time.

In dynamic coastal habitats, it is important to monitor biodiversity to detect impending species declines, assess impacts of environmental changes, and evaluate the effectiveness of restoration and management practices (e.g. Lindenmayer et al. 2012; Pocock et al. 2015; Baumgardt et al. 2019). Monitoring of all species in these ecosystems is often impractical; however, some targeted taxa may be used as proxies for biodiversity. Previous studies indicate that birds may be useful indicators of long-term environmental trends and are acceptable proxies for biodiversity in ecosystems with heterogeneous landscapes (Eglington et al. 2012; Gregory et al. 2003; Gregory and Strein 2010; Schikorr and Swain 1995; Temple and Wiens 1989). In addition, many coastal birds are currently experiencing population declines (Brown et al. 2001; Kushlan et al. 2002). These birds serve ecological functions and provide a myriad of ecosystem services (Anderson and Polis 1999; Charalambidou and Santamaria 2005; Devault et al. 2003; Sekercioglu 2006; Tabur and Ayvaz 2015; Whelan et al. 2015; Wootton 1991), highlighting the importance of conserving these at-risk taxa. Both the North American Waterbird Conservation Plan and the United States Shorebird Conservation Plan emphasize monitoring in order to better inform conservation and management strategies for protecting and restoring coastal bird populations (Brown et al. 2001; Kushlan et al. 2002). Furthermore, both conservation plans suggest habitat-based conservation and restoration to best meet the needs of these at-risk taxa (Brown et al. 2001; Kushlan et al. 2002).

The overall goal of this study is to provide data on the avian community within the biodiverse estuary of Mosquito Lagoon, the northern portion of the Indian River Lagoon system. To achieve this goal, the aims of this study were to 1) assess the bird abundance and diversity in Mosquito Lagoon; 2) determine seasonal trends in bird abundance and diversity in the region; and 3) evaluate the use of various habitat features in the region by specific bird taxa.

Field-site Description

The Indian River Lagoon (IRL) system is an estuary along the eastern coast of Florida, stretching 251 km from Ponce Inlet in Volusia County to Jupiter Inlet in Palm Beach County. It is composed of three interconnected regions: Mosquito Lagoon, the Banana River, and the Indian River. This region lies in a transition zone between a temperate climate zone to the north, and a subtropical climate zone to the south (Gilmore 1995; Lang and Hines 2005; Schmalzer 1995). The IRL contains a mosaic of habitats, including seagrass beds, mangrove forests, soft non-vegetated bottom, and oyster reefs. These factors contribute to a high level of biodiversity within the IRL, which is widely considered one of the most biodiverse estuaries in North America (Gilmore 1995; Lang and Hines 2005; Provancha et al. 1992; Schmalzer 1995; Smith and Breininger 1995). Mosquito Lagoon is the northernmost portion of the IRL system; thus, its biota includes more temperate species and fewer subtropical species than are found in the more southern portions of the system (Provancha et al. 1992). The salinity in Mosquito Lagoon ranges from 25-45 ppt annually, and the average depth of the lagoon is 1.5 m (Walters et al. 2001). The lagoon is microtidal, with the principal lunar semi-diurnal (M_2) tidal amplitudes between 0-5 cm (Smith 1993). Water levels vary based on season, with highest water levels occurring in the fall (Smith 1993).

The avian fauna within Mosquito Lagoon includes a variety of both resident and migratory birds (IRLNEP 2019). More than a dozen of the birds commonly found within the IRL are listed by the state of Florida as threatened species, including *Haematopus palliates* (American oystercatcher), *Egretta caerulea* (Little blue heron), *Egretta rufescens* (Reddish egret), *Sternula antillarum* (Least tern), and *Mycteria americana* (Woodstork); the last of which is also listed federally as a threatened species (FFWCC 2018). One of the largest birding festivals in the United States, the Space Coast Birding and Wildlife Festival, takes place annually in areas surrounding the Indian River Lagoon, and brings in many birders and tourists to the region every January; in 2020 this festival had an estimated economic impact of approximately $900,000 in Brevard County (Witenhafer 2020).

To elucidate the bird diversity in the region, I surveyed all birds including, but not limited to, wading birds, shorebirds, seabirds, songbirds, and waterfowl along a 14.5 km transect through the central/northern portion of Mosquito Lagoon, spanning from Oak Hill in the south to Edgewater in the north. I selected the route to serve as a representative sample of the heterogeneity of habitats within Mosquito Lagoon. The transect route included intertidal oyster reefs and mangrove fringe throughout its length. The route also included one intersection with the Intracoastal Waterway, and there were many popular fishing spots throughout the transect. I analyzed seasonal variations in the bird community and bird usage of the various habitat types found within Mosquito Lagoon.

Methods

Sampling methods

I conducted sampling seasonally for two years from December of 2018 through November of 2020. For this study, December through February were designated as winter, March through May as spring, June through August as summer, and September through November as fall. A minimum of 5 sampling transects were conducted each season, and a maximum of 11 per season for a total of 55 transects. The 14.5 km transect route was followed by boat (Figure 1) and photographs were taken with a Nikon D7500 digital 35 mm camera with AF-S Nikkor 200-500 mm lens of all birds observed along the route within 50 meters on either side of the boat. The total area of the transect was approximately 300 hectares. I was aware of previous studies indicating a bias toward observing white birds, due to their conspicuousness against the landscape (Schikorr and Swain 1995) and made efforts to minimize this bias. At least two to three trained observers were present during each transect and binoculars were used to scan the landscape. Transects took approximately 1 hour to complete and the direction of the transect (north or south) was haphazardly chosen prior to each trip.

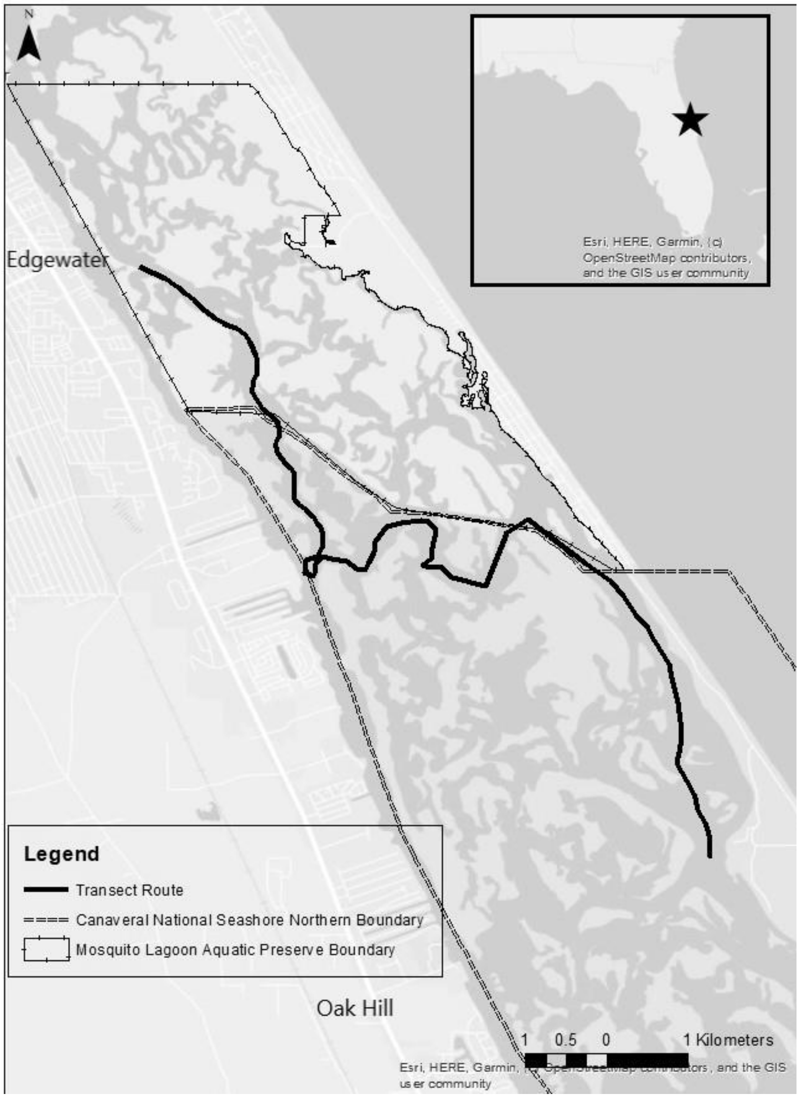

Figure 1 Mosquito Lagoon, Florida. Bird photograph transect route in bold, along with boundaries of Canaveral National Seashore (CANA) and Mosquito Lagoon Aquatic Preserve (MLAP). The Intracoastal Waterway runs along the western border of both CANA and MLAP. Whether the transect was started at the north or south end of the route was haphazardly determined for each sampling event.

I sorted the photographs based on habitat if the individual was loafing or foraging [live oyster reef, dead oyster reef, live mangroves, dead tree branches (any species), artificial structures, sandbar] or behavior (flying, floating, wading) and identified birds in each photograph to the species level. Some birds in the photographs could not be identified to species level due to image darkness, distance, or camera angles. In these instances, I categorized the birds as “unidentified”. The live oyster reef category included birds observed on or within one meter of natural or restored oyster reefs, and the dead oyster reef category included birds observed on or within one meter of dead oyster reefs. Dead oyster reefs consist of piles of loose, disarticulated shells that sometimes reach elevations as high as one m above the high tide line (Grizzle et al. 2002). The mangrove category included birds observed perched on live mangrove branches or wading within one meter of mangrove shorelines. The dead tree branch category included birds perched on branches of “standing dead” trees, including, but not limited to, mangroves, pine trees, and palm trees. The artificial structures category included birds found on any man-made (or human-placed) structures including signposts made of polyvinyl chloride (PVC) or wood, metal signs, PVC pilings, docks (floating and fixed), wooden and metal utility poles, riprap, and aquaculture equipment for oyster growing (placed in Mosquito Lagoon on transect route in late 2018). The sandbar category included birds on sandbars that were fully or partially exposed. The floating and wading behavior categories included birds that were floating or wading in open water (not within one meter of either oyster reefs or mangrove shorelines). I used aerial imagery from Google Earth Pro to estimate the areas of oyster reefs, sandbars, and aquaculture equipment within the transect area, and counted the numbers of artificial structures such as sign posts, pilings, and docks (Table 1).

Table 1 Various habitat features that occur along the transect route with total area or numbers of structures, as appropriate. I used these categories when determining if there were differences in community assemblages using different habitat features, and to determine which species were most closely associated with certain habitat features.

Habitat Category	Includes	Total Area or Number
Live Oyster Reefs	Natural Oyster Reefs	5.12 ha
	Restored Oyster Reefs	1.09 ha
Dead Oyster Reefs	Dead Oyster Reefs	0.38 ha
Sandbars	Sandbars	3.37 ha
Mangroves	Live Mangrove Branches	---
	Mangrove Prop Roots	---
	Mangrove Shoreline	23.23 km
Dead Tree Branches	Dead Branches of any Tree	---
Artificial Structures	Signs	42 total
	Pilings	80 total
	Utility Poles	33 total
	Aquaculture Equipment	0.21 ha
	Docks	24 total
Total Area of Transect Route	---	303 ha

I used Weather Underground (2020) to determine the temperature and mean wind speed at the time of each transect. I did not complete surveys if wind speed exceeded 24 kph or if it was raining. Transects were conducted at various times of the day and included various tidal periods. Due to seasonal differences in water levels, I categorized the water level for each transect (regardless of tidal period) as either high (no oyster reefs or sandbars completely exposed), medium (oyster reefs and sandbars partially exposed), or low (oyster reef and sandbars exposed). High water levels may be caused by either high water season or by high tide during low water seasons.

Statistical methods

Using the data collected from Weather Underground, I calculated summary statistics for air temperature (^{o}C) and average wind speed (kph) for each season. I used ANOVAs to determine differences in air temperature or average wind speed based on season and Tukey HSD post-hoc testing for pairwise comparisons of seasons. To assess the likelihood that my sampling efforts captured the representative diversity of the study region, I used the iNext package in R to generate a rarefaction curve (Hsieh et al. 2019). For each species, I calculated the observation percentage by dividing the number of birds of each species encountered on all transects by the total number of birds encountered on all transects. This calculation was repeated to determine the observation percentage of each species for each habitat type. I next calculated the percent occurrence for each species by dividing the number of transects in which the species occurred by the total number of transects performed. This calculation was completed for total number of birds observed in each transect and broken down by habitat type. The data were highly dispersed count data, so I used negative binomial generalized linear models (GLMs) and Akaike information criterion (AIC) model selection to determine which factors impacted the total number of birds observed. The predictors included in the models were season, average wind speed, and wind gust speed. Neither temperature nor water level were included in the models, as they were correlated to season. I also ran separate negative binomial models to determine the effect of water level on wading birds and shorebirds. I calculated diversity indices (Shannon Diversity, Simpson Diversity, Pielou’s Evenness, and species richness) for the region using the Vegan package in R (Oksanen et al. 2019) and used an ANOVA to determine any seasonal differences in these indices. To assess the differences in community assemblages based on habitat and behavior, generated ordination plots were generated based on habitat or behavior using non-metric multidimensional scaling (NMDS) in the Vegan package in R. I conducted PERMANOVA tests to determine if there were community differences based on habitat or behavior (Oksanen et al. 2019). Flying birds were only included in the overall abundance analyses and were not included in this analysis. I summed the bird observations from the individual transect data for each season to use in this analysis in order to reduce the number of zeros and to reduce stress in the ordination plot. Stress represents the difference between the distances on the two-dimensional plot and the distances in complete multidimensional space, and stress values below 0.2 are typically considered a fair fit for ecological data. Multi-level pattern analysis, which assesses the strength of the relationships between species abundance or occurrence with specific sites or groups of sites, was used to generate lists of representative species associated with specific habitat features (De Caceres and Legendre 2009). Rstudio version 3.6.2 was used for all statistical analyses (R Core Team 2019; RStudio Team 2018).

Results

Abiotic Factors

For the two-year study time frame, the mean air temperature at the time of sampling (± 95% confidence intervals) was 26.6 ± 1.6 ^{o}C, and mean wind speed was 6.1 ± 1.0 km/h (Table 2). Mean air temperature was lower in winter than in summer ($p < 0.001$) and fall ($p < 0.001$) but was similar to spring (Figure 2A). Summer air temperatures were similar to temperatures in spring and fall ($p = 0.05$ and $p = 0.72$, respectively). The highest mean air temperatures were in summer (30.6 ± 1.6 ^{o}C) and lowest in winter (21.1 ± 3.7 ^{o}C). Mean wind speed and mean wind gust speed were both similar for all seasons (Figure 2B and C).

Table 2 Summary statistics for air temperature, average wind speed, and wind gust speed for all observations and separated by season, including means, 95% confidence intervals (CI), and ranges (Min-max) for each metric.

		Air Temperature (°C)	Average Wind Speed (km/h)	Average Wind Gust Speed (km/h)
All Data	Mean	26.6	6.1	8.8
	CI	1.6	1.0	1.3
	Min-max	9.0-36.1	0-15.3	0-20.9
Winter	Mean	21.1	5.4	8.1
	CI	3.7	2.6	3.6
	Min-max	9.0-28.5	0.6-15.3	1-20.9
Spring	Mean	25.3	7.0	9.7
	CI	4.4	2.5	3.5
	Min-max	10.2-31.4	8.0-19.3	0-16.6
Summer	Mean	30.5	5.0	8.3
	CI	1.6	1.3	1.9
	Min-max	25.4-35.7	2.1-8.9	2.7-14.0
Fall	Mean	28.7	6.8	9.3
	CI	1.6	2.1	2.7
	Min-max	24.2-36.1	0-14.8	0-18.5

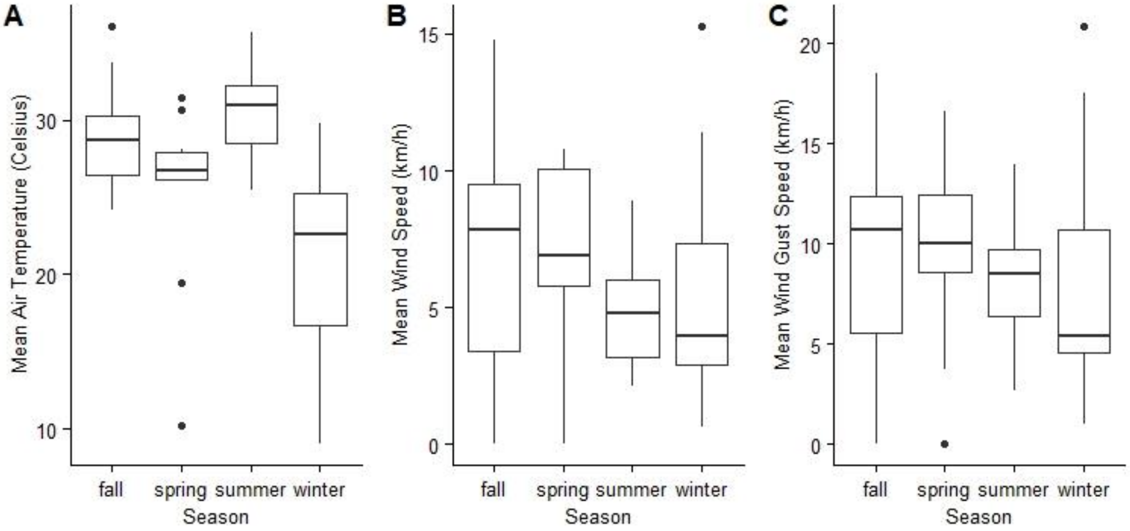

Figure 2 Boxplots comparing seasonal (A) air temperature, (B) average wind speed, and (C) wind gust speed. Boxes represent the middle 50% of the data, bold lines represent medians, whiskers represent the upper and lower 25% of the data values (excluding outliers), and points represent outliers. Data was obtained from Weather Underground based on the start time of each transect.

Abundance and Diversity

I identified 67 different species and counted a total of 22,085 birds. The mean number of birds I observed per transect was 397.56, or 1.31 birds/ha. 292 birds (1.3% of total birds) were unidentifiable to species level due to dark photographs, distance, or camera angle. The rarefaction curve reached an asymptote, indicating that my sampling efforts provided a representative sample of the diversity of the study region (Figure 3). Results of AIC model selection (Table 3) determined that the model that best predicted bird abundance only included season as a predictor. Abundance (± 95% confidence intervals) was highest in winter (1013.00 ± 594.28) and was significantly higher than in any other season ($p < 0.001$). Similarly, species richness (Figure 4B) was highest in winter (25.79 ± 2.13) and was also significantly higher than all other seasons ($p < 0.001$ for all). Pielou's evenness (Figure 4C) was lowest in winter (0.08 ± 0.01) and was significantly lower than in all other seasons ($p < 0.001$ for all). Shannon diversity values (Figure 4D) were similar for all seasons ($p = 0.13$) and Simpson's diversity values (Figure 4E) were significantly higher in summer (0.88 ± 0.02) than in winter ($p = 0.010$).

