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DOES INTERTIDAL OYSTER REEF RESTORATION AFFECT AVIAN COMMUNITY STRUCTURE AND BEHAVIOR IN A SHALLOW ESTUARINE SYSTEM? A POST-RESTORATION ANALYSIS

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Abstract.—As urbanization and human population growth continue to drive global habitat loss, restoration efforts are focused on returning ecosystem services to degraded habitats. While methods continue to evolve, some projects, such as Florida's Mosquito Lagoon intertidal oyster reef restoration, have had successes in restoring native foundation species such as the eastern oyster (*Crassostrea virginica*). Our study evaluates how these intertidal oyster reef restorations influence bird communities that depend on these reefs for food and resting locations. We conducted monthly observational bird surveys from September 2016 through August 2017 on 24 intertidal oyster reefs in Mosquito Lagoon. Observational bird surveys were conducted during morning low tides each month. During these surveys, six reef types (restored 2009, restored 2012, restored 2015, restored 2016, natural, and damaged), with four replicates of each type, were evaluated for species abundances, diversity, and behaviors. We additionally recorded abiotic variables (salinity, wind speed, air and water temperatures) at each site on each date. Our results did not show a significant difference in avian communities between reef type, species richness, or abiotic variables. However, frequency of foraging was significantly greater on natural and restored oyster reefs than damaged oyster reefs by birds that probe the sediment for prey. This research contributes to the growing body of knowledge on the effects of ecological restoration on avian communities, providing insight on the importance of habitat restoration to support bird species.

Key words: estuary, Mosquito Lagoon, oyster reef restoration, bird communities, bird behaviors, foraging, loafing

Habitat selection is an important process exhibited by coastal and wading bird species worldwide (e.g., Pierce and Gawlik 2010, Pickens and King 2014, Beerens et al. 2015, Brush et al. 2017, Christensen-Dalsgaard et al. 2017). Mangrove stands, mudflats, salt marshes, kelp forests, and intertidal oyster reefs all provide resource opportunities for birds (e.g., Leopoldo and Collazo 1997, Olin et al. 2017, Piersma et al. 2017, Poli et al. 2017). These resources include locations for feeding, migratory stopovers, and breeding grounds (Christensen-Dalsgaard et al. 2017, Olin et al. 2017, Piersma et al. 2017, Poli et al. 2017). Coastal regions are also favored by humans for their economic and aesthetic values. Estuaries are affected by urbanization and human population growth, which results in habitat degradation and habitat loss (McKinney and Raposa 2012, Polidoro et al. 2017). Globally, the loss of wetland habitat during the twentieth century is between 64% and 71% compared to the total wetland area present in 1900 AD (Davidson 2014). Oyster reefs have also declined and Beck et al. (2011) estimated 85% of shellfish reefs have been lost globally over the past century.

The loss of oyster reefs has many negative implications for the ecology and economy surrounding these systems. Oyster reefs provide many ecosystem services including water filtration, sequestration of suspended biomass and nutrients, stabilization of adjacent shorelines and habitats, and provision of habitat for foraging marine species (Grabowski and Peterson 2007, Grabowski et al 2012, Chambers et al. 2018). For example, Grabowski et al. (2012) explains that the interception of suspended particles by an oyster reef increases the transfer of energy among trophic levels, transferring energy through the bottom-feeding crustaceans all the way up to apex predators, such as birds. Therefore, restoration has been conducted on a global scale to help restore these ecosystem services.

Restoration aims to return degraded habitats from either human or natural disturbances to previous conditions (e.g., Burdick et al. 1997, Bastyan and Cambridge 2008, Garvis et al. 2015, Kerr et al. 2016). While methods of ecological restoration continue to evolve, many projects have already returned degraded habitats into areas where birds can once again thrive. The San Francisco estuary marsh grass project, Western Australia's Oyster Harbour seagrass transplant project, National Estuarine Research Reserve System (NERRS) tidal wetland restoration projects, and Florida's Mosquito Lagoon intertidal oyster reef restoration project are all successful examples of long-term coastal restoration (Bastyan and Cambridge 2008, Garvis et al. 2015, Kerr et al. 2016, Raposa et al. 2017). Resident and migrant bird species depend on these habitats for nesting, roosting, and foraging. This is especially true in Florida, which is situated along the Atlantic flyway, a primary route for migratory birds and seasonal nesters (Audubon 2018). Florida's thriving ecotourism is also dependent upon wildlife viewing; approximately

2.7 billion dollars is spent annually on wildlife viewing in Florida, with 57% of that generated from birders (Anonymous 2013).