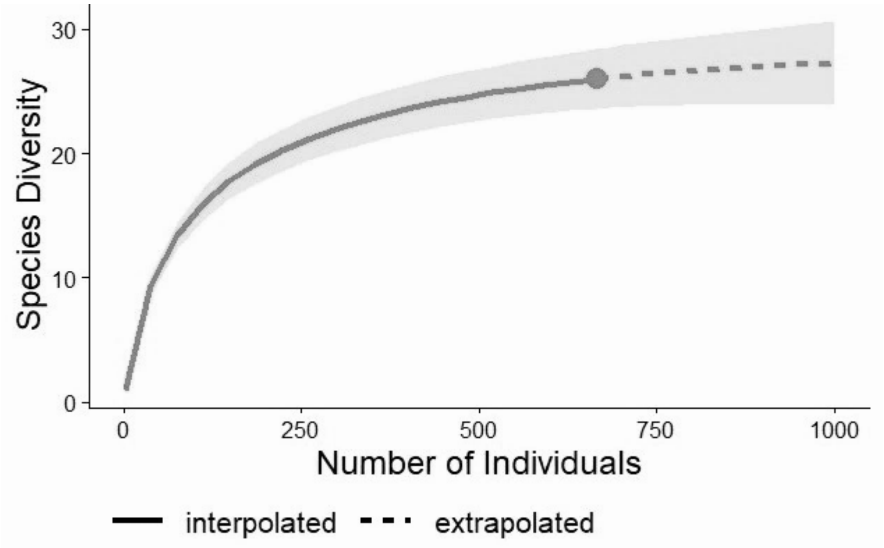

Figure 3 Rarefaction curve reaches an asymptote, indicating that my sampling efforts were effective at capturing an accurate representation of the species diversity of the region.

Table 3 AIC table for negative binomial generalized linear models predicting total bird abundance. AIC_c, delta AIC_c, degrees of freedom, and AIC_c weight are given.

	AIC_c	ΔAIC_c	df	AIC_c weight
Season	727.1	0.0	5	0.41
Average wind speed	776.0	49.0	3	<0.001
Wind gust speed	776.0	49.0	3	<0.001
Season + average wind	728.9	1.8	6	0.16
Season + wind gust	727.8	0.8	6	0.28
Season + average wind + wind gusts	729.0	2.0	7	0.15
Average wind + wind gust	778.4	51.3	4	<0.001

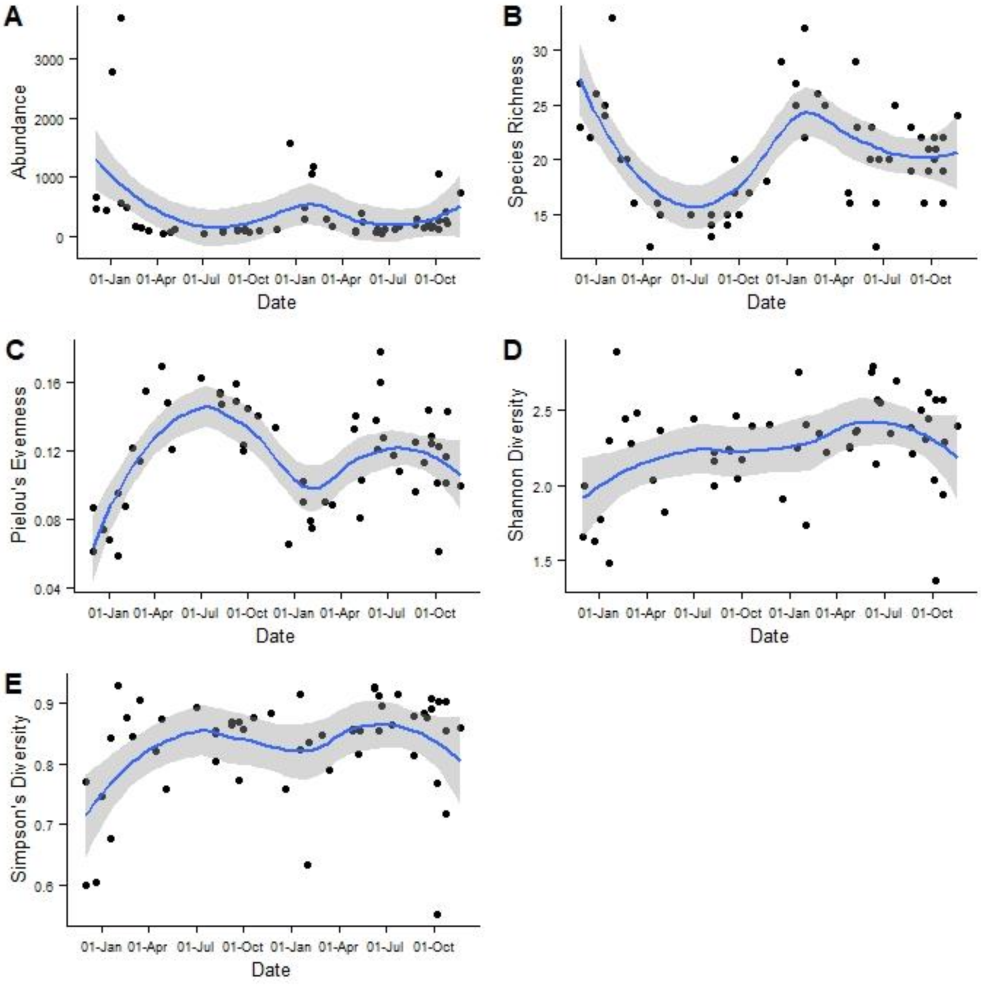

Figure 4 Abundance and diversity metrics over the study period. Abundance (A), species richness (B), Pielou's evenness (C), Shannon diversity (D), and Simpson's Diversity (E) shown with trend lines (black lines) and 95% confidence intervals (gray shading).

The five most numerically abundant bird families observed were Laridae (Gulls and Terns, 27.0%), Anatidae (Ducks, 22.2%), Ardeidae (Herons and Egrets, 13.6%), Scolopacidae

(Sandpipers, 9.2%), and Threskiornithidae (Ibises, 4.6%). These families accounted for 76.6% of all birds observed throughout the study. Twenty additional families comprised the remaining 23.3%. Laridae, Ardeidae, and Threskiornithidae were present in 100% of the transects throughout all seasons. Although Anatidae were the second most abundant family, they were only present in 60.0% of transects (Table 4), with none present in summer 2019. In the spring of 2020, I observed a lone surf scoter floating in open water, and in summer of 2020 I made 10 observations of *Anas fulvigula* (Mottled ducks), which are endemic to Florida and were the only non-migratory waterfowl species observed in this study.

Table 4 Total counts from all transects for the five most commonly observed bird families. Percent of observations value represents the number of birds in each family observed for all transect photographs divided by the total number of birds counted throughout all transect photographs. Percent occurrence values represent the percentage of transects in which any member of the family occurred in any photographs.

Family	Count	Percent of Observations	Percent Occurrence
Laridae (gulls and terns)	5957	27.0%	100%
Anatidae (ducks)	4911	22.2%	60.0%
Ardeidae (herons and egrets)	3013	13.6%	100%
Scolopacidae (sandpipers)	2023	9.2%	67.3%
Threskiornithidae (ibises)	1012	4.6%	100%
Total count of top 5 families	16918	76.6%	
Total count for all other birds	5167	23.3%	

Both wading bird and shorebird abundances were impacted by water level. Shorebirds, which included plovers, sandpipers, and oystercatchers, were more abundant during low water observations than in both high ($p < 0.001$) and medium ($p = 0.037$) water levels. Wading birds, which included herons, egrets, ibises, spoonbills, and storks, were most abundant in medium water conditions. Wading bird abundances were similar between medium and low water conditions ($p = 0.113$) and were similar between low and high water conditions ($p = 0.124$), but abundance was greater in medium water conditions than in high water conditions ($p = 0.002$).

Assemblages by Habitat or Behavior

Results from the PERMANOVA test indicates significant differences between communities based on habitat or behavior ($p = 0.001$). The ordination plot results suggest that the bird assemblages observed perched on dead treetops differed from those found on sandbars, wading in shallow water, on dead oyster reefs, floating in open water, and on mangroves or mangrove shorelines, as there was no overlap with the confidence interval ellipses (Figure 5). There was some overlap between the ellipse for the birds on dead treetops and the ellipses for birds on live oyster reefs and birds on artificial structures, indicating some similarities in those assemblages. Additionally, bird assemblages observed floating in open water differ from those associated with live oyster reefs and mangroves, with minimal overlap with birds associated with sandbars and wading in shallow water, and more overlap with birds on artificial structures and on dead oyster reefs. The more significant overlaps in the confidence interval ellipses for birds associated with wading shallow, mangroves, and live oyster reefs, indicates similarities in those bird assemblages. There is little to no overlap between the confidence intervals for the assemblages associated with sandbars and those associated with floating in open water, artificial structures, mangroves, or dead treetops, indicating differences in those assemblages. The confidence interval ellipses for birds on oyster reefs and shallow wading overlap with birds associated with mangroves, suggesting that those assemblages are also similar (Figure 5). Percent of observations for all species for each habitat type or behavior can be found in Appendix 1.

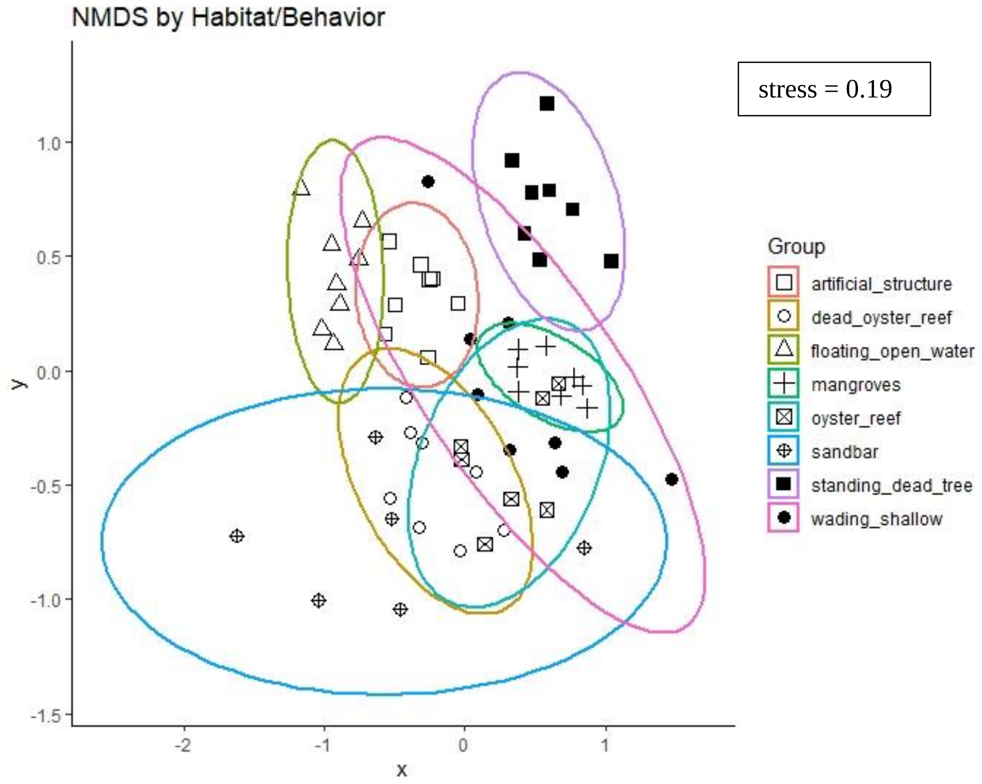

Figure 5 NMDS ordination plot of species assemblages for different habitat features. Different symbols represent bird assemblages during a particular season for each specific habitat type. Ellipses represent 95% confidence intervals for habitat groupings.

Species Associated with Habitat Features

There were 35 representative species which were associated with various habitat features or behaviors, including combinations (Table 5). Of these, there were 14 species that were associated with one habitat type or behavior. Two of the top four species most associated with live oyster reefs were *Egretta rufescens* (Reddish egret) and *Rynchops niger* (Black skimmer), both of which are listed as threatened on the FWC Imperiled Species List. The single species associated with dead oyster reefs was *Sternula antillarum* (Least tern), which is also a threatened species in the state of Florida. In some instances, certain species were associated with more than one habitat type. There were an additional 21 species that were representative of a combination of 2 habitats or behaviors. Species that were most closely associated with oyster reefs plus mangroves included wading birds, such as *Eudocimus albus* (White ibis) and several species of herons and egrets. Raptors, specifically *Pandion haliaetus* (Osprey) and *Cathartes aura* (Turkey vulture), were associated with both dead treetops and artificial structures. The complete list of species associated with specific habitat features can be found in Table 5.

Table 5 Representative species by habitat types. The indicator value (IndVal) is based on both statistics A and B. Statistic A is the positive predictive value of the species and represents an estimate of the probability that a site belongs to a particular habitat type based on the presence of the species. Statistic B is the fidelity value of the species and represents an estimate of the probability of finding the species at that particular habitat feature. All values given are statistically significant at the p < 0.05 level.

Species	**IndVal**	**A**	**B**
Live Oyster Reefs			
Tringa semipalmata (Willet)	0.62	0.60	0.64
Egretta rufescens (Reddish egret)	0.30	0.82	0.11
Rynchops niger (Black skimmer)	0.28	0.93	0.08
Actitis macularius (Spotted sandpiper)	0.25	0.74	0.08
Dead Oyster Reefs			
Sternula antillarum (Least tern)	0.35	0.99	0.12
Mangroves and Mangrove Shorelines			
Anhinga anhinga (Anhinga)	0.52	0.68	0.39
Nycticorax nycticorax (Black-crowned night heron)	0.46	0.88	0.24
Dead Treetops			
Cathartes aura (Turkey vulture)	0.36	0.66	0.19
Tyrannus dominicensis (Gray kingbird)	0.34	1.00	0.12
Sandbars			
Hydroprogne caspia (Caspian tern)	0.54	0.72	0.41
Charadrius semipalmatus (Semi-palmated plover)	0.53	0.78	0.35
Floating in Open Water			
Mergus serrator (Red-breasted merganser)	0.59	0.96	0.37
Gavia immer (Common loon)	0.40	0.96	0.16
Melanitta perspicillata (Surf scoter)	0.25	1.00	0.06
Artificial Structures + Dead Treetops			
Pandion haliaetus (Osprey)	0.79	0.77	0.80
Coragyps atratus (Black vulture)	0.27	1.00	0.07
Artificial Structures + Floating in Open Water			
Phalacrocorax auratus (Double-crested cormorant)	0.73	0.64	0.82
Pelecanus occidentalis (Brown pelican)	0.51	0.45	0.58
Artificial Structures + Live Oyster Reefs			
Leucophaeus atricilla (Laughing gull)	0.59	0.67	0.52
Artificial Structures + Sandbars			
Thalasseus maximus (Royal tern)	0.68	0.58	0.81
Dead Oyster Reefs + Live Oyster Reefs			
Haematopus palliatus (American oystercatcher)	0.62	0.86	0.44

Species	IndVal	A	B
Arenaria interpres (Ruddy turnstone)	0.44	0.89	0.22
Dead Treetops + Mangroves			
Megaceryl alcyon (Belted kingfisher)	0.54	0.78	0.38
Floating in Open Water + Live Oyster Reefs			
Larus delawarensis (Ring-billed gull)	0.50	0.80	0.32
Mangroves + Live Oyster Reefs			
Eudocimus albus (White ibis)	0.84	0.83	0.84
Ardea herodias (Great blue heron)	0.81	0.80	0.82
Ardea alba (Great egret)	0.81	0.91	0.71
Egretta thula (Snowy egret)	0.72	0.93	0.56
Egretta caerulea (Little blue heron)	0.52	0.65	0.41
Nyctanassa violacea (Yellow-crowned night heron)	0.51	0.97	0.27
Egretta tricolor (Tricolored heron)	0.49	0.87	0.28
Butorides virescens (Green heron)	0.32	1.00	0.10
Live Oyster Reefs + Sandbars			
Pluvialis squatarola (Black-bellied plover)	0.62	0.86	0.45
Calidris alpine (Dunlin)	0.39	0.98	0.15
Sterna forsteri (Forster’s tern)	0.29	0.61	0.13

Discussion

Birds are both ecologically and economically important members of the Mosquito Lagoon community, underlining the need for monitoring and assessment of avian taxa within the lagoon. The mean density of all birds in this study was 1.31 birds/ha. Previous studies in the nearby Kennedy Space Center/Merritt Island National Wildlife Refuge focused on nesting bird densities or only reported bird densities for wading birds. Trost (1968) reported an estimated mean wading bird density of 0.9 birds/ha in the KSC/MINWR area prior to the creation of mosquito impoundments (areas that have been diked in order to control water level). Stolen (2006) reported a mean wading bird density of 0.26 birds/ha in KSC/MINWR impoundments. In the current study of the northern portion of Mosquito Lagoon, the mean density of wading birds was 0.24 birds/ha, so mean wading bird densities are similar to those found in KSC/MINWR impoundments. More recent studies in Mosquito Lagoon focused on bird use of oyster reefs and a restored shoreline. Shaffer et al. (2019) identified 41 species in their surveys of bird use of oyster reefs in Mosquito Lagoon, 38 of which were also observed in this study. They observed

Charadrius vociferus (Killdeer), *Calidris alba* (Sanderling), and *Charadrius wilsona* (Wilson's plover), which were not observed in my study. Similarly, Litwak and Rifenberg (2021) identified 16 bird species on a restored shoreline in Mosquito Lagoon, 14 of which were also observed in the current study. They observed *Calidris mauri* (Western sandpiper) and *Setophaga palmarum* (Palm warbler), which were not observed in my study. The combined total number of species identified by Shaffer et al. (2019) and Litwack and Rifenberg (2021) was 44, and I identified 67 species in this study. My study adds to the previous studies of birds in Mosquito Lagoon and other parts of the Indian River Lagoon system, but provides important, recent, and regional-specific information about the bird community in Mosquito Lagoon. My data elucidates seasonal trends in both resident and migratory bird abundance and diversity in the lagoon. Additionally, this study highlights the importance of the mosaic of habitat features within Mosquito Lagoon in supporting a diverse bird community.

Seasonal Abundance

In this study, overall bird abundance was highest during the winter seasons. The higher abundance in winter was in contrast to previous studies of wading birds in the region of KSC/MINWR. In two previous studies that included mosquito impoundments, the highest wading bird abundances were reported from February-June and lowest abundances in winter, which they defined as October-January (Smith and Breininger 1995; Stolen et al. 2002). Some of this discrepancy was due to differences in how seasons were defined. Smith and Breininger (1995) and Stolen et al. (2002) defined seasons based on the nesting seasons of the birds. In the current study, I analyzed data based on meteorological seasons rather than nesting seasons. I defined October and November as part of fall, and February was included in winter data. Additionally, the salinity of the impoundments in these study areas varies based on rainfall and water level (ranging from 0–35 ppt) and is lower than typical salinities in Mosquito Lagoon, which ranges from 18-45 ppt (Barber et al. 2010; Breininger and Smith 1990). KSC/MINWR serves as a nesting site for many of Florida's wading birds (Schikorr and Swain 1995; Stolen et al. 2002), which explains why the abundances of wading birds would be higher in that region during pre-nesting and nesting seasons. Stolen (2006) observed the distances which *Ardea alba* (Great egrets) and *Egretta thula* (Snowy egrets), nesting in KSC/MINWR, flew from their nests to forage and found that the average distances were 6.2 km and 4.7 km, respectively. The distance between the southernmost point of the bird transect route and the northernmost region of KSC/MINWR was nearly 9 km. Wading birds may use Mosquito Lagoon as foraging habitat in the fall and winter but not during spring and summer, due to nesting behaviors.

In their 1995 study, Smith and Breininger only focused only on wading birds, and lacked any migratory waterfowl, shorebirds, or seabirds in their analyses. An earlier study showed that in open impoundments within the Kennedy Space Center region, duck abundance was highest starting in November and peaked in February, and shorebird and wading bird abundances were highest in spring, when water levels were lowest (Breininger and Smith 1990). I found peaks in the abundances of waterfowl, wading birds, and seabirds in both winters. The most abundant waterfowl in this study was *Mergus serrator* (Red-breasted merganser), which were present in high numbers during both winter seasons of the study (3,322 and 1,381 observations, respectively), completely absent in summer and fall, and rare in spring with 3 observations in spring of 2019 and 2 observations in spring of 2020. The high abundance of Red-breasted mergansers in winter is consistent with the life history of this species, as they migrate to Florida each November, and then return to northern breeding grounds (e.g. Great Lakes, New England) in March (Johnsgard 2016).

Wading birds were present in every transect throughout the study, with Great egrets and White ibises being the most abundant waders. The abundances of both these species also peaked in the winter. Both are permanent residents in Florida, the increase in Great egret abundance during the winter was likely due to an influx of individuals from more northern Atlantic states (Virginia, Maryland, and Delaware) (Melvin et al. 1999; Nellis 2010). Birds from these areas tend to begin southward migration in October to avoid freezing conditions, and return north in February and March (Melvin et al. 1999; Nellis 2010). White ibis nestlings may become salt stressed, so during nesting (April-September) they tend to forage in freshwater ecosystems, which likely explains why their numbers were lower in Mosquito Lagoon during those seasons than in winter (Nellis 2000). The high densities of wading birds present during the spring in the 1990 study (up to nearly 4.5 birds/ha) at KSC may be due to the close proximity of that area to important breeding grounds for waders (Breininger and Smith 1990). For some wading birds, such as Great egrets, human disturbance (especially boating within 50 m of nesting-sites) is one of the main factors affecting nesting-site suitability (Chapman and Howard 1984). Unlike Mosquito Lagoon, KSC has designated areas with no public access. This lack of human disturbance makes KSC a more suitable wading bird nesting habitat than central Mosquito Lagoon.

The most abundant seabirds were Ring-billed gulls, Laughing gulls, and Royal terns. Ring-billed gulls were present almost exclusively in winter, with 1 observed in spring of 2019 and some birds observed during late fall of 2019. This species is migratory, typically beginning southward migration to wintering grounds in September, and beginning the return northward in March, explaining the high abundances in Mosquito Lagoon during winter and general absence during other seasons (Nellis 2000). Both Laughing gulls and Royal terns are resident species in

Mosquito Lagoon and were present in ≥ 80% of transects. Both species were most abundant in winter, as populations from northern regions of the United States migrate south for winter (Nellis 2000). Additionally, Laughing gulls tend to forage on terrestrial prey items more frequently than marine prey items during nesting (Washburn et al. 2013), which may contribute to their reduced abundance on oyster reefs and sandbars during summer months.

In the current study, winter and spring seasons had the highest shorebird abundances. These results are similar to those from an 8-year study of shorebird use of impounded wetlands in MINWR, which found that shorebird numbers were highest from December through April, and then lower from May through November (Epstein 2019). The most abundant shorebirds in my study were Dunlins, which were present in high numbers during the winter of 2018/2019. The high abundance of Dunlins that I observed is consistent with Epstein's (2019) results, as well as those from a study in which Dunlins were found to be the most abundant wintering shorebird in 59 of 60 coastal Florida study sites, including sites near KSC/MINWR (Sprandel et al. 2000). They were also observed in winter of 2019/2020, but in lower numbers than the previous winter. It is interesting to note that in the fall of 2020, falcons (Peregrines, Merlins) were observed on four separate occasions. Falcons are natural predators of Dunlins, and previous research has indicated that non-breeding populations of Dunlins may be reduced by the presence of Falcons (Ydenberg et al. 2017). Further research would be needed to determine if this predator-prey interaction is occurring in Mosquito Lagoon.

Bird Abundance and Water Level

A 1995 study of wading bird abundance in the Indian River Lagoon and nearby Upper Basin of the St. John's marsh system found that tidal condition was the main factor affecting numbers of birds, with up to three-times more birds occurring during drawdown events that artificially lowered water levels (Schikorr and Swain 1995). Studies in wetlands in other parts of the world indicate that there were increases in shorebird abundances at lower water levels, when more shallow water habitat was available (Collazo et al. 2019; Velasquez 1992). In the current study, wading bird abundance was highest during medium water level conditions, in which live oyster reefs and sandbars were partially, but not entirely, exposed. Wading birds, such as herons and egrets, have relatively long legs, allowing them to wade through deeper water than shorebirds. Herons and egrets primarily feed on fish and mobile invertebrates (Nellis 2000), which may be concentrated in areas surrounding mangrove shorelines and on oyster reefs during periods of falling tide (Barber et al. 2010; Boudreaux et al. 2006). As the tide falls, small fish and mobile invertebrates must retreat from their more sheltered areas among mangroves, and may become trapped in small ephemeral pools within the complex structure of oyster reefs.

Shorebird abundance was highest at low water levels, when live oyster reefs and sandbars were completely exposed. Previous shorebird research in the KSC/MINWR area found that shorebird abundance was negatively related to water level (Collazo et al. 2019). Prey items for shorebirds, such as plovers and sandpipers, include marine worms, gastropods, small crustaceans, and other small invertebrates (Nellis 2000) which may be available on or within sandy or muddy sediments. In my study, shorebirds were most frequently observed foraging on sandbars or oyster reefs, both of which are most readily available at the lowest water levels, and which provide sediments for common shorebird prey items (Harris 2020).

Both wading bird and shorebird abundances were lowest during high water conditions, when live oyster reefs and sandbars were completely submerged. This decrease in abundance during periods of high water level is consistent with the earlier studies (Collazo et al. 2019; Schikorr and Swain 1995; Velasquez 1992). During high water season, however, water level did not have a significant impact on the total number of birds. This may be, in part, due to the fact that during the high water season the water levels were too high for live oyster reefs and sandbars to be exposed, even at low tide. Some species that frequently utilize live oyster reefs, such as American oystercatchers and *Actitis macularius* (Spotted sandpipers) were completely absent from all transects during the fall seasons.

Seasonal Species Richness, Evenness, and Diversity

In addition to higher bird abundance, species richness peaked in winter (Figure 4). The increase in number of species observed in winter corresponds with the timing of migratory birds, such as Red-breasted mergansers and Surf scoters, wintering in Florida (Johnsgard 2016; Nellis 2000). Thus, the combination of resident and migratory species is most likely the main contributor to the higher richness during winter months. Conversely, Pielou’s evenness was lowest during winter months. In winter, migratory waterfowl made up a large proportion of the birds observed. For example, on one winter occasion more than 65% of the birds observed were migratory waterfowl (including Red-breasted mergansers, Hooded mergansers, Black scoters, and Surf scoters). This over-abundance of certain species explains why evenness would be lower during winter months. Even though species richness was highest in winter, Simpson’s diversity was higher in the summer than in the winter. This is likely due to the low evenness in winter, as the Simpson’s diversity index is more sensitive to changes in evenness.

Bird Use of Habitat Features

Mosquito Lagoon exhibits a mosaic of habitat categories (Table 1) and based on the results from the NMDS plot and analyses of species associations with habitat features, this variety may be important in supporting the diverse bird community. Different bird groups showed preferences for certain habitat features.

Oyster Reefs. Several bird species were closely associated with either live oyster reefs, dead oyster reefs, or the combination of the two. The willet was the top species most closely associated with live oyster reefs. Typical prey items for Willets include both mobile and infaunal invertebrates, such as crabs, snails, amphipods, and worms (Nellis 2000), all of which are readily available food sources on either the surface or in the subsurface sediment of live oyster reefs (Harris 2020; Rodney and Paynter 2006; zu Ermgassen et al. 2016). American oystercatchers, a species that is threatened in Florida, and Ruddy turnstones were associated with the combination of dead and live oyster reefs. The main food source for American oystercatchers is marine bivalves (Nellis 2000), so in Mosquito Lagoon they forage primarily on live *Crassostrea virginica* clustered on intertidal reefs, making live reefs ideal foraging habitats. American oystercatchers have been documented nesting on dead oyster reefs in Mosquito Lagoon, which may explain their abundance on dead reefs. I observed 61 (87.0%) Ruddy turnstones on dead oyster reefs on transects that took place during high water conditions, and none were observed on live oyster reefs during high water transects. On transects that took place during medium or low water conditions, Ruddy turnstones were observed on both live and dead oyster reefs, with 34 (50.0%) observed on live and 14 (20.6%) observed on dead reefs. As their name implies, one type of foraging behavior exhibited by these birds is the turning over of loose stones or shell in search of invertebrate prey items (Groves 1978). Since dead oyster reefs are composed of loose, disarticulated oyster shells, they serve as important foraging habitat for Ruddy turnstones, particularly during periods of high water, when live oyster reefs are submerged. A 2019 study also found that Ruddy turnstones were the dominant species foraging on dead oyster reefs in

Mosquito Lagoon (Shaffer et al. 2019). An additional foraging style for turnstones involves scavenging remnants of food left behind by oystercatchers (Nellis 2000), which could explain their presence on live oyster reefs. Least terns, another state-level threatened species, were associated with dead oyster reefs, where they were observed nesting in Mosquito Lagoon in the summers of 2019 and 2020. A previous study of Least tern nesting on the Gulf Coast of Florida suggested that disarticulated oyster shell was a preferred substrate for nest site-selection (Mazzocchi and Forys 2005).

Mangroves and Oyster Reefs. Wading birds were most frequently observed in live mangroves within a meter of trees, and on live oyster reefs. Eight different wading bird species were determined to be associated with the combination of these two habitat types. Of these, 7 were herons and egrets, including the Little blue heron and Tricolored heron, both of which are state-level threatened species. Herons and egrets were most commonly observed on live mangroves or on mangrove shorelines (1354 observations), but during periods of medium and low water level they were also abundant on live oyster reefs (811 observations). The main prey items for herons and egrets are crustaceans and fish (Miranda and Collazo, 1997; Nellis, 2001), both of which are more abundant in structured habitats, such as mangrove prop roots and oyster reefs, than unstructured habitats (Barber et al. 2010; Bloomfield and Gillanders, 2005; Boudreaux et al., 2006; zu Ermgassen et al., 2016). Dietary analysis of herons and egrets in a tropical mangrove swamp in Puerto Rico suggested that some of the most important fish prey items were members of the families Mugilidae (mullets) and Gobiidae (gobies) (Miranda and Collazo, 1997). Stolen (2006) found that within impounded salt marshes in the northern IRL, fish densities were always higher in vegetated areas than in adjacent unvegetated areas. A recent fish survey in Mosquito Lagoon found mullets in 50% of all seine net catches near living shorelines and 18% of catches near oyster reefs (Lewis et al. 2020). Likewise, gobies were found in 73% of living shoreline catches and 25% of oyster reef catches (Lewis et al. 2020). Miranda and Collazo (1997) also found crabs and shrimp to be important dietary components of herons and egrets. In a survey of the macroinvertebrates along living shorelines and oyster reefs in Mosquito Lagoon, crabs and shrimp were abundant, making up over 90.8% of individuals caught on natural (non-restored) oyster reefs and 90.9% of individuals caught on natural mangrove shorelines (Searles 2019). The abundance of prey items concentrated near mangroves and oyster reefs explains the preference of wading birds for such habitats.

Sandbars and Oyster Reefs. Shorebirds showed preference for sandbars, with plovers and sandpipers making up 49.2% of the birds observed using this habitat feature. The shorebird species most closely associated with sandbars was the Semi-palmated plover. They are small and short-billed, and forage by pecking at small marine invertebrate prey from the surface of sand or mudflats (Nellis 2000). Black-bellied plovers and Dunlins were both associated with the combination of sandbars and live oyster reefs. The larger body size and longer leg length of the Black-bellied plover (the largest of all plover species) may allow for more maneuverability around the complexities of oyster reefs, and the longer bill length of the Dunlin may allow for probing into oyster reef sediments between oyster clusters, accounting for the abilities of these species to exploit live oyster reefs for foraging, in addition to sandbars (Bent 1929, Cornell Lab of Ornithology 2020).

Artificial Structures, Sandbars, and Oyster Reefs. Seabirds, including gulls, terns, pelicans, and cormorants, were frequently observed loafing on oyster reefs and sandbars and perched on artificial structures such as signs and pilings. Previous research on bird use of oyster reefs in Mosquito Lagoon reported that seabirds (gulls, terns, pelicans, and cormorants) were among the dominant species seen loafing (which includes any behaviors not associated with feeding or breeding) on dead oyster reefs, and gulls were also among the most abundant birds observed on live oyster reefs (Shaffer et al. 2019). I documented birds utilizing all habitat features in Mosquito Lagoon, rather than only those associated with oyster reefs. In my study, sandbars and artificial structures were frequented by seabirds. Royal terns were associated with the combination of artificial structures and sandbars. Royal terns are diving foragers, picking off fish from the upper 60 cm of the water (Nellis 2000). Previous research indicates that Royal terns utilize artificial structures for perch hunting (Watts 2000), so pilings and sign posts in Mosquito Lagoon likely provide a perch to give the terns an aerial view when searching for prey. These perches may also simply provide a place of rest, particularly during periods when the water levels are too high for sandbars to be exposed for loafing. In my study, the number of Royal terns observed perched on artificial structures was significantly higher during high water than during either medium or low water conditions ($p < 0.001$ for both). Laughing gulls were associated with the combination of artificial structures and live oyster reefs. Similar to the Royal terns, they likely use the signs and pilings as resting places when oyster reefs are submerged. The number of Laughing gulls perched on artificial structures was also significantly higher during high water than during medium or low water conditions ($p = 0.001$ and $p = 0.002$, respectively). Additionally, Laughing gulls, which are not as adept at diving as terns, are known to steal food from other seabirds (Burger, 1988); this may explain their behavior of perching on signs and pilings near Royal terns.

Artificial Structures and Standing Dead Treetops. Birds of prey were often observed perched either on artificial structures such as signs, pilings, and utility poles or on dead treetops. Osprey was the species most associated with the combination of artificial structures and dead treetops.

Dead tree branches, utility poles, and sign posts all provide perches for Ospreys to both scan for prey and to consume fish prey (Watts 2000). Similarly, I frequently observed Osprey eating fish while perched on these structures. While both standing dead trees and artificial structures may serve the same purpose as an aerial perch, their locations might impact which structure an Osprey may choose to utilize. For example, when the water turbidity is high due to factors such as algal blooms or storms, Osprey might select the pilings and sign-posts if they are in closer proximity to the surface of the water. I did not assess turbidity, so more research would be needed to ascertain whether certain conditions affect Osprey preferences for perch types.

Open Water. Waterfowl were almost exclusively seen floating in open water and three waterfowl species were associated with this behavior. The species most associated with floating in open water was Red-breasted merganser, the most abundant waterfowl observed in this study, making up 96.5% of the waterfowl observed. They forage primarily on fish in calm water that is less than 4 m in depth (Nellis 2000). Mosquito Lagoon is sheltered from coastal waves, and has an average depth of 1.5 m (Walters et al. 2001); therefore, there is ample, suitable open water habitat for foraging Red-breasted mergansers.

Restoration of Important Bird Habitat

The decline of mangroves and oyster reefs has led to extensive restoration efforts throughout Mosquito Lagoon. In the past 14 years, the Coastal and Estuarine Ecology Lab at the University of Central Florida has restored 91 oyster reefs and planted mangroves along 4.2 km of shoreline in these waters (e.g. McClenachan et al. 2020; Walters et al. 2021). Research suggests that due to the high mobility of birds and their ability to locate and utilize newly-available habitat, bird abundance may be a good measure of the success of restoration projects (Melvin et al. 1999). Shaffer et al. (2019) found similarities in species evenness and proportions of foraging birds between restored and natural oyster reefs in Mosquito Lagoon, suggesting that the restoration efforts are benefiting the bird community. Additionally, a 6-month study using trail cameras along a newly-restored portion of a newly-stabilized mangrove shoreline in Mosquito Lagoon captured 17 bird taxa (189 total observations) utilizing the shoreline (Litwak and Rifenberg, 2021). More research is needed to determine how bird use of these restored shorelines compares to that of natural mangrove shorelines. Restoration appears to be having a positive impact on birds in Mosquito Lagoon, but more frequent and consistent monitoring will be necessary to elucidate these impacts, and to assess the overall ecological health of the lagoon.

CHAPTER THREE: BIRD USE OF NATURAL, RESTORED, AND DEAD OYSTER (*CRASSOSTREA VIRGINICA*) REEFS IN MOSQUITO LAGOON, FL

Introduction

Shorebirds, wading birds, and sea birds rely on coastal ecosystems for foraging and nesting habitats (Bildstein et al. 1991; Connors et al. 1979; Powell 1987; Kushlan et al. 2002; Piersma et al. 2017; Schreiber and Burger 2002). The ability of any coastal habitat to support communities of foraging birds is dependent on two main factors: prey availability and habitat extent (Galbraith et al. 2002). Gawlick (2002) conducted a study in the Florida Everglades in which prey density and prey vulnerability were artificially controlled. The study found that wading birds such as *Mycteria americana* (Wood stork), *Eudocimus albus* (White ibis), and *Egretta thula* (Snowy egret) were negatively impacted by decreased prey density and decreased prey vulnerability, and all three species had experienced population declines in the study region (Gawlik 2002). However, the amount of available habitat imposed a restriction on how many birds can forage at any particular site, regardless of prey availability (Galbraith et al. 2002; Goss-Custard 1977). As foraging densities increase, density-dependent factors, such as competition take effect, ultimately leading to an overall reduction in bird abundance (Galbraith et al. 2002; Goss-Custard 1977; Goss-Custard 1980). Therefore, if foraging habitat in an ecosystem is lost, the capacity of that site to support bird populations would also decrease. Goss-Custard and Moser (1988) found that loss of foraging grounds due to the spread of the cordgrass *Spartina anglica* led to decreases in *Calidris alpina* (Dunlin) abundances in several estuaries in Europe. Similarly, Meire (1991) found that reductions in intertidal foraging habitat due to the construction of several dams resulted in declines in *Haematopus ostralegus* (Eurasian oystercatcher) populations in an estuary in the Netherlands.

For some coastal bird species, loss of nesting habitat may pose a greater threat than loss of foraging habitat (Hunter et al 2015; Nol 1989; Ogden et al 2014). This has been documented for beach nesting birds, and there is evidence to suggest that many shorebird and tern populations are at risk of decline in the southeastern United States due to loss of nesting habitat (Hunter et al. 2015; Ogden et al. 2014). Ogden et al. (2014) suggested that both *Haematopus palliatus* (American oystercatchers) and *Sternula antillarum* (Least terns) experienced population declines in South Florida resulting from loss or anthropogenic alteration of nesting habitat. Hunter et al. (2015) used modelling to predict the potential impacts of coastal habitat loss due to sea level rise, and predicted that ground nesting coastal birds, such as American oystercatchers and *Charadrius wilsonia* (Wilson's plovers), would likely be more negatively impacted by the loss of their nesting habitat than by loss of foraging habitat. A study on several breeding populations of American oystercatchers in Virginia also found that reproductive output was not impacted by prey availability, and suggested that availability of suitable nesting habitat is more important for reproductive success (Nol 1989).