Along the central east coast of Florida, Mosquito Lagoon (ML) has experienced many anthropogenic stressors over the last two decades, including mosquito ditching, septic tank failures, runoff, and habitat loss through filling and seawall construction (Brockmeyer et al. 1996, Kleppel et al. 1996, Nielsen et al. 2000, Provancha and Scheidt 2000). Live intertidal oyster (*Crassostrea virginica*) reef acreage in Canaveral National Seashore declined 40% between 1943 and 2009 (Garvis et al. 2015). Simultaneously, damaged reefs became apparent along all major boating channels in ML (Grizzle et al. 2002). Damaged reefs begin as piles of disarticulated shell on the seaward edge of reefs, formed by recreational boat wakes removing sediment around the bases of live oyster clusters until nothing remains to hold them in place (Campbell 2015, Manis et al. 2015). The loose clusters are then moved above the mean high water line in this microtidal system by additional large wakes. These oysters soon perish due to lack of water for filter-feeding (Walters et al. 2007). The main goal of oyster reef restoration in ML is to restore these damaged oyster reefs back to their historical live footprint (Barber et al. 2010). This is done by leveling the damaged portion of the oyster reef and installing stabilized shell on top of the reef, forming a "carpet" of benthos substrate for oyster spat settlement. Since 2007, 89 oyster reefs have been restored, resulting in over three acres of oyster restoration (L. Walters unpublished data).

Research is limited on how coastal habitat restoration, especially intertidal oyster reef restoration, affects coastal Florida bird communities. Coastal birds use intertidal oyster reefs for foraging and loafing, because these oyster reefs can provide a variety of avian food sources, including *C. virginica* itself. Infauna and macrofauna living on or near reefs are also available to foraging birds; abundant species include pinfish (*Lagodon rhombiodes*), grass shrimp (*Palaemonetes spp*.), and mud crabs (Panopeidae) (Frederick et al. 2016, Gain et al. 2017). In one Florida study, Frederick et al. (2016) found that 49% of bird observations at intertidal oyster reefs in Florida's Big Bend region occurred on restored oyster reefs. However, the study by Frederick et al. (2016) evaluated oyster reefs restored at a single time, rather than over a temporal range. Our study aims to answer the following questions over eight years of oyster restoration in ML: 1) What is the diversity and abundance of birds observed at restored, natural, and damaged intertidal oyster reefs?, 2) How does the age of a restored oyster reef affect avian community structure?, and 3) What behaviors are birds exhibiting on each reef type?

Methods

Study site

Bird surveys were conducted on intertidal oyster reefs along the east coast of central Florida, within the Indian River Lagoon system (IRL) (Fig. 1). The IRL is approximately 250 km^2 in area with three major inlets (Smith 1993). The IRL system is biologically diverse with over 3,500 plant and animal species (Anonymous 2014); in particular, the IRL plus neighboring St. Johns River marshes represent 25% of Florida's breeding wading bird populations (Schikorr and Swain 1995). Three distinct estuaries make up the IRL system, from north to south: 1) Mosquito Lagoon (ML), 2) Indian River, and 3) Banana River. All bird surveys were conducted in Mosquito Lagoon. Mosquito Lagoon is made up of a mosaic of 10 distinct but connected estuarine habitats, including wetlands, oyster reefs, seagrass beds, and mudflats. Within Mosquito Lagoon, there are at least seven state-designated threatened avian species and one federally-designated threatened avian species as of 2017, including the Roseate Spoonbill (*Platalea ajaja,* ST*),* Reddish Egret (*Egretta rufescens,* ST*),* American Oystercatcher (*Haematopus palliatus,* ST*)*, and Wood Stork (*Mycteria americana,* FT) (ST = state-designated threatened species; FT = federally-designated threatened species) (Florida Fish and Wildlife Conservation Commission 2017).

Salinity in ML ranges from 18 to 45 parts per thousand, while water temperatures range annually from 16.1 to 31.1 °C (Boudreaux et al. 2006, Barber et al. 2010). The mean water depth in ML is 1.7 m, with microtidal patterns that vary seasonally (Smith 1993). Wind has the most influence on currents within this system, with minimal influence from tidal currents (Smith 1987, Manis et al. 2015). During the fall and early winter months, generally August through February, the mean water level in ML is approximately 25 cm higher than the mean water level during spring and summer months (Smith 1986). This is known as the "high water season."