Globally, coastal habitats such as mangroves, saltmarshes, beaches, vegetated dunes, and oyster reefs have experienced severe losses during the last century due to sea level rise and anthropogenic factors such as coastal development (e.g. Beck et al. 2011; Bindoff et al. 2019). These declines have led to habitat restoration efforts all over the world (e.g. Beck et al. 2011; Coen et al. 2007; Garvis et al. 2015; Hashim et al. 2010; Kaly and Jones 1998; Liu et al. 2016). It is important to assess the success of these restoration efforts in terms of restoration of ecosystem functions such as habitat provision. Birds have often been used as indicators of biodiversity and ecosystem health (Gregory et al. 2003; Gregory and Strien 2010; Temple and Wiens 1989).

Melvin et al. (1999) suggests that birds are useful as indicators of restoration success due to their mobile nature and ability to find and use newly-available habitat.

Birds utilize oyster reefs for foraging, loafing (any behavior that is not related to either foraging or breeding), and nesting habitat. It is estimated that, on a global scale, oyster reefs have experienced losses of 85% compared to historical abundances (Beck et al. 2011), and oyster reef restoration has become a common practice to mitigate these losses (Beck et al. 2011; Coen et al. 2007; Garvis et al. 2015). While many of these efforts have been deemed successful in terms of oyster metrics (Barber et al. 2010), I am also interested in how successful oyster reef restoration translates into providing foraging habitat for coastal birds. Shaffer et al. (2019) surveyed bird activity for one year on restored oyster reefs of various ages (ranging from 1 to 8 years post-restoration) in a Florida estuary and found that the proportion of birds foraging on restored oyster reefs was similar to the proportion of birds foraging on live, natural oyster reefs (hereafter referred to as “live” reefs). Coastal bird communities include a variety of groups, each with specific prey preferences (Table 6). Previous studies have suggested that oyster reef restoration may increase the abundance of oyster reef-associated fauna, including mobile invertebrates, infaunal invertebrates, and fishes (Grabowski et al. 2005; Harris 2020; Meyer and Townsend 2000; Rodney and Paynter 2006), all of which are known food sources for estuarine birds. Infaunal invertebrates, including species of the classes Malacostraca, Gastropoda, Bivalvia, and Polychaeta, have also been identified as some of the most widely represented food sources for shorebirds (Skagen and Oman 1996). These invertebrates also serve as important food sources for juvenile fish (Grabowski et al. 2005), which may, in turn, serve as prey items for piscivorous birds.

Table 6 Summary of prey items for different bird groups found within Mosquito Lagoon.

Group	Example Species	Prey Items	Citations
Birds of Prey	*Pandion haliaetus* (Osprey) *Haliaeetus leucocephalus* (Bald eagle)	Fish	Glass and Watts 2009; Nellis 2001
Wading Birds	*Egretta caerulea* (Little Blue heron) *Ardea 36erodias* (Great Blue heron) *Eudocimus albus* (White ibis)	Fish Crustaceans Worms	Miranda and Collazo 1997; Kushlan 1979; Pranty et al. 2006
Seabirds	*Leucophaeus atricilla* (Laughing gull) *Thalasseus maximus* (Royal tern) *Pelecanus occidentalis* (Brown pelican)	Fish Mollusks Crustaceans	Barrett et al. 2007; Pranty et al. 2006
Shorebirds	*Arenaria interpres* (Ruddy turnstone) *Tringa semipalmatta* (Willet) *Pluvialia squatarola* (Blackbellied plover)	Mollusks Crustaceans Worms Insects	Skagen and Oman 1996; Alsop 2002; Pranty et al. 2006

By providing foraging and loafing habitat, the extensive network of live and restored oyster reefs in Mosquito Lagoon, the northernmost portion of the Indian River Lagoon system, contributes to the diversity of bird species in the region (Shaffer et al. 2019). Recreational boating in Mosquito Lagoon has contributed to the formation of dead reefs, which are piles of dead, disarticulated shell that may reach elevations of up to 1 m above mean high tide (Wall et al. 2005). The University of Central Florida's Coastal and Estuarine Ecology Laboratory has been restoring oyster reef habitat in Mosquito Lagoon for over a decade. Their methodology involves leveling the dead reef profile and then adding stabilized shell substrate for oyster spat to attach to and grow, eventually leading to the formation of restored biogenic reefs (Garvis et al. 2015, Walters et al. 2021). Restored reefs in Mosquito Lagoon have been deemed successful based on oyster abundance, oyster density, shell heights, reef heights, reef thickness, and adjacent seagrass recruitment (IRLNEP 2019; Walters et al. 2021). One goal of my study was to determine if bird abundance, diversity, and behavior on restored oyster reefs became more similar over time to that of live reefs in Mosquito Lagoon. As infaunal invertebrates serve as an important food source for birds foraging on oyster reefs, a second goal of this study was to determine if the abundance of infaunal invertebrates on restored reefs becomes similar to that of live reefs in Mosquito Lagoon.

While live and restored reefs provide important foraging habitat, dead reefs and shell rakes are also utilized by birds in Mosquito Lagoon. Walters et al. (2021) have documented the formation of dead reefs. Boat wakes cause live oysters clusters to dislodge and pile up on top of the reef, and as the piles exceed the high tide line the oysters die due to desiccation. What begins as a dead margin on the channel side of the reef eventually grows to cover the whole reef, resulting in an entirely dead reef composed of dead, disarticulated shell (Walters et al. 2021). The movement of loose shells and clusters moves the reef away from the direction of boating activity at an average rate of 0.85 m per year (Garvis et al. 2015). Shell rakes in Mosquito Lagoon are the result of dredge sand spoil piles becoming covered, due to wave action, with a veneer of dead oyster shells ranging from approximately 15 - 30 cm thick. Birds have been documented utilizing these dead areas in Mosquito Lagoon for loafing and nesting (FWC, personal communication; National Parks Service, personal communication; Shaffer et al. 2020).

American oystercatchers and Least terns have both been documented nesting on dead oyster reefs and shell rakes in Mosquito Lagoon (FWC, personal communication; National Parks Service, personal communication). Both of these species traditionally nest in areas of open sand or shell substrate (Bent 1929; Nellis 2001), and the two species have been known to nest in close proximity (Bent 1929). In recent decades, coastal development, shoreline armoring, and sea level rise have led to drastic reductions in nesting habitat for both the American oystercatchers and Least terns, contributing to their threatened status at the state-level (Florida Fish and Wildlife Conservation Commission 2019, Ogden et al. 2014). Due to loss of coastal habitat and human activity, both American oystercatchers and Least terns have been documented nesting in nontraditional locations.

American oystercatchers have been documented to nest on spoil islands, shell rakes, marshes, and forest edges (Davis et al. 2016; Jodice et al. 2014). The substrate on which American oystercatchers typically nest varies by region, and includes sand, shell, mixtures of sand and shell, mixtures of sand and rock, wrack, and leaf litter (Lauro and Burger 1989; Toland 1999; Traut et al. 2006; Wilke et al. 2005). In the states along the southeast Atlantic coast of the United States (from Virginia to Florida), 35%-50% of American oystercatcher nesting now takes place on shell rakes (Jodice et al. 2014). In other regions within the nesting range of American oystercatchers, they tend to nest in open sandy or shell-rich intertidal areas with sparse vegetation (Lauro and Burger 1989; Toland 1999; Vega-Ruiz et al. 2019). Vega-Ruiz et al. (2019) found that on the Pacific Coast of Mexico when a mosaic of habitat types were available, the western subspecies of American oystercatchers preferred to nest in areas without mangroves. They found that some nesting did occur near mangroves < 1 m in height, but did not occur at all in areas where mangrove height was > 2 m (Vega-Ruiz et al. 2019). Elevation is also an important component in successful nesting. Jodice et al. (2014) found that on shell rake nesting sites in North Carolina, overwash into nests due to inadequate substrate elevation was the main cause of nest failure. Of all nests that failed over five years, overwash accounted for 25-90% of nest failures (Jodice et al. 2014). The overwash events were attributed to both naturally occurring high water levels due to rain and spring tides as well as large wakes created by barges and yachts (Jodice et al. 2014).

Least terns, which are traditionally beach nesting birds, have also been documented nesting on spoil islands and shell rakes, and have even taken to nesting on gravel rooftops due to lack of more traditional nesting sites (Gore 1991; Krogh and Schweitzer 1999). Mazzocchi and Forys (2005) found slope, elevation, and sediment composition to be the most important variables in nest site selection (Mazzocchi and Forys 2005). This species typically prefers to create nests on shell-rich substrate over finer sediments, as silt (grain size: 0.008-0.063 mm) can cause breakage of eggs due to a phenomenon called “egg-sticking”, in which the fine sediments adhere to the shell and decrease hatching success (Mazzocchi and Forys 2005). Additionally, white shell absorbs less heat than darker sediments such as sand and silt, which decreases thermal stress on the eggs (Mallach and Leberg 1999). White shell also provides better camouflage for eggs and for chicks at most nest sites (Mallach and Leberg 1999). Least terns often prefer ridges and slopes over flat nesting areas, as they provide a better elevation to limit overwash of nests and also allow for a less inhibited view of potential predators (Burger and Gochfeld 1990; Mallach and Leberg 1999; Mazzocchi and Forys 2005). Mazzocchi and Forys (2005) found that Least tern nests on the Gulf Coast of Florida had a mean elevation (± SE) of 0.76 m ± 0.19 above sea level. Least terns also prefer areas where any vegetation is short and sparse. Studies suggest that some short, sparse ground-cover (e.g. sea purslane, sandwort, saltwort, or marsh grass) is preferable to provide hiding places for chicks, but dense or tall vegetation may provide cover from potential predators (Burger and Gochfeld 1990; Krogh and Schweitzer 1999; Mallach and Leberg 1999; Mazzocchi and Forys 2005).

While both American oystercatchers and Least terns have been observed nesting on shell rakes and some dead reefs within Mosquito Lagoon, no research has been done regarding nesting site selection in this area. A final goal of this study was to characterize these dead areas in Mosquito Lagoon which have been utilized by nesting Least terns and American oystercatchers and determine if elevation, slope, base-substrate composition, or mangrove height differ between sites where nesting has been documented and similar-looking sites where nesting has not been observed.

The main objectives of this study are to 1) determine if bird abundance, diversity, and behaviors on restored reefs are similar to natural reefs; 2) determine if the bird assemblages utilizing restored reefs are similar to those utilizing natural reefs; 3) determine if the infaunal abundances in the sediments of restored reefs are similar to those of natural reefs; and 4) determine which physical and biological characteristics of Least tern and American oystercatcher nesting sites differ from sites not being used for nesting. Combined, all of the objectives of this study will provide new information on the ways in which birds utilize live, restored, and dead oyster reefs within Mosquito Lagoon for foraging, loafing, and nesting, so that restoration efforts may be designed in ways that maximize benefits to the bird community.

Methods

Bird Survey Methods

I utilized the methods outlined by Shaffer et al. (2020) to survey bird activity on reefs beginning one week after restoration and continuing for three years. The surveys began in June of 2017 and ended in June of 2020. I surveyed 12 reefs each month: four dead reefs, four live reefs, and four reefs that were restored by UCF’s Coastal and Estuarine Ecology Lab in June of 2017 (Figure 6). The dead and live reefs were selected prior to the start of this study and then remained constant throughout. Oyster reefs are naturally skewed toward the northern portion of ML, and within this portion of the lagoon reefs were selected from various regions to represent the spatial distribution of oyster reefs. I accessed the reef areas by boat withing two hours of predicted morning low tides, when oyster reefs were more likely to be exposed and, therefore, visible and available for birds to utilize (Conway 2011; Schikorr & Swain 1995). If a reef was completely submerged (i.e., unavailable for bird use) data was not collected. To prevent disrupting any birds already present on the reefs, the reefs were approached at minimal speed with no wake and took efforts to minimize noise created by both the approach and anchorage of the boat. I remained a minimum of 30 meters away from each reef throughout the surveys, so as not to discourage birds from landing on the reefs during the observational period. I measured and recorded air and water temperatures (using a thermometer), average wind speed (using an anemometer), and salinity (using a portable refractometer) at each site. Two researchers with binoculars observed each reef for 20 minutes and recorded the species and behaviors (foraging or loafing) of all birds utilizing the reef during that time frame.

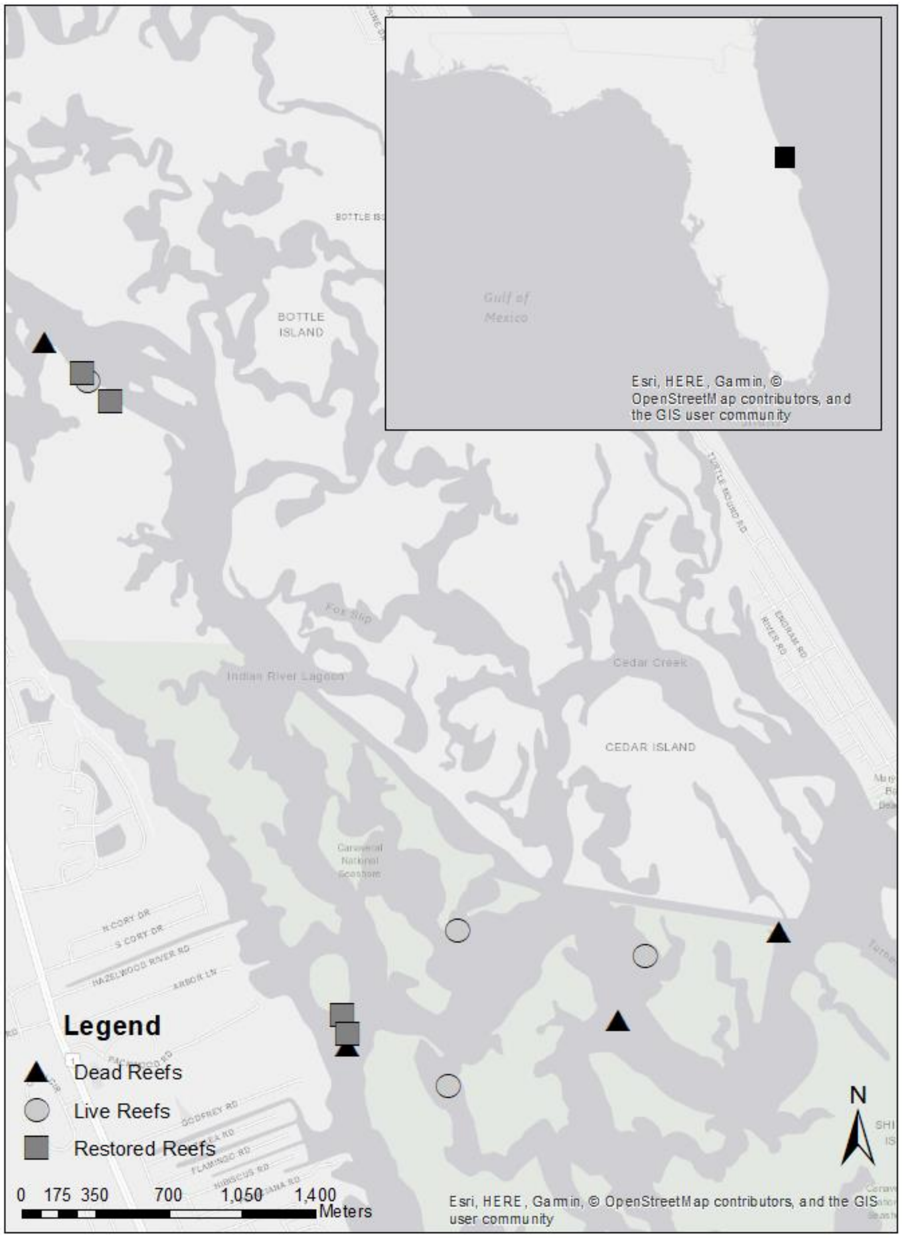

Figure 6 Northern Mosquito Lagoon, FL. Symbols represent live, restored, and dead oyster replicate reefs used for bird surveys and infauna sampling. Live and dead reefs were selected prior to the study. Restored reefs were restored in June of 2017.

Statistical Methods for Bird Survey Data

Using the abiotic data, I calculated summary statistics for air temperature (°C), water temperature (°C), average wind speed (kph), and salinity (ppt) for the overall study period and for meteorological seasons (summer: June – August, fall: September – November, winter:

December – February, and spring: March – May). I used ANOVA tests to determine if there were differences in air temperature or average wind speed based on season and Tukey HSD post-hoc tests for pairwise comparisons of seasons.

I used zero-inflated negative binomial GLMs with Akaike information criterion (AIC) model selection to determine which variables best predicted bird presence and abundance, including season, reef type, and reef size in my models. I also used zero-inflated negative binomial GLMs to determine if bird abundance on restored reefs differed between year 1, year 2, and year 3 of the study. I used analysis of deviance to compare the proportions of birds foraging and loafing on different reef types.

To assess the differences in community assemblages based on reef type, I used non-metric multidimensional scaling (NMDS) in the Vegan package in R to generate an ordination plot for all birds (Oksanen et al. 2019). Birds were grouped into families for these analyses, in order to reduce the number of zero values and decrease stress. To account for differences in reef sizes, I used bird densities (number of birds/10 m^2) rather than counts. I generated additional ordination plots for foraging birds for each reef type and for loafing birds for each reef type to visualize differences in the community assemblages. To determine if there were differences between reef types I used PERMANOVA tests. For these analyses, birds were grouped into families in order to reduce the number of zero values and decrease stress.

I determined diversity indices, including Shannon diversity, Simpson’s diversity, species richness, and Pielou’s evenness for live, dead, and restored reefs using the Vegan package in R (Oksanen et al. 2019). For these analyses the data were condensed into seasons and I used bird densities rather than counts to account for differences in reef sizes. I used ANOVA tests to determine if these diversity metrics differed between reef types. When differences were detected, I used Tukey HSD testing for pairwise comparisons. I used multi-level pattern analysis to determine representative species for each of the different reef types (De Caceres and Legendre 2009). I also ran separate multi-level pattern analyses for foraging birds and for loafing birds for each of the reef types. For the representative species analyses I used density data rather than counts. All statistical analyses were conducted using R and RStudio (R Core Team 2020; RStudio Team 2019).

Infauna Sampling and Sorting Methods

I collected three sediment samples from each of the 12 bird survey reefs pre-restoration (June 2017) and 1 month (July 2017), 6 months (January 2018), 1 year (July 2018), 2 years (July 2019), and 3 years (July 2020) post-restoration. Methods from Rumohr (2009) were utilized for field sampling and laboratory treatment of samples. A quadrat was used to maintain a 15 cm x 15 cm area on the reef (selected haphazardly) and I collected sediment within the quadrat to a depth of 15 cm. Using a bucket with plastic mesh (pore size: 2 cm) in place of the bottom I pre-sieved the sediment samples to remove large shell fragments. Then, I passed the remaining contents through stacked 2,000 µm and a 500 µm sieves, and retained all specimens caught in the 2,000 µm sieve along with all sediment collected in the 500 µm sieve and added a 4:1 sea water to formaldehyde and rose Bengal solution to each sample. After a minimum of one week, I again sieved each sample through a 500 µm sieve and transferred to a 70% ethanol solution (Rumohr 2009). Using a dissecting microscope with a magnification of 40x, I observed each sample and infauna were counted and sorted into categories: polychaetes, amphipods, isopods, gastropods, bivalves, and decapods. Additionally, for each sample I counted the number of larger specimens ($\geq$ 1 cm length for polychaetes, or carapace width of $\geq$ 0.5 cm for decapods) as these should be more obvious to both visual and tactile predators.