Oyster reef bird surveys

Bird surveys were conducted monthly on 24 oyster reefs in ML for 12 months, between September 2016 and August 2017 (Fig. 1). Three reef types surveyed were: 1) restored oyster reefs, 2) damaged reefs, and 3) natural reefs. The same restoration methods were used across all restored oyster reefs over the eight-year time span. The restored oyster reefs were divided into four classes: 2009, 2012, 2015, and 2016 based on year of restoration (Table 1). This allowed us to consider reef age as a factor of habitat selection, as it takes time for oyster settlement and growth as well as development of faunal communities. Each reef type had four replicates (Table 1).

Bird surveys were conducted monthly over two consecutive days for all 24 reefs. Surveys were done within two hours of predicted morning low tides (NOAA tide tables) in order to optimize the detection probability of birds using the oyster reefs (Schikorr and Swain 1995, Conway 2011). Surveys were conducted with Nikon Monarch™ 10x 42 binoculars at a minimum distance of 30 m. Survey design for each reef included four one-minute scan samples, during which the abundance and species of each bird present on or flying over a reef or reef segment was recorded. Following each scan sample were four-minute focal observations. For each focal sample, the abundance, species, and behaviors (foraging, loafing, flying) were observed for all birds present. This study defines foraging as actively seeking prey on an observed oyster reef, loafing as resting or preening on an observed oyster reefs, and flying as flying directly over an observed oyster reef without landing. Bird observations were recorded on each reef for 20 minutes on each monitoring day for a total of 240 minutes per reef over the course of this study.

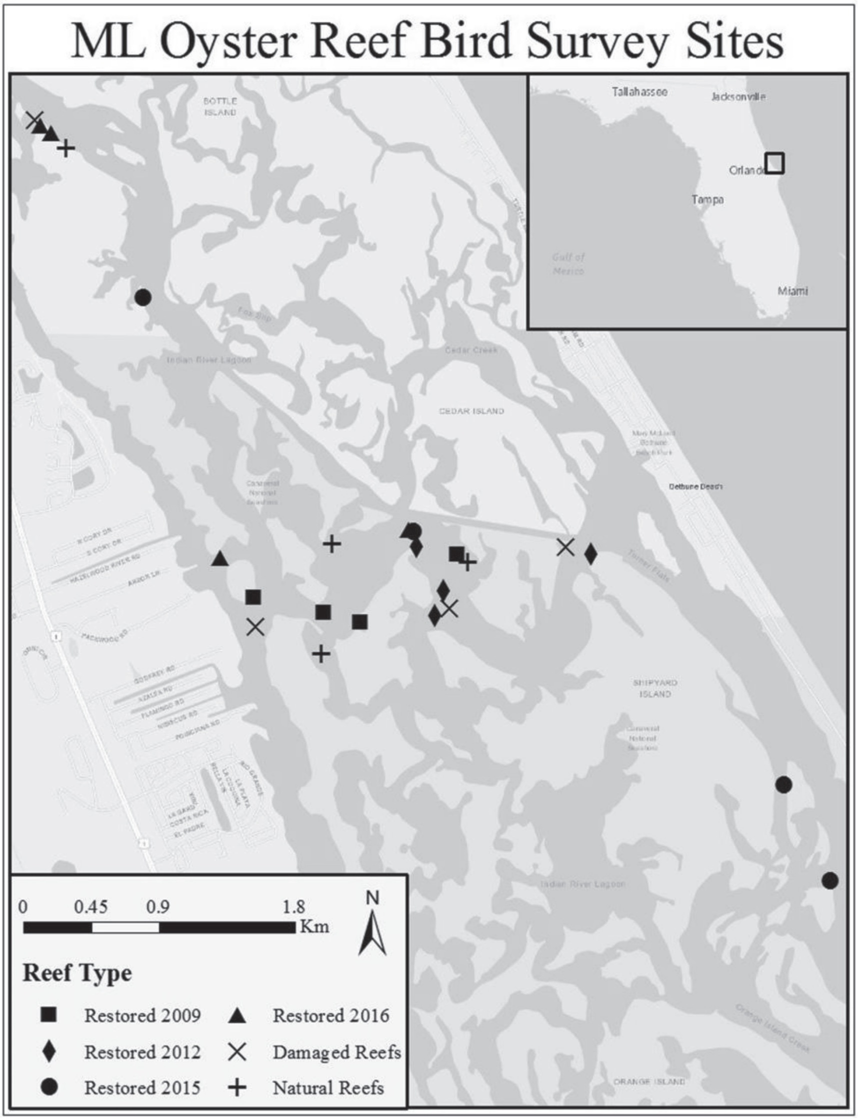

Figure 1. Locations of intertidal oyster reefs in Mosquito Lagoon, Florida where bird surveys were conducted.