Statistical Methods for Infauna Data

I conducted negative binomial generalized linear models (GLMs) with reef type as the predictor variable and total number for the six groups of infaunal invertebrates as the response variable for each sampling period. I also performed negative binomial GLMs with reef type as the predictor variable and total number of larger specimens as the response variable. To determine the change in mean total of the six taxonomic groups over time, I performed negative binomial GLMs with time as the predictor variable and total number as the response variable.

Nesting Site Characterization Methods

I selected the only four sites where nesting by either or both American oystercatchers or Least terns have been observed in the past five years to serve as reference reefs (hereafter referred to as “reference sites”). I used aerial imagery and field checking to select 17 other dead areas where nesting has not been previously observed (hereafter referred to as “potential nesting sites”) (Figure 7). I used real-time kinematic (RTK) positioning with an iGage RTK surveyor (vertical accuracy: 2-4 cm) to determine the average elevation of each site. I ran transects along each dead reef or shell rake, with the number of transects per reef varying by reef dimensions. The number of transects per reef ranged from 6-20, with fewer transects on smaller reefs and more on larger reefs. Transects were separated by approximately 2-3 m. I took elevation measurements at specific positions on each transect to represent the topographical variations along the transect (i.e. highest point, lowest point, each ridge, each valley) as well as the height were dead area transitioned into muddy bottom. The total number of elevation data points collected per reef ranged from 24-92. I measured slope using a stadia rod, a transect tape, and a laser level (Walters et al. 2021). I recorded heights of the laser level at the highest point and the lowest point, as well as the distance between the two points and then calculated slope by and dividing the height difference by the distance between the two, and then converted the values to degrees. I determined the slope from the highest point on the reef, along with 5 other haphazardly selected locations on the reef to determine the average slope of the reef (Walters et al. 2021).

Figure 7 Mosquito Lagoon, FL. Symbols represent dead oyster reefs and shell rakes selected for Least tern and American oystercatcher nesting site study. The 4 reference nesting sites are locations where nesting by one or both birds has been documented within the past 5 years. The 17 potential nesting sites are locations where nesting has not been observed by either species within the past 5 years.

Mangroves were the tallest plants on both dead reefs and shell rakes, so I measured the heights of all mangroves to determine the average plant stand height for each site. To assess base substrate composition and vegetative cover, I ran 10 transects across each reef. I measured the length of each reef (reefs ranged from 9-60 m in length) and used a random number generator to determine the placements of the 10 transects. I then placed five 0.25 m^2 quadrats equal distance apart on the same side of each transect. Within each quadrat, I used the point-intercept method to visually determine the percentage of vegetation, percentage of dead shell substrate, percentage of live oyster clusters, and percentage of sand substrate using 25 points within the quadrat (Donnelly et al. 2017).

Statistical Methods for Nesting Site Data

I conducted t-tests tests to determine if elevation, slope, and mangrove heights differed between the reference sites and the potential nesting sites. Log transformations were applied when necessary to improve normality of the data prior to performing t-tests. I used analysis of deviance to determine if percent of vegetation, shell, sand, and live oysters differed between sites.

Results

Bird Survey Results

In total, I observed 1,528 birds from 36 unique species on oyster reefs, with 10.8% of the birds observed on live reefs, 2.2% on restored reefs, and 87.0% on dead reefs (Table 7). The most common species observed on live reefs was *Eudocimus albus* (White ibis), making up 21.2% of the total observations. The most common species observed on restored reefs was *Arenaria interpres* (Ruddy turnstone), making up 14.7% of observations. On dead reefs, the most common species observed was *Thalasseus maximus* (Royal tern), which made up 37.5% of birds observed.

Table 7 Total counts and percent of observations for each bird species for each reef type.

		Percent of Observations		
Species	**Total Count**	**LOR**	**ROR**	**DOR**
Actitis macularius (Spotted sandpiper)	4	1.21	2.94	0.08
Ardea alba (Great egret)	4	1.82	0.00	0.08
Ardea herodias (Great Blue heron)	11	1.82	5.88	0.45
Arenaria interpres (Ruddy turnstone)	92	3.64	14.71	6.09
Butorides virescens (Green heron)	1	0.00	2.94	0.00
Calidris alba (Sanderling)	4	1.21	0.00	0.15
Calidris mauri (Western sandpiper)	1	0.00	2.94	0.00
Cathartes aura (Turkey vulture)	3	1.82	0.00	0.00
Charadrius vociferus (Killdeer)	1	0.00	0.00	0.08
Charadrius semipalmatus (Semi-palmated plover)	26	1.21	0.00	1.80
Coragyps atratus (Black vulture)	2	1.21	0.00	0.00
Egretta caerulea (Little Blue heron)	14	6.67	5.88	0.08
Egretta rufescens (Reddish egret)	6	1.21	0.00	0.30
Egretta thula (Snowy egret)	13	6.06	2.94	0.15
Egretta tricolor (Tri-colored heron)	2	0.61	0.00	0.08
Eudocimus albus (White ibis)	41	21.21	2.94	0.38
Haematopus palliatus (American oystercatcher)	16	1.82	8.82	0.75
Haliaeetus leucocephalus (Bald eagle)	2	0.00	5.88	0.00
Hydroprogne caspia (Caspian tern)	9	0.00	0.00	0.68
Larus argentatus (Herring gull)	16	0.00	0.00	1.20
Larus delawarensis (Ring-billed gull)	21	4.85	0.00	0.98
Leucophaeus atricilla (Laughing gull)	437	9.70	8.82	31.40
Megaceryle alcyon (Belted kingfisher)	5	2.42	0.00	0.08
Mergus serrator (Red-breasted merganser)	3	0.00	0.00	0.23
Nyctanassa violacea (Yellow-crowned night heron)	1	0.00	0.00	0.08
Pandion haliaetus (Osprey)	22	7.88	5.88	0.53
Pelecanus occidentalis (Brown pelican)	27	0.00	0.00	2.03
Phalacrocorax auritus (Double-crested cormorant)	43	0.00	5.88	3.09
Pluvialis squatarola (Black-bellied plover)	29	7.88	0.00	1.20
Quiscalus major (Boat-tailed grackle)	1	0.00	0.00	0.08
Rynchops niger (Black skimmer)	1	0.00	0.00	0.08
Sterna forsteri (Forster's tern)	11	0.00	0.00	0.83
Sternula antillarum (Least tern)	64	1.82	2.94	4.51
Thalasseus maximus (Royal tern)	500	0.61	2.94	37.42
Thalasseus sandvicensis (Sandwich tern)	5	0.00	0.00	0.38
Tringa semipalmata (Willet)	86	13.33	0.00	4.81
All Birds	1,529	10.78	2.22	86.86

LOR = live oyster reefs, ROR = restored oyster reefs, DOR = dead oyster reefs

Abiotic Data. There were differences in air temperature, water temperature, wind speed, and salinity based on season ($p < 0.001$ for all). As expected, air temperatures and water temperatures were highest in the summer, and lowest in the winter, and differed between all seasons except for spring and fall (Table 8, Figure 8). Wind speeds on observation dates in winter, spring, and fall were similar to one another, and all were higher than wind speeds in summer ($p < 0.001$, $p = 0.020$, and $p = 0.013$, respectively). Similarly, salinity in winter, spring, and fall were similar, and all were higher than salinity in summer during the wet season ($p < 0.001$ for all).

Table 8 Summary statistics for air temperature, water temperature, average wind speed, and salinity for all surveys and by season, including means, 95% confidence intervals (95% CI), and ranges (Min-Max) for each metric. Summer included June-August, fall included September-November, winter included December-February, and spring included March-May.

		Air Temp (°C)	Water Temp (°C)	Wind Speed (kph)	Salinity (ppt)
All Data	Mean	23.5	24.1	8.1	33.3
	95% CI	0.6	0.5	0.5	0.5
	Min-Max	5.0-39.0	12.0-31.3	0-25.9	20.0-44.0
Summer	Mean	28.0	28.8	6.5	29.2
	95% CI	0.3	0.3	0.7	0.6
	Min-Max	24.0-34.3	25.0-32.3	0-17.5	23.0-42.0
Fall	Mean	23.0	23.7	8.9	34.4
	95% CI	1.8	1.2	1.3	1.6
	Min-Max	8.0-39.0	14.0-31.0	2.3-25.9	20.0-43.0
Winter	Mean	18.6	18.7	9.4	35.3
	95% CI	1.0	0.7	1.0	1.1
	Min-Max	5.0-27.0	12.0-26.0	1.0-24.1	21.0-41.0
Spring	Mean	22.6	23.5	8.4	36.0
	95% CI	1.1	0.6	1.2	0.7
	Min-Max	9.5-30.0	16.0-29.0	0-25.6	27.0-44.0

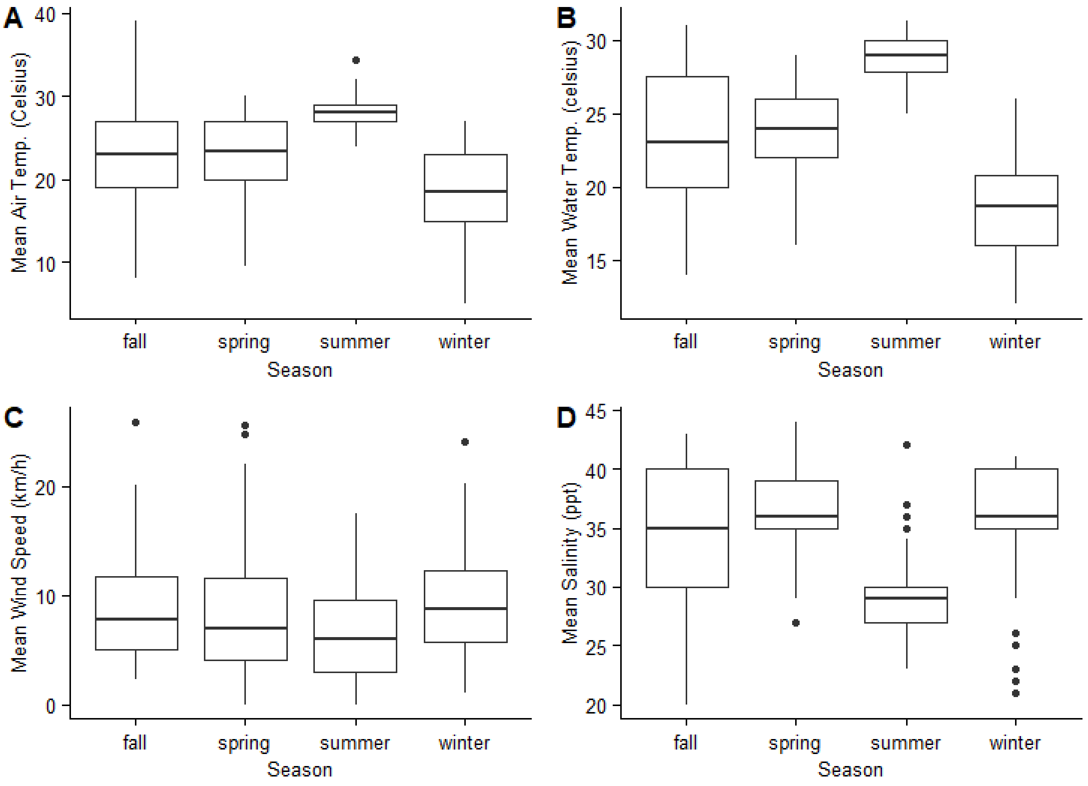

Figure 8 Boxplots comparing (A) air temperature (B) water temperature, (C) wind speed, and (D) salinity during different seasons. Boxes represent the middle 50% of the data, bold lines represent medians, whiskers represent the upper and lower 25% of the data values (excluding outliers), and points represent outliers.

Bird Abundances by Reef Type. The most plausible zero-inflated negative binomial model included reef type, reef size, and season as predictors of overall bird abundance and reef size as the predictor for presence or absence of birds (McFadden pseudo-R^2=0.120, Table 9). Dead reefs had higher bird abundances than restored reefs ($p < 0.001$, Figure 4) and live and restored reefs had similar abundances ($p = 0.077$). Additionally, season was a predictor for bird abundance, with the highest bird abundances in spring, winter, and fall and the lowest bird abundance in summer. Reef size also predicted the abundance of birds ($p < 0.001$). The total number of birds observed on restored reefs during year 1, year 2, and year 3 of the study were all similar to one another.

Table 9 AIC table for zero-inflated negative binomial models predicting bird abundance. AIC_c, delta AIC_c, degrees of freedom, and AIC_c weight are given.

	AIC_c	ΔAIC_c	df	AIC_c weight
Reef type	1192.9	45.0	7	<0.001
Reef size	1288.1	140.2	5	<0.001
Season	1269.3	121.4	9	<0.001
Reef type + reef size | reef type	1186.1	38.2	8	<0.001
Reef type + season	1177.9	30.0	13	<0.001
Reef type + season | reef type	1174.5	26.6	10	<0.001
Reef_type + season + reef_size | season	1171.1	23.2	12	<0.001
Reef type + season + reef size | reef size	1147.9	0	10	1
Reef size + season	1243.1	95.2	9	<0.001
Reef size + season | reef size	1223.2	75.3	8	<0.001

Although dead reefs had higher bird abundances, bird behaviors differed by reef types. The proportion of birds foraging and loafing on restored reefs was similar to the proportion on live reefs and differed from dead reefs (*p* = 0.017). The proportion of birds foraging was higher on live and restored reefs, and the proportion of birds loafing was higher on dead reefs (Figure 9).

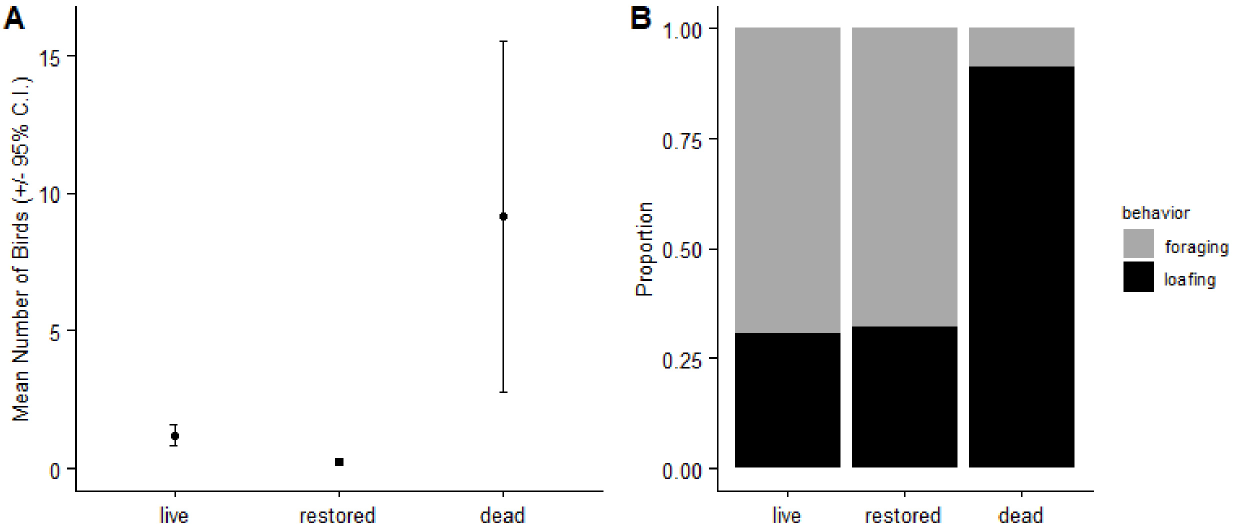

Figure 9 Mean total number of birds (± 95% confidence intervals) for each reef type (A) and proportion of bird behaviors for each reef type (B).

Community Assemblages. When assessing all birds observed on oyster reefs (Figure 10-A), there were differences in the bird assemblages based on reef type (*p* = 0.001). There were similarities between live and restored reefs and similarities between dead and restored reefs, but differences between live and dead reefs (*p* = 0.003). There were also significant differences in communities of foraging birds (Figure 10-B) on different reef types (*p* = 0.001). Restored reefs were similar to both live and dead, but live and dead reefs differed (*p* = 0.006). There was no significant difference in loafing bird communities based on reef type (*p* = 0.37), and the NMDS plot shows significant overlap between ellipses for all three reef types (Figure 10-C). The stress values for each of the three ordination plots were below 0.1. Stress values < 0.1 indicate that the ordination is a good fit for the data (Kruskal and Wish 1978; Clarke 1993).

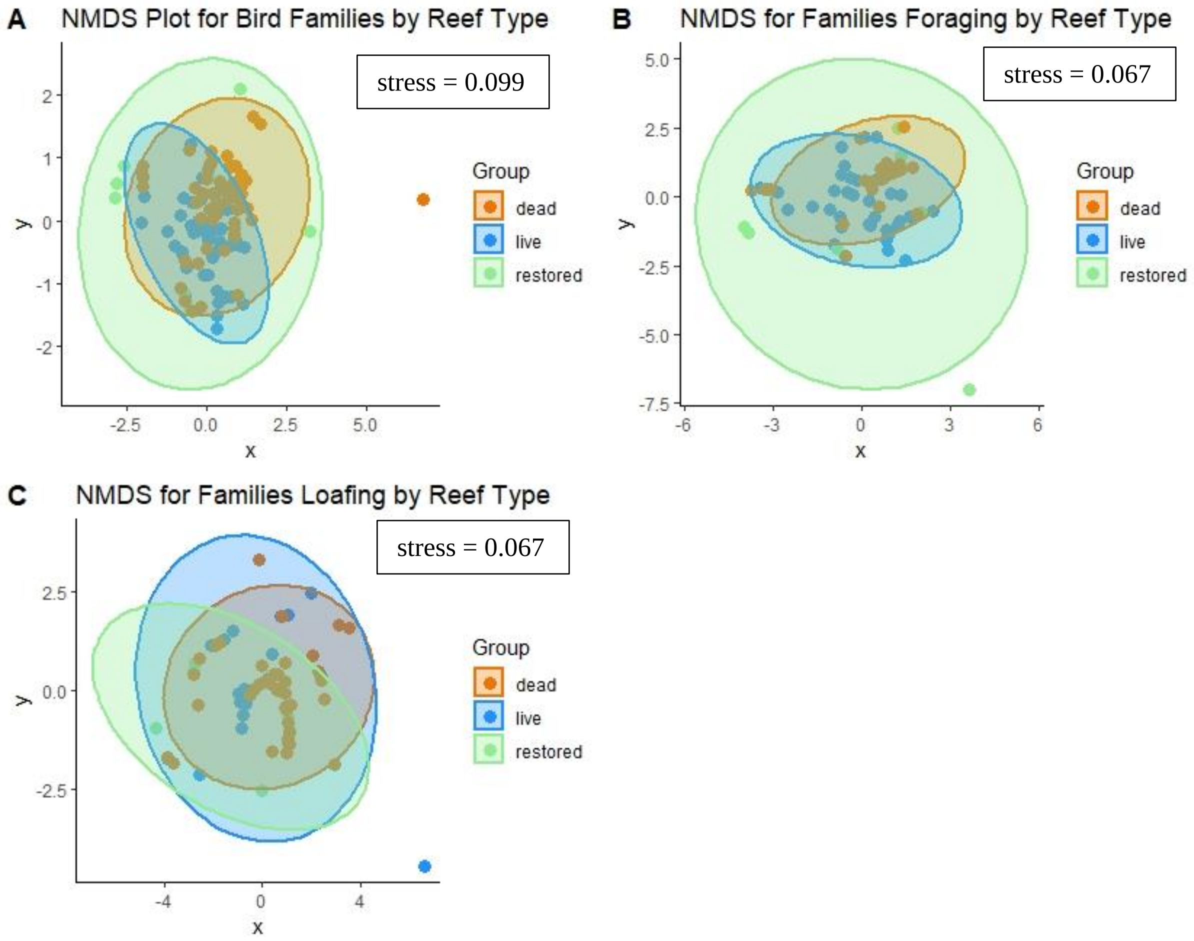

Figure 10 NMDS ordination plots for (A) all bird families, (B) foraging bird families, and (C) loafing bird families observed on live, restored, and dead reefs. Points represent community assemblages on each reef type for each survey event. Ellipses represent 95% confidence intervals for reef type groupings.

Diversity Indices and Representative Species. Shannon diversity and species richness were higher for live and dead reefs than for restored reefs, but Simpson's diversity and Pielou's evenness for restored reefs were similar to both live and dead (Table 10, Figure 11). There was no statistical difference detected in any of the diversity metrics for the restored reefs over time. There were 8 representative species for dead reefs, including seven seabirds and one shorebird. *Tringa semipalmatta* (Willet), *Eudocimus albus* (White ibis), and *Pluvialia squatarola* (Black-bellied plover) were associated with the combination of live and dead reefs. There were no species which were representative species for live reefs alone or for restored reefs (Table 11-A). When using only the data for foraging birds, White Ibis was associated with foraging on live reefs and *Arenaria interpres* (Ruddy turnstone) was associated with foraging on dead reefs (Table 11-B). There were 9 species associated with loafing on dead reefs, 7 of which were also included in the results for all birds (Table 11-C).

*Table 10 p-values for ANOVA results comparing Shannon diversity, Simpson's diversity, species richness, and Pielou's evenness between reef types. Values that are significant at the p < 0.05 level indicated with **

	Restored v. Live	Restored v. Dead	Live v. Dead
Shannon diversity	$p = 0.002$ *	$p < 0.001$ *	$p = 0.262$
Simpson's diversity	$p = 0.297$	$p = 0.129$	$p = 0.882$
Species richness	$p = 0.001$ *	$p < 0.001$ *	$p = 0.031$ *
Pielou's evenness	$p = 0.555$	$p = 0.209$	$p = 0.733$

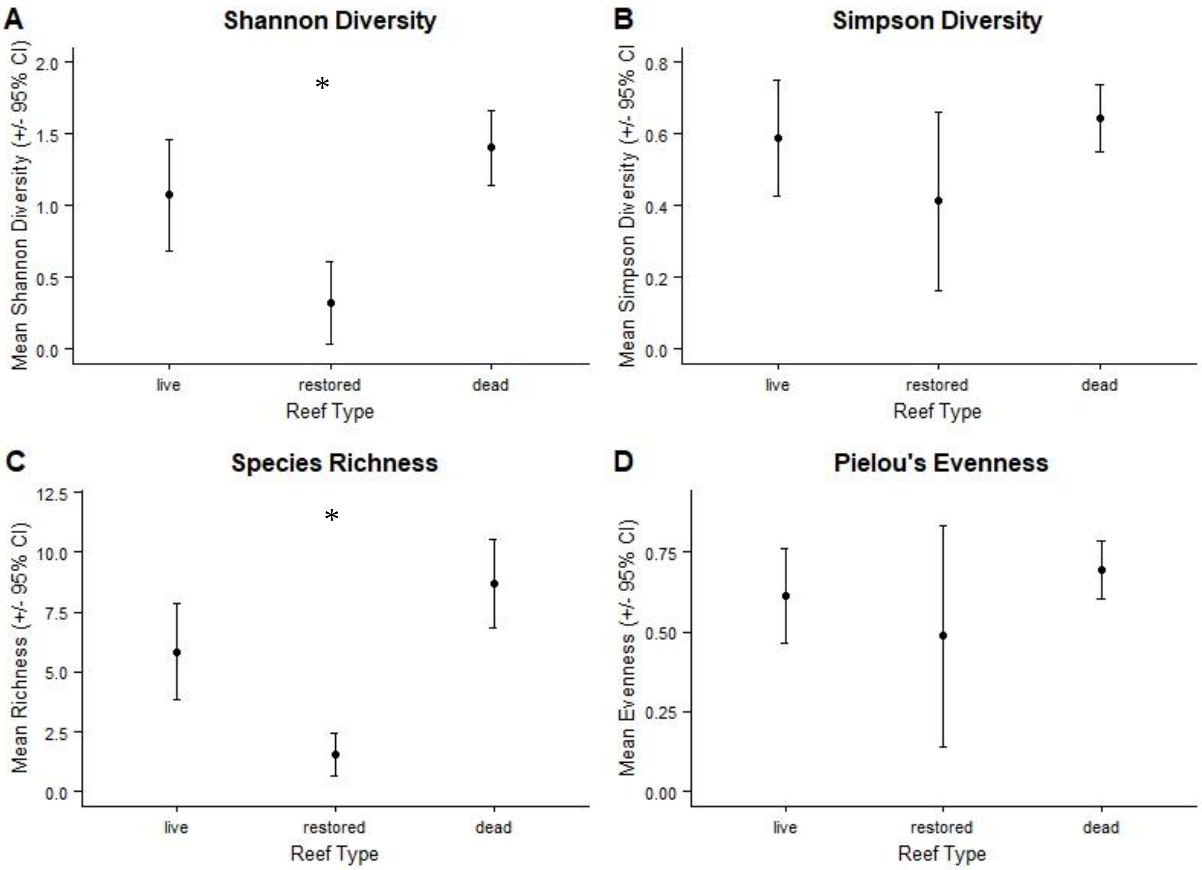

*Figure 11 Comparisons of mean (A) Shannon diversity, (B) Simpson's diversity, (C) species richness, and (D) Pielou's evenness between live, restored, and dead reefs. Error bars represent 95% confidence intervals. Differences significant at the p < 0.05 level indicated by **

Table 11 Representative species results by reef type. The indicator value (IndVal) is determined based on statistics A and B. Statistic A (the positive predictive value) represents an estimate of the probability that a site belongs to a particular reef type based on the presence of the species. Statistic B (the fidelity value) represents an estimate of the probability of finding the species at that particular reef type. All values given are statistically significant at the p < 0.05 level.

Table 11-A Representative species for all bird observations by reef type.

Species	**IndVal**	**A**	**B**
Dead Oyster Reefs			
Leucophaeus atricilla (Laughing gull)	0.359	0.813	0.159
Thalasseus maximus (Royal tern)	0.329	0.979	0.110
Arenaria interpres (Ruddy turnstone)	0.286	0.660	0.124
Larus delawarensis (Ring-billed gull)	0.245	0.874	0,069
Pelecanus occidentalis (Brown pelican)	0.220	1.000	0.048
Sterna forsteri (Forster’s tern)	0.203	1.000	0.041
Larus argentatus (Herring gull)	0.186	1.000	0.034
Hydroprogne caspia (Caspian tern)	0.166	1.000	0.028
Dead + Live Reefs			
Tringa semipalmatta (Willet)	0.318	1.000	0.101
Eudocimus albus (White ibis)	0.278	0.928	0.083
Pluvialia squatarola (Black-bellied plover)	0.166	1.000	0.028

Table 11-B. Representative species for foraging birds by reef type.

Species	**IndVal**	**A**	**B**
Dead Oyster Reefs			
Arenaria interpres (Ruddy turnstone)	0.293	0.735	0.117
Live Oyster Reefs			
Eudocimus albus (White ibis)	0.342	0.814	0.144
Dead + Live Reefs			
Tringa semipalmata (Willet)	0.294	1.000	0.087
Pluvialis squatarola (Black-bellied plover)	0.208	1.000	0.043

Table 11-C Representative species for loafing birds by reef type.

Species	**IndVal**	**A**	**B**
Dead Oyster Reefs			
Leucophaeus atricilla (Laughing gull)	0.357	0.838	0.151
Thalasseus maximus (Royal tern)	0.332	1.000	0.110
Larus delawarensis (Ring-billed gull)	0.233	0.874	0.062
Pelecanus occidentalis (Brown pelican)	0.220	1.000	0.048
Sterna forsteri (Forster’s tern)	0.203	1.000	0.041
Ardea herodias (Great Blue heron)	0.186	1.000	0.034
Tringa semipalmata (Willet)	0.185	0.988	0.034
Larus argentatus (Herring gull)	0.166	1.000	0.028
Hydroprogne caspia (Caspian tern)	0.166	1.00	0.028

Infauna Results

Infaunal Abundance. The most abundant infaunal group in sediments from all reef types were polychaete worms (Figure 12). The mean number of polychaetes (± 95% confidence intervals) for all 15 x 15 x 15 cm samples was 328.04 ± 40.49, which was 10x – 30x higher than the mean abundance of any other taxa. The second most abundant taxa in live and restored reef sediments were amphipods, with the mean abundances for live and restored reefs being 27.74 ± 13.25 and 70.78 ± 23.16, respectively (Figure 12). Gastropods were the second most abundant taxa in dead reef sediments with a mean abundance of 46.71 ± 25.32, which was 10x greater than restored reef sediments and 65x greater than live reef sediments. Over time, the community composition of the taxa in restored reef sediments became more similar to live reef sediments and less similar to dead reef sediments (Figure 12). Pre-restoration and one-month post-restoration the mean total of the six infaunal groups in samples from restored reefs was lower than in samples from live reefs and was higher than in samples from dead reefs. By 6 months post-restoration, the mean total in restored reef samples was similar to live reefs and was higher than dead reefs. In each time period up to two years, samples from live reefs had significantly higher numbers than samples from dead reefs. However, three years post-restoration, there were no significant differences between the mean totals for any of the three reef types (Table 12-A).

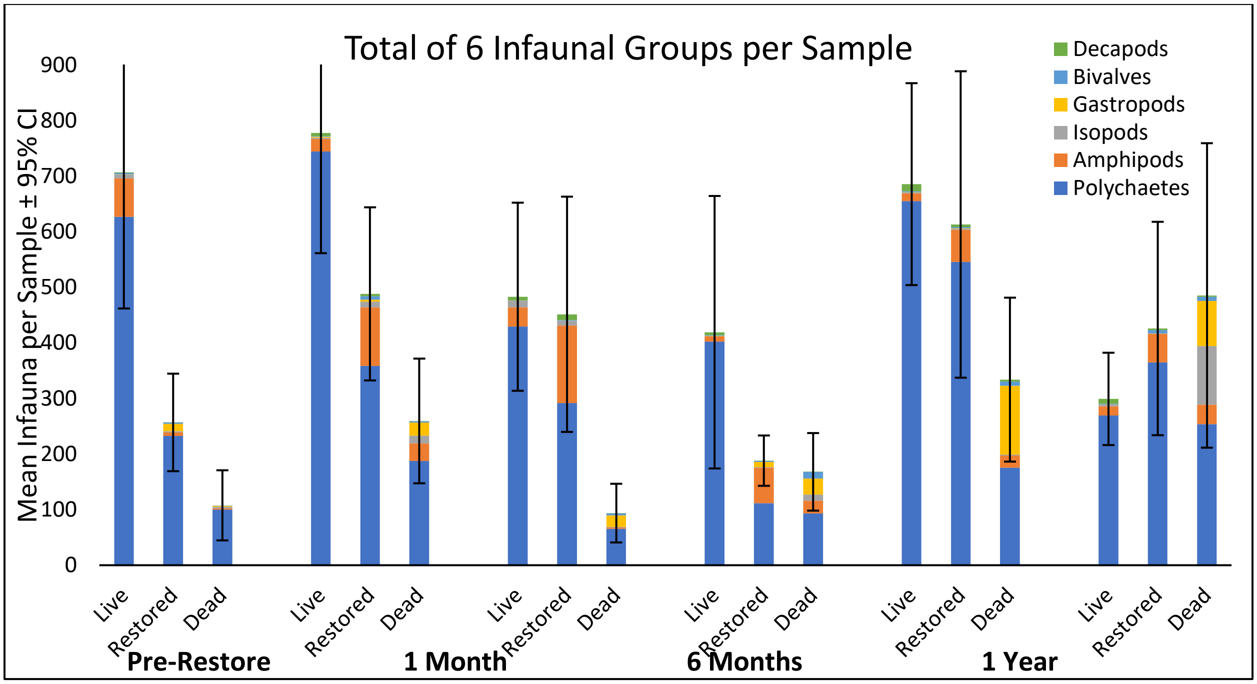

Figure 12 Mean total number of all 6 groups of infauna for each reef type for all sampling periods. The different colors within the bars represent the totals for each infaunal group. Error bars represent 95% confidence intervals.

Abundance of Large Infauna. Common organisms included in the larger polychaete category (length ≥ 1 cm) included members of the families Eunicidae, Hesionidae, Spionidae, and Nereididae, and common organisms within the larger decapod category (carapace width ≥ 0.5 cm) included members of the families Porcellanidae and Panopeidae. Pre-restoration, there was no difference in the mean number of larger infaunal organisms between any of the three reef types. One-month post-restoration, the mean total number of larger organisms in restored reef samples was similar to the samples from dead reefs, but lower than the live reef samples. In all other post-restoration samples, the mean totals of larger infauna in restored reef samples were similar to live reef samples, and both were higher than the mean totals in dead reef samples (Table 12-B, Figure 13).

Table 12 p-values for negative binomial GLM results comparing (A) mean infaunal abundance and (B) mean abundance of large infauna between reef types. Values that differed significantly at the $p < 0.05$ *level indicated by **

Table 12-A

	Restored v. Live	Restored v. Dead	Live v. Dead
Pre-Restoration	$p < 0.001$	$p < 0.001$ *	$p < 0.001$ *
1 Month	$p = 0.034$ *	$p = 0.004$ *	$p < 0.001$ *
6 Months	$p = 0.809$	$p < 0.001$ *	$p < 0.001$ *
1 Year	$p = 0.003$ *	$p = 0.809$	$p = 0.001$ *
2 Years	$p = 0.664$	$p = 0.018$ *	$p = 0.004$ *
3 Years	$p = 0.218$	$p = 0.648$	$p = 0.091$

Table 12-B

	Restored v. Live	Restored v. Dead	Live v. Dead
Pre-Restoration	$p = 0.176$	$p = 0.771$	$p = 0.286$
1 Month	$p = 0.004$ *	$p = 0.131$	$p < 0.001$ *
6 Months	$p = 0.305$	$p < 0.001$ *	$p < 0.001$ *
1 Year	$p = 0.500$	$p < 0.001$ *	$p < 0.001$ *
2 Years	$p = 0.454$	$p < 0.001$ *	$p = 0.002$ *
3 Years	$p = 0.935$	$p = 0.001$ *	$p = 0.001$ *

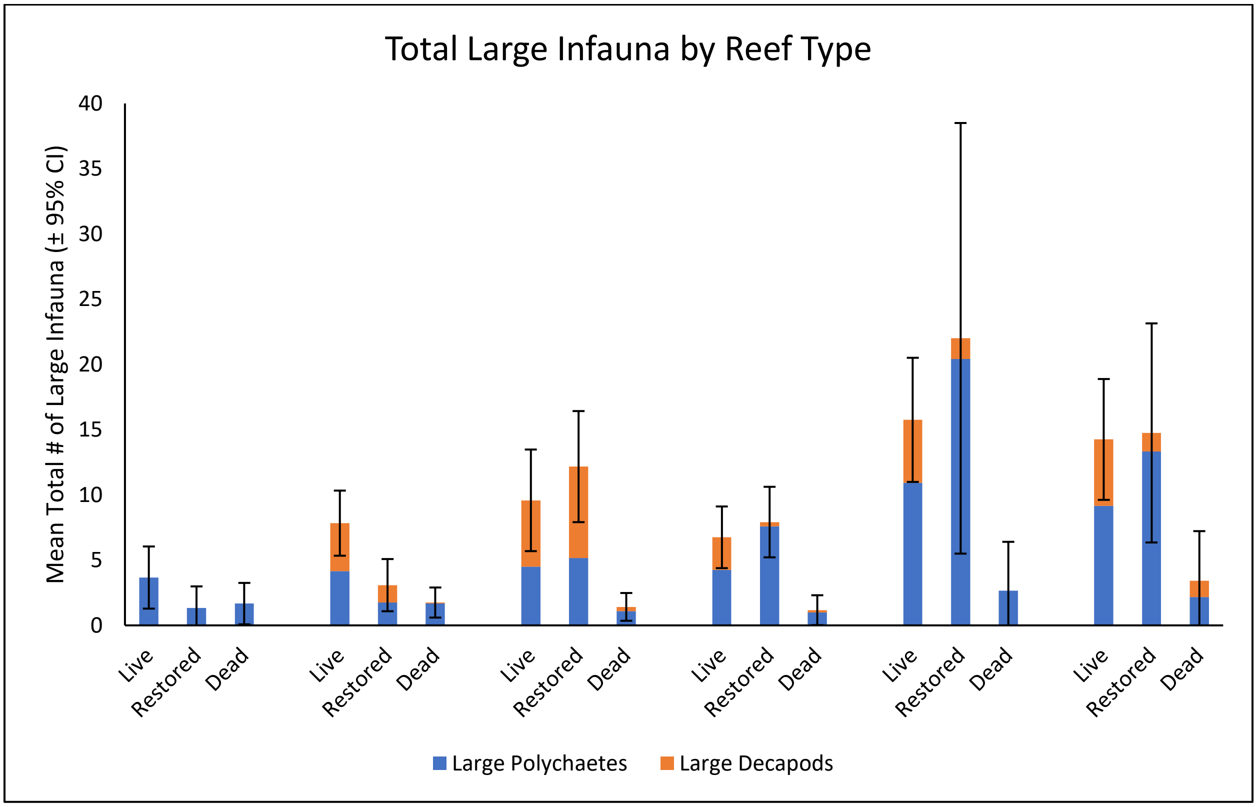

Figure 13 Mean totals of larger infaunal organisms (polychaetes length ≥ 1 cm and decapods with carapace width ≥ 0.5cm) by reef type for each of the sampling periods. Error bars represent 95% confidence intervals.

Changes in Infaunal Abundance Over Time. For restored reefs, all post-restoration mean totals, with the exception of 1 year post-restoration, were significantly higher than the pre-restoration mean total infauna. However, the mean totals in samples from dead reefs were also significantly higher at 1 month, 2 years, and 3 years post-restoration than the mean total infauna prior to restoration. Live reef samples had significantly lower mean totals at 1 year and 3 years post-restoration than pre-restoration (Table 13-A).

By 6 months post-restoration and beyond, live and restored reefs both had higher mean totals of large infauna than the mean totals pre-restoration. Dead reef samples showed no differences in total large infauna in post-restoration data compared to the pre-restoration data (Table 13-B).

*Table 13 p-values for negative binomial GLM results for (A) mean infaunal abundance and (B) mean abundance of large infauna in live, restored, and dead reef sediments for post-restoration time frames compared to pre-restoration means. Values that are significant at the $p<0.05$ level indicated with **

Table 13-A

	Live	Restored	Dead
1 Month	$p = 0.656$	$p = 0.007$ *	$p = 0.275$
6 Months	$p = 0.103$	$p = 0.014$ *	$p = 0.022$ *
1 Year	$p = 0.019$ *	$p = 0.185$	$p = 0.696$
2 Years	$p = 0.872$	$p < 0.001$ *	$p = 0.064$
3 Years	$p < 0.001$ *	$p = 0.036$ *	$p = 0.002$ *

Table 13-B

	Live	Restored	Dead
1 Month	$p = 0.004$ *	$p = 0.075$	$p = 0.946$
6 Months	$p < 0.001$ *	$p < 0.001$ *	$p = 0.822$
1 Year	$p = 0.022$ *	$p < 0.001$ *	$p = 0.625$
2 Years	$p < 0.001$ *	$p < 0.001$ *	$p = 0.244$
3 Years	$p < 0.001$ *	$p < 0.001$ *	$p = 0.304$

Bird Nesting Site Results

Mean mangrove height, slope, elevation, proportion of vegetation base substrate, and proportion of live oyster base substrate all differed between reference nesting sites and potential nesting sites (Table 14, Figure 14). Reference sites had a higher mean mangrove height, mean slope, and mean elevation than potential reefs (*p* = 0.001, *p* = 0.022, and *p* < 0.001, respectively). The mean height of mangroves on reference sites (± 95% confidence intervals) was 86.82 ± 7.46 cm, while the mean mangrove height on potential sites was 69.18 ± 6.30 cm. The mean slope of reference sites was 10.85 ± 2.05° and the mean slope of potential sites was 8.49 ± 0.95°. Mean elevation of reference sites was 1.73 ± 0.02 m and the mean elevation of potential sites was 1.49 ± 0.01 m. The mean proportion of vegetation was higher on reference sites than on potential sites (*p* = 0.003). The mean proportion of vegetation on references cites was 0.05 ± 0.02, while on potential sites it was 0.02 ± 0.01. Mean proportion of live oysters was lower on reference sites than on potential sites (p < 0.001), with potential sites having a mean of 0.05 ± 0.01 and reference sites having 0.02 ± 0.01. Neither proportion of dead shell nor proportion of sand differed between reef types (Figure 14).

*Table 14 Mean (± 95% CI) mangrove height, slope, elevation, and percent base substrate values for reference nesting reefs and potential nesting reefs. Characteristics that differed significantly (p < 0.05) between reference and potential sites indicated with **

	Mean ± 95% C.I.	
	Reference Nesting Sites	Potential Nesting Sites
Mangrove Height (cm) *	86.82 ± 7.46	69.18 ± 6.30
Slope (°) *	10.85 ± 2.05	8.49 ± 0.95
Elevation (m) *	1.73 ± 0.02	1.49 ± 0.01
% Vegetation *	4.55 ± 2.46	2.00 ± 0.59
% Shell	91.86 ± 2.62	90.94 ± 0.89
% Sand	1.85 ± 0.79	1.85 ± 0.44
% Live Oysters *	1.75 ± 0.74	5.20 ± 0.58

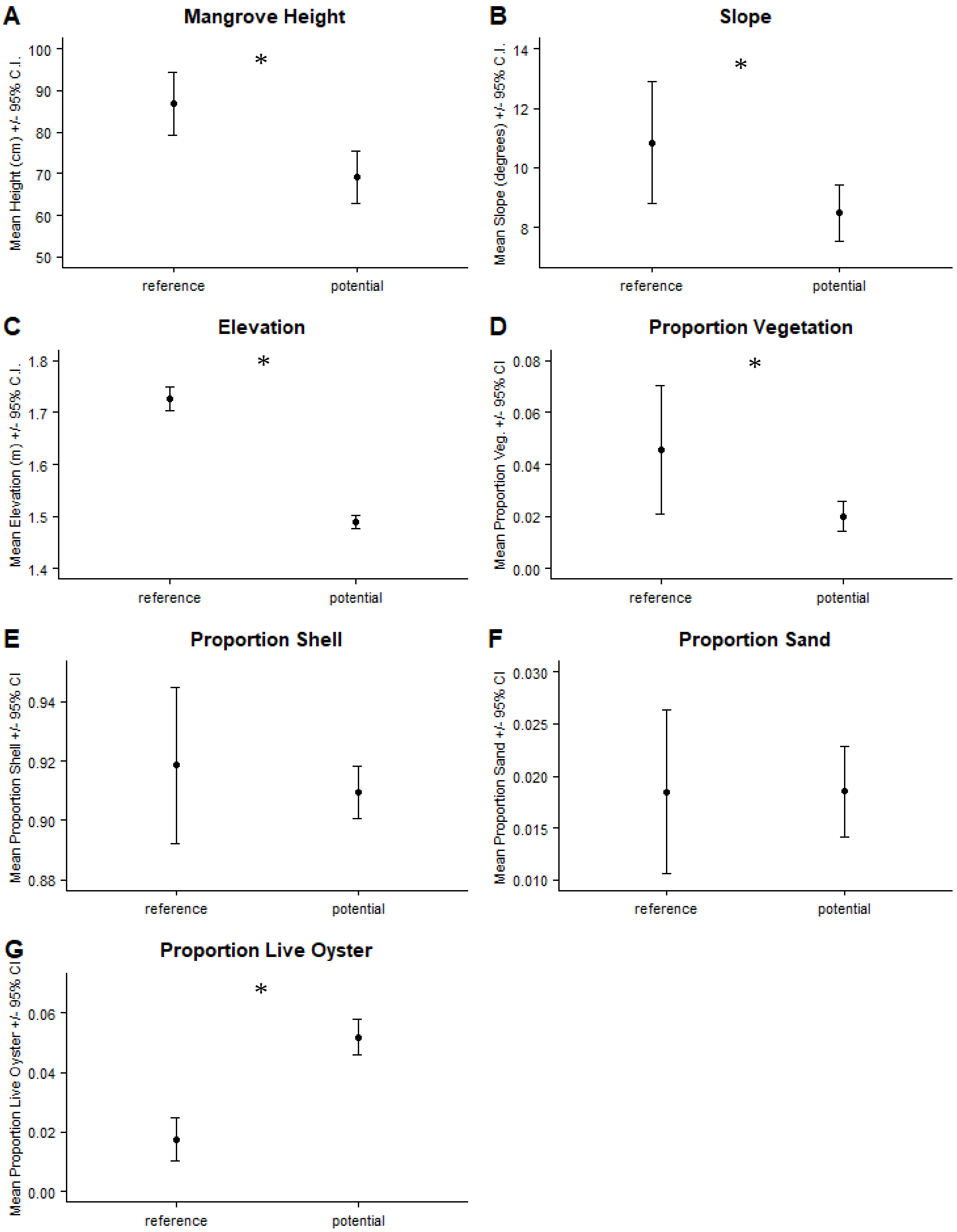

*Figure 14 Comparisons of the mean (A) mangrove height, (B) slope, (C) elevation, (D) proportion of vegetation base substrate, (E) proportion of shell base substate, (F) proportion of sand base substrate, and (G) proportion of live oyster base substrate between reference and potential nesting sites. Differences significant at the p < 0.05 level indicated by **

Discussion

While oyster densities, shell lengths, and reef heights are important metrics that are recommended when evaluating the success of oyster reef restoration, there has been a push for monitoring ecosystem service metrics such as the ability of restored oyster reefs to provide habitat for other faunal groups (Baggett et al. 2015; Brumbaugh et al. 2006; Coen et al. 2007). Based on comparisons of infaunal abundances and bird behaviors on live and dead oyster reefs, I found that live reefs provide important bird foraging habitat, and that restored oyster reefs appear to be becoming more similar to live reefs over time in terms of foraging habitat provision. Thus, efforts to reestablish damaged oyster reefs back to their former functionality as bird foraging habitat via oyster reef restoration methods in Mosquito Lagoon have been successful. However, dead oyster reefs and shell rakes with certain physical features, such as a high elevation, sloped ridges, and sparse vegetation, may be more valuable as possible nesting sites for threatened birds.

Impacts of Oyster Reef Restoration

Previous research has shown that oyster reef restoration can lead to increases in epifauna (Luckenbach et al. 2005; Rodney and Paynter 2006), infaunal invertebrates (Harris 2020; Rodney and Paynter 2006), sessile macroinvertebrates (Rodney and Paynter 2006), mobile macroinvertebrates (De Santiago et al. 2019; Meyer and Townsend 2000; Rodney and Paynter 2006), and small fish (Grabowski et al. 2005; La Peyre et al. 2014). Additionally, through stable isotope analyses Rezek et al. (2017) found that community food resources and food chain lengths on restored reefs were similar to natural reefs, indicating that restored reefs can support similar trophic structures as natural reefs. Coastal birds, like those monitored in this study, often occupy high trophic levels; thus, they are sensitive to changes in trophic structure (Eglington et al. 2012;

Gregory and Strein 2010). Their high trophic level as well as their ability to locate and utilize newly available habitat make birds good candidates for evaluating oyster reef restoration success (Melvin et al. 1999). In this study I aimed to evaluate the success of oyster reef restoration in Mosquito Lagoon by monitoring the use of live, restored, and dead reefs by birds.

Abundance and Behaviors

Dead oyster reefs had the highest mean bird abundances of all three reef types. This may be, in part, due to the high elevation of dead reefs. Dead reefs may reach 1 m above the mean high water (Wall et al. 2005), allowing them to be exposed and available for bird use even during high tide and high water season. Mosquito Lagoon experiences a high-water season in the fall months (Smith and Pierce 1993) in which live and restored oyster reefs may remain submerged even during low tide. Restored reefs had the lowest bird abundances of all three reef types; however, the results indicated that reef size was a significant factor for bird counts on reefs. Restored reefs had the smallest mean area (Table 15), which could explain why the counts of birds were lowest on restored reefs. Dead reefs also had the highest mean bird density; however, when looking only at foraging bird densities all three reef types were similar (Figure 15).

Table 15 Means ± 95% confidence intervals (95% CI) for reef sizes, bird densities, foraging bird densities, and loafing bird densities for live, restored, and dead reefs.

	Mean Reef Size (m^2) ± 95% CI	Mean Bird Density (# of birds/$10m^2$) ± 95% CI	Mean Foraging Bird Density (# of birds/$10m^2$) ± 95% CI	Mean Loafing Bird Density (# of birds/$10m^2$) ± 95% CI
Live	1,543.800 ± 3114.135	0.024 ± 0.012	0.011 ± 0.006	0.004 ± 0.003
Restored	61.275 ± 62.370	0.049 ± 0.031	0.013 ± 0.008	0.019 ± 0.019
Dead	386.625 ± 576.407	0.198 ± 0.105	0.014 ± 0.006	0.118 ± 0.080

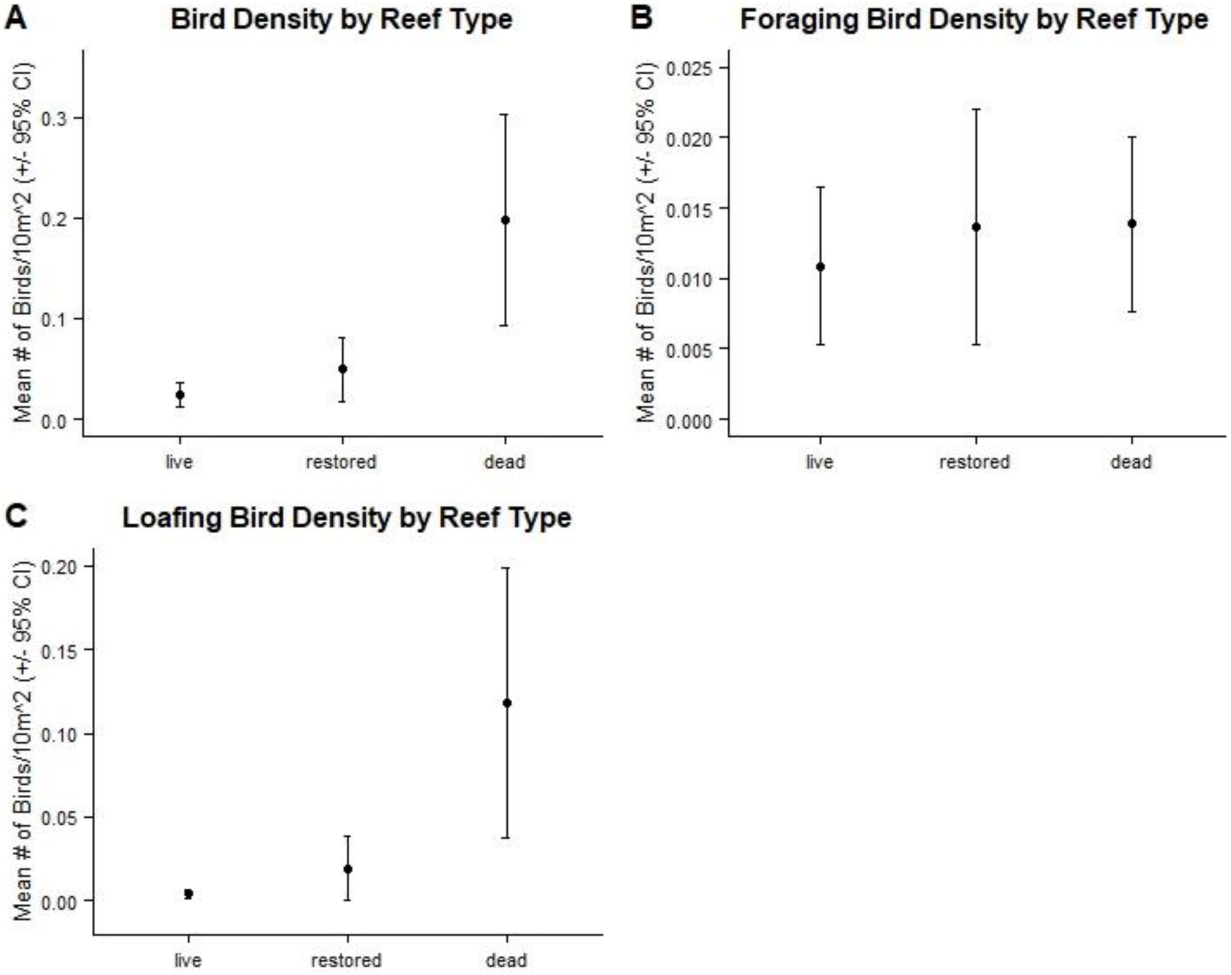

Figure 15 Comparisons of mean total bird densities (A), mean foraging bird densities (B), and mean loafing bird densities (C) between reef types. Error bars represent 95% confidence intervals.

The difference in bird behaviors on dead reefs versus behaviors on live and restored reefs indicates that the different reef types serve different purposes for the birds. I observed birds utilizing the dead reefs most frequently for loafing. I often observed large flocks of *Laridae* (gulls and terns) loafing on dead oyster reefs. *Leucophaeus atricilla* (Laughing gull), *Thalasseus maximus* (Royal tern), and *Sterna forsteri* (Forster's tern), *Larus delawarensis* (Ring-billed gull), *Larus argentatus* (Herring gull), and *Hydroprogne caspia* (Caspian tern) were all associated with loafing on dead reefs. These members of the *Laridae* family are gregarious, and typically observed in large interspecific flocks (Alsop 2002; Nelson 1962). This, along with the higher elevation and longer periods of exposure for these reefs may account for the high numbers of loafing seabirds on dead reefs, contributing to their higher overall bird abundance. Shaffer et al. (2019) also observed high proportions of seabirds, specifically Laughing gulls and *Pelecanus occidentalis* (Brown pelicans), loafing on dead reefs in Mosquito Lagoon. In the current study, not only were birds most abundant on dead reefs, but they were most abundant on dead reefs during late fall, winter, and early spring. This increase in abundance from late fall to early spring correlates with the life histories of Forster's terns, Ring-billed gulls, and Herring gulls, which are all migratory species that arrive in Florida toward the end fall, remain through the winter, and leave during the spring (Pranty et al. 2006).

Habitat extent and prey availability are the two main factors that influence the ability of coastal habitats to support communities of foraging marine birds (Galbraith et al. 2002). In my study, birds were more frequently observed foraging on live and restored reefs. My results agree with a previous study in Mosquito Lagoon, in which Shaffer et al. (2020) found similarities in proportions of foraging birds between live reefs and restored reefs ranging from 1-8 years in age. Successful oyster reef restoration inherently increases the extent of foraging habitat by providing additional reef acreage, and my current study indicates that oyster reef restoration also increases coastal bird prey availability. Post-restoration abundances of important infaunal prey taxa increased in the restored reef sediments and became similar to those of live oyster reefs. Additionally, the total abundance of larger infaunal prey items increased in restored reef sediments post-restoration, and by 6 months became similar to those of live reefs. Grabowski et al. (2005) likewise found infaunal abundances increased in restored oyster reef sediments over time.

The larger infauna may be of particular importance as direct prey items for birds, as they would be more visible to visual hunters (i.e. herons and egrets) and more easily sensed by tactile feeders (i.e. White Ibis). Pre-restoration and one-month post-restoration, the mean number of large infaunal organisms on a restored reef (based on the mean reef size of restored reefs) was approximately 60. These large organisms accounted for 0.6% of the total infauna on restored reefs during these time frames. When looking at all other post-restoration time frames, the mean number of large infauna increased to over 326 per restored reef, and made up 2.8% of the total infauna. The increase in these lower trophic level organisms on restored reefs provides the necessary prey base for higher trophic level organisms. Lenihan et al. (2001) found that piscivorous fish abundances around restored reefs were similar to those around natural reefs in a North Carolina estuary. In Mosquito Lagoon, J. Loch (personal communication, 2021) also found an increase in juvenile sport fish around restored reefs. The ability of these restored reefs to support higher trophic level organisms such as piscivorous fish and birds indicates success in restoring the trophic structure on these reefs.

Diversity and Community Assemblages

The lower species richness and Shannon diversity values on the restored reefs compared to live and dead reefs may be explained by two things. One possibility is that the smaller sizes of the restored reefs may be a contributing factor. In a study on the effects of forest patch size on avian diversity, McIntyre (1995) found that diversity was higher when forest patch sizes were large and decreased with decreasing patch size. The small size of the restored reefs may limit their ability to reach the same levels of richness and Shannon diversity as the larger live and dead reefs. A second explanation for the lower Shannon diversity is that Shannon diversity places more emphasis on rare species than common species. In this study, there were 16 bird species that appeared 5 or fewer times. Of those 16 species, 8 were observed on live reefs and 11 were observed on dead reefs, while only 3 were observed on restored reefs. The less frequent use of restored reefs by these rarer species may be contributing to the lower Shannon diversity value for restored reefs.

However, despite the small size of the restored reefs, Pielou's evenness and Simpson's diversity on restored reefs were both similar to live and dead reefs. Simpson's diversity is more sensitive to changes in evenness than richness, so the higher Pielou's evenness on the restored reefs resulted in the higher Simpson's diversity. Conversely to Shannon diversity, Simpson's diversity puts more weight on common species than on rare species. Of the 5 most common species in this study, 4 of them were observed on all 3 reef types. The use of all 3 reef types by these more common species may be contributing to their similarities in Simpson's diversity values.

In addition to similarities in foraging behavior of birds on live and restored reefs, I found that the assemblages of all birds and the assemblages of foraging birds on restored reefs were similar to both live and dead reefs. This suggests that the restored reefs may be in an intermediate state between dead and live. Troast (2019) monitored the fish assemblages on the same reefs monitored in my study, and after 15 months found that the small resident fish communities on restored reefs were in an intermediate state between live and dead. As small fish serve as prey items for many bird groups in this study (Table 6), the restored reefs would provide an intermediate prey base between dead and live reefs. This may be contributing to the bird assemblages on restored reefs being in-between those of dead and live reefs. Continued monitoring would be needed in order to determine if the restored reef bird assemblages eventually become more similar to live reefs and less similar to dead reefs.

There were differences in the birds most associated with foraging and loafing on live reefs and dead reefs. White ibis, a species whose diet is mostly composed of decapod crustaceans and small fish (Kushlan 1979; Miranda and Collazo 1997), was a representative species for foraging on live oyster reefs, suggesting that these reefs provide the preferred prey items for this species. This is also supported by the high abundances of infauna in live oyster reef sediments, which directly provide food for the birds and also provide food for prey fish. This study did not reveal any species associated with restored reefs. However, in the previous chapter of this thesis I found multiple species that were associated with the combination of live and restored oyster reefs ranging from 1-12 years old, including shorebird species who feed primarily on invertebrates. All observations in the current study took place once monthly during morning low tide, while observations in the previous study were done at varying times of the day and in various tidal conditions. This, perhaps, could have contributed to some of the differences in representative species results from the two studies.

The species associated with dead reefs were mostly gulls and terns, as discussed previously, but also included *Arenaria interpres* (Ruddy turnstone). Ruddy turnstone was the only species associated with foraging on dead reefs. This species primarily forages by turning over loose pieces of stone, shell, or debris to search for invertebrate prey items which may be hiding (Groves 1978). As the dead oyster reefs are composed of loose shell, they provide appropriate habitat for the foraging style of Ruddy turnstones. Ruddy turnstones were also the most commonly observed species on restored oyster reefs in this study (Table 7), which contributes to some of the similarities in the foraging bird assemblages on dead and restored reefs.

Unexpected Infaunal Results

In nearly all time frames, the infaunal abundances were higher in live reef sediments than in dead reef sediments, with the exception of year 3. In this time frame, the infaunal abundances on all three reef types were similar. One factor which contributed to the higher numbers of infauna in the 3-year dead reef samples was that one of the reefs experienced a dramatic increase in the number of isopods. Warburg et al. (1984) reported unexplained population explosions of terrestrial isopods, and Kensley et al. (1995) reported dramatic, unexplained increases in marine isopod abundances during specific years at certain sites within the Indian River Lagoon system. One possible explanation is that the increase in isopods was due to an event that occurred in spring of that year which resulted in the uprooting of the only vegetation on this dead reef, a solitary black mangrove (*Avicennia germinans*) with numerous pneumatophores. The abundant infauna in the year 3 samples from this dead reef were from the genus *Sphaeroma*, which contains many wood-boring species, which show preference for mangrove roots (Brooks and Bell 2001; Perry and Brusca 1989; Rehm 1976; Xin et al. 2020). It is possible that the isopods were displaced from the roots into the sediment when the mangrove was uprooted.

Dead Oyster Reefs as Bird Nesting Habitat

The formation of dead oyster reefs in Mosquito Lagoon may be considered negative, as it is the result of a loss of natural, live oyster reefs, usually due to anthropogenic factors such as boat wakes (Garvis et al. 2015; Wall et al. 2005). My results indicate that the dead oyster reefs and shell rakes in Mosquito Lagoon are being utilized by some bird species for foraging. None of these foraging species are on any endangered/threatened species lists. The largest dead reefs and shell rakes in Mosquito Lagoon also provided nesting habitat for Least terns and American oystercatchers. Both of these species are state-level threatened and have experienced losses of traditional beach nesting habitat (Ogden et al. 2014).

Elevation is often cited as one of the most important factors in American oystercatcher and Least tern nest site selection and nesting success (Jodice et al. 2014; Mazzocchi and Forys 2005; Rounds et al. 2004; Thompson and Slack 1982). Rounds et al. (2004) documented American oystercatcher nests at elevations between 1.1 and 1.4 m above sea level. Mazzocchi and Forys (2005) and Thompson and Slack (1982) documented Least tern nests at elevations (± SE) of 0.76 ± 0.53 m above sea level and 1.1 ± 0.3 m above sea level, respectively. In my study, the reference nesting sites had a mean elevation (± 95% CI) of 1.73 ± 0.02 m above sea level, and the potential sites had a mean elevation of 1.49 ± 0.01 m. This suggests that both reference and potential sites may have adequate elevations for nesting by both species; however, for relatively small birds such as American oystercatchers (maximum size 51 cm) and Least terns (maximum size 23 cm), the difference of 24 cm between the mean elevations at reference and potential sites may be substantial. Additionally, the range of elevations for the potential sites was between -0.25 – 2.12 m above sea level and the range for the reference sites was between 1.26 – 2.23 m above sea level. This suggests that there are portions of the potential sites that are below the typical nesting elevations, including negative elevations which suggest that those portions are below sea level. However, every elevation measurement on the reference sites exceeded published elevations (Mazzocchi and Forys 2005; Rounds et al. 2004; Thompson and Slack 1982). This difference in elevation may be due to the nature of the shell rakes, as they tend to have higher elevation due to the underlying dredge spoil pile. Even during Mosquito Lagoon’s annual fall high water season the two shell rake reference sites were exposed, whereas all other dead reefs were submerged in 2020 (L. Walters, personal communication).

Previous studies suggest that vegetation height is an important factor in American oystercatcher and Least tern nest site selection, as mangroves may serve as hiding places for potential predators (Mazzocchi and Forys 2005; Vega-Ruiz et al. 2019). Mazzocchi and Forys (2005) found that that the mean distance (± SE) from Least tern nests to vegetation > 1 m in height was 18.42 ± 2.79 m. In my study, the mean mangrove height on reference nesting sites was 0.87 ± 0.07 m and the mean height on potential sites was 0.69 ± 0.06 m. Two of the reference nesting sites are shell rakes, which are made up of spoil piles with a veneer of shell, whereas most of the potential sites were dead reefs. The underlying spoil sediment might allow for increased mangrove growth on shell rakes compared to dead reefs that do not have the underlying sediment. Previous research on mangrove seedling recruitment on dead oyster reefs in Mosquito Lagoon suggests that most seedlings are dislodged before they reach adulthood (M. Witt, personal communication). Based on m results, both reference and potential sites have mean mangrove heights below 1 m; however, the maximum mangrove heights of some individual mangroves at these sites exceed 2 m. Vega-Ruiz et al. (2019) did not document any nesting by American oystercatchers in areas where mangroves exceeded 2 m, and found that most nesting occurred in areas where mangroves were < 1 m in height. Additionally, Mazzocchi and Forys (2005) found that that the mean distance (± SE) from Least tern nests to vegetation > 1 m in height was 18.42 ± 2.79 m. At the two shell rake nesting sites, the mangroves were clustered in the middle of the rake, and the rakes only extend 12 m on either side of the clusters.

Previous research on preferred slope of nesting sites for American oystercatchers and Least terns is mixed. Some studies suggest that both species prefer a neutral or more gradual slope (Mazzocchi and Forys 2005; Rounds et al. 2004), while another suggests that ridges and slope are preferred (Burger and Gochfeld 1990). In my study, mean slope at reference sites was steeper than the potential sites. Again, this difference may be due to the fact that two of the four reference sites were shell rakes, which have steeper slopes due to the less-mobile underlying spoil pile. In my study area, it appears that a steeper slope is preferred, possibly because it helps provide better view of potential threats. Two of the reference nesting sites are shell rakes located adjacent to the Intracoastal Waterway, which experiences heavy boat traffic and human activity. In the summer of 2019, two Least tern colonies that were composed of at least three nests each and one American oystercatcher nest at these sites failed after a fisherman allowed his dogs to run free on the sites (FWC, personal communication). In addition to human disturbance, predation may also be problematic for nesting birds at these sites, and nest placement higher on ridges would allow for a view of incoming predators. In 2020, two Least tern nesting colonies consisting of a total of 55 nests on two of the sites failed again, possibly due to predation. Large groups of night herons and Great Blue herons, both species that have been documented to preying on tern chicks (Chapman and Forbes 1984; Collins 1970), were observed on a nearby reef during the nesting season. Additionally, a pair of American Bald eagles were observed diving toward the nesting sites and being chased by adult Least terns. These events occurred just prior to the Florida Department of Environmental Protection declaring that the nesting colonies had failed (FLDEP, personal communication). Additionally, one of the failed nesting sites had 2 mangroves that exceeded 2 m in height and the other had 5 that exceeded 2 m. These taller mangroves may have inhibited the parental birds from being able to detect incoming threats.

Neither the percentage of shell nor the percentage of sand base-substrate differed between reef types in this study, and both reef types had over 90% shell base-substrate. These are much higher percentages than previous studies, in which Least tern nesting sites were found to have between 2.43% – 27.1% shell substrate (Burger and Gochfeld, 1990; Mazzocchi and Forys, 2005; Thompson and Slack, 1982). However, these previous studies focused on beach nesting sites and some spoil islands where restoration efforts such as renourishment or planting of native vegetation had taken place. As the study sites are shell rakes and dead oyster reefs, they naturally contain higher percentages of shell than those other nesting locations.

In previous studies, vegetation cover percentages at Least tern or American oystercatcher nesting sites ranged from 1.11 – 27.94% (Gochfeld 1983; Lauro and Burger 1989; Mazzocchi and Forys 2005; Thompson and Slack 1982). While the two site types in this study did not differ in sand or shell base-substrate percentages, they did differ in percentage of vegetation and percentage of live oysters. Reference reefs had a higher mean percentage of vegetation (4.55 ± 2.46 %) compared to the potential reefs (2.00 ± 0.59 %). Both the reference and potential nesting reefs in my study are within the range of vegetation percentage reported by these previous studies.

In my study, reference sites had a lower mean percentage of live oysters (1.75 ± 0.37%) than potential sites (5.20 ± 0.30%). This is likely a result of the elevation differences in the two reef types. Since the potential sites had lower maximum elevations, they were likely in the earlier stages of conversion from a previously live reef into a dead reef (Walters et al. 2021). These reefs would, therefore, have a greater chance of having adjacent live oysters which may wash up onto the reefs compared to the higher elevation reference sites. The potential reefs had higher percentage of live oysters, which would serve as a direct food source for nesting American oystercatchers, but nesting has not been documented at these sites. In a study of American oystercatchers nesting on shell rakes in South Carolina, Jodice et al. (2014) found that all nesting attempts occurred in areas where there was foraging habitat (live oyster reef) within 500 m of the nesting site. All sites within this study (both reference and potential sites) are within 500 m of either natural or restored live oyster reefs, which would provide foraging habitat for nesting pairs of American oystercatchers.

Research suggests that while Least terns typically return to the same general area each year to nest (between 1.5 – 80.0 km of their previous location), they do not show strong nest-site fidelity (Renken and Smith 1995). The maximum distance between all sites in the study area is only 12.5 km. If additional or alternate nesting sites within this study area become available and more suitable, then they may be selected by Least terns in future nesting seasons. Some of the potential sites which have adequate elevation and slopes, limited mangrove heights, and are located farther from areas of human disturbance might be selected. Monitoring of these sites should be conducted during future nesting seasons.

Conclusions

My results indicate that live, restored, and dead oyster reefs are all being utilized by birds in Mosquito Lagoon. The differences in abundances, behaviors, and community assemblages suggest that different reef types may serve alternate purposes. Additionally, dead reefs and shell rakes are utilized by nesting birds in Mosquito Lagoon. Therefore, care should be taken when considering whether a dead reef in Mosquito Lagoon should be restored or left as potential bird nesting habitat. A mosaic of reef types and shell rakes should be maintained in order to provide foraging, loafing, and nesting habitat for birds.

APPENDIX: CHAPTER 1 SUPPLEMENTARY TABLE

Table 16 Total counts and percent observations for each species for each habitat/behavior.

		Total Count	Percent of Observations							
Scientific Name	Common Name		LOR	DOR	AS	MS	DT	SB	WS	FL
Actitis macularius	Spotted sandpiper	15	0.09	0.13	0.00	0.00	0.00	0.00	0.00	0.00
Agelaius phoeniceus	Red-winged blackbird	233	0.00	0.00	0.00	0.11	0.50	0.00	0.00	0.00
Anas discors	Blue-winged teal	66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Anas fulvigula	Mottled duck	18	0.02	0.00	0.00	0.11	0.00	0.00	0.00	0.02
Anas platyrhynchos	Mallard	6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Anhinga anghinga	Anhinga	65	0.09	0.00	0.06	1.64	0.99	0.00	0.00	0.06
Ardea alba	Great egret	1662	12.89	0.63	0.49	39.81	3.47	0.00	23.31	0.02
Ardea herodias	Great blue heron	643	2.38	2.34	0.55	18.74	2.48	0.29	13.51	0.00
Arenaria interpres	Ruddy turnstone	145	0.78	4.42	0.67	0.00	0.00	0.29	0.00	0.00
Bubulcus ibis	Cattle egret	6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Buteo jamaicensis	Red-tailed hawk	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Buteo lineatus	Red-shouldered hawk	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Butorides virescens	Green heron	24	0.12	0.00	0.00	0.48	0.00	0.00	0.00	0.00
Calidris alpina	Dunlin	1337	15.06	0.13	1.10	0.00	0.00	36.82	0.00	0.00
Calidris minutilla	Least sandpiper	144	0.12	0.76	0.00	0.00	0.00	3.53	0.00	0.00
Cathartes aura	Turkey vulture	127	0.00	0.00	0.12	0.37	4.71	0.00	0.00	0.00
Charadrius semipalmatus	Semipalmated plover	42	0.00	0.44	0.00	0.00	0.00	3.09	0.00	0.00
Circus hudsonius	Northern harrier	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coccyzus americanus	Yellow-billed cuckoo	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Columbina passerina	Common ground dove	8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coragyps atratus	Black vulture	33	0.00	0.00	0.43	0.00	0.74	0.00	0.00	0.00
Corvus ossifragus	Fish crow	883	0.05	0.63	0.00	0.11	2.48	0.00	0.00	0.00
Egretta caerulea	Little blue heron	191	0.90	2.40	0.06	1.64	0.00	0.15	0.68	0.00
Egretta rufescens	Reddish egret	25	0.19	0.00	0.00	0.05	0.00	0.00	0.34	0.00
Egretta thula	Snowy egret	263	1.70	0.13	0.12	5.98	0.74	0.15	1.35	0.00
Egretta tricolor	Tricolored heron	91	0.19	0.00	0.00	2.12	0.25	0.00	1.35	0.00
Eudocimus albus	American white ibis	1001	10.06	0.88	0.00	14.61	3.72	2.80	20.95	0.00
Falco columbarius	Merlin	5	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Falco peregrinus	Peregrine falcon	3	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Gavia immer	Common loon	28	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.46
Grus canadensis	Sandhill crane	15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Haematopus palliatus	American oystercatcher	142	2.15	1.96	0.00	0.00	0.00	1.03	1.35	0.00
Haliaeetus leucocephalus	Bald eagle	27	0.05	0.00	0.43	0.00	0.99	0.15	0.00	0.00
Hirundo rustica	Barn swallow	9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydroprogne caspia	Caspian tern	203	0.43	2.28	2.14	0.00	0.00	12.52	0.68	0.02
Larus argentatus	Herring gull	6	0.02	0.00	0.06	0.00	0.00	0.44	0.00	0.00
Larus delawarensis	Ring-billed gull	2278	14.38	3.92	12.13	0.26	0.00	8.10	4.05	13.27
Leucophaeus atricilla	Laughing gull	1501	16.06	21.05	8.95	0.00	0.25	6.63	0.34	0.70
Lophodytes cucullatus	Hooded merganser	13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Megaceryle alcyon	Belted kingfisher	154	0.00	0.00	1.16	2.06	5.96	0.00	0.00	0.00
Melanitta americana	Black scoter	22	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.22

		Total				Percent of Observations				
Scientific Name	Common Name	Count	LOR	DOR	AS	MS	DT	SB	WS	FL
Melanitta perspicillata	Surf scoter	27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
Mergus serrator	Red-breasted merganser	4738	2.83	0.13	0.00	0.42	0.00	0.00	0.00	77.86
Mycteria americana	Wood stork	12	0.07	0.00	0.00	0.11	0.00	0.00	0.00	0.00
Nyctanassa violacea	Yellow-crowned night heron	66	0.78	0.00	0.00	1.32	0.50	0.00	0.00	0.00
Nycticorax nycticorax	Black-crowned night heron	42	0.05	0.00	0.00	1.54	0.25	0.00	0.00	0.00
Pandion haliaetus	Osprey	934	0.73	0.32	7.66	2.86	63.77	0.00	2.03	0.00
Pelecanus erythrorhynchos	American white pelican	51	0.00	1.52	0.00	0.00	0.00	0.00	0.00	0.28
Pelecanus occidentalis	Brown pelican	846	2.05	4.61	8.76	4.39	0.00	2.06	1.69	2.46
Phalacrocorax auritus	Double-crested cormorant	895	0.64	8.34	19.36	0.64	1.74	3.09	3.72	3.71
Platalea ajaja	Roseate spoonbill	11	0.00	0.00	0.00	0.00	0.00	0.44	0.00	0.00
Pluvialis squatarola	Black-bellied plover	225	3.68	2.91	0.00	0.00	0.00	2.95	0.00	0.00
Podiceps auritus	Horned grebe	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quiscalus major	Boattailed grackle	16	0.26	0.00	0.00	0.00	0.99	0.00	0.00	0.00
Rallus crepitans	Clapper rail	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rynchops niger	Black skimmer	112	1.91	0.57	0.00	0.00	0.00	0.00	0.00	0.00
Sterna forsteri	Forster’s tern	59	0.31	0.38	0.61	0.00	0.00	0.29	0.00	0.00
Sternula antillarum	Least tern	298	0.00	16.12	0.12	0.00	0.00	0.00	0.00	0.00
Sternus vulgaris	European starling	170	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Streptopelia decaocto	Eurasian collared dove	10	0.00	0.00	0.00	0.00	1.49	0.00	0.00	0.00
Tachycineta bicolor	Tree swallow	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thalasseus maximus	Royal tern	1416	3.61	20.67	33.82	0.00	0.00	12.67	3.38	0.02
Thalasseus sandvicensis	Sandwich tern	15	0.09	0.38	0.00	0.00	0.00	0.00	0.00	0.00
Tringa melanoleuca	Greater yellowlegs	1	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Tringa semipalmata	Willet	383	4.96	1.52	0.74	0.42	0.00	2.50	21.28	0.00
Tyrannus dominicensis	Gray kingbird	11	0.00	0.00	0.00	0.00	1.99	0.00	0.00	0.00
Zenaida macroura	Mourning dove	11	0.00	0.13	0.00	0.00	0.25	0.00	0.00	0.00
	Unidentified birds	291	0.14	0.19	1.47	0.21	1.24	0.00	0.00	0.44
	Total birds	22085	19.18	7.16	7.39	8.55	1.82	3.07	1.34	24.64

LOR=live oyster reefs, DOR=dead oyster reefs, AS=artificial structures, MS=mangroves and mangrove shorelines, DT=dead tree branches, SB=sandbar, WS=wading shallow, FL=floating in open water

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