Abiotic data were collected from the boat during each monthly survey and included: 1) water salinity (Extech™ portable refractometer), 2) three-minute measurement of average wind speed (Kestrel 3000™ wind gauge), and 3) water and air temperatures (Hach™ protected field thermometer). Seasonal water and weather conditions were also recorded, such as reefs completely submerged at low tide during the annual fall "high water season" in ML (Smith 1986, Stolen et al. 2009).

Table 1. Mosquito Lagoon oyster reefs surveyed during this study. This table includes data for all 24 of the surveyed reefs by reef type, years since restoration, area in square meters, and oyster density as count per m². Age for restored reefs were determined by time since restoration. Age for natural reefs were determined by 26-year old aerial photography of each reef (e.g. 26 + years old for natural reefs).

Reef Name	Year of Restoration	Reef Age (yrs.)	Reef Area (m²)	Oyster Density (count/m²)
Restored 1	2009	8	160	134.47
Restored 2	2009	8	50	36.50
Restored 3	2009	8	80	96.27
Restored 4	2009	8	50	144.97
Restored 5	2012	5	128	38.97
Restored 6	2012	5	275	49.17
Restored 7	2012	5	20	115.60
Restored 8	2012	5	100	77.53
Restored 9	2015	2	100	103.63
Restored 10	2015	2	180	110.73
Restored 11	2015	2	450	123.67
Restored 12	2015	2	125	58.67
Restored 13	2016	1	100	103.07
Restored 14	2016	1	141	86.83
Restored 15	2016	1	70	33.23
Restored 16	2016	1	485	57.27
Natural 1	N/A	26 +	1390	301.20
Natural 2	N/A	26 +	503	120.40
Natural 3	N/A	26 +	4652	184.20
Natural 4	N/A	26 +	635	80.00
Damaged 1	N/A	0	217	1.40
Damaged 2	N/A	0	835	0.40
Damaged 3	N/A	0	141	10.40
Damaged 4	N/A	0	642	0.40

NMS community structure analyses

We compared community structure between reef types using nonmetric multidimensional analysis (NMS) in PC-ORD. NMS is an ordination technique designed to visualize the level of similarity of individual cases for a dataset with all pairwise distances among points compared. NMS differs from other ordination methods in that there are no hidden axes of variation, does not produce a unique solution but rather a "most acceptable" solution, and does not make assumptions about the nature of the data, making it suitable for a wide variety of data sets. Data is analyzed in a primary and secondary data matrix and can be analyzed with any distance measure (in this case Sorenson distance measure). The primary data matrix included the total number of observations of each bird species for individual reefs observed during all monthly surveys. Observed bird species with a total number of observations of less than five for all reef types were excluded from the NMS analysis (Table 2).

The primary matrix included species observed loafing, foraging, and flying over the reef during surveys in order to represent all birds potentially utilizing oyster habitats based on proximity to the reef. In addition, we wanted to evaluate if community struc-

Table 2. Bird species observed during surveys by reef type. Numbers per species at each reef type: the top number is relative abundance, the middle number is foraging frequency, and the third number is loafing frequency. Relative abundance includes flying; flying frequency is not included separately. Primary foraging style for each species is included, and a total abundance count is found at the bottom of the table. Any species with < five abundance count is annotated with an asterisk. All frequencies are rounded to the thousandths.

Species			Relative Abundance, Foraging, and Loafing					
English Name	Scientific Name	Foraging Style	Restored 2009	Restored 2012	Restored 2015	Restored 2016	Natural	Damaged
American Oystercatcher	*Haematopus palliatus*	Prober	0.000	0.007	0.009	0.000	0.038	0.024
(n = 15)			0.000	1.000	1.000	0.000	1.000	0.286
			0.000	0.000	0.000	0.000	0.000	0.714
Bald Eagle	*Haliaeetus leucocephalus*	Soaring	0.000	0.007	0.000	0.011	0.000	0.010
(n = 5)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Belted Kingfisher	*Megaceryle alcyon*	Aerial Diver	0.000	0.026	0.009	0.011	0.006	0.000
(n = 7)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.250	0.000	0.000	0.000	0.000
Black-bellied Plover	*Pluvialis squatarola*	Ground Forager	0.000	0.033	0.000	0.000	0.000	0.003
(n = 6)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	1.000	0.000	0.000	0.000	1.000
*Black Skimmer	*Rynchops niger*	Aerial Forager	0.000	0.000	0.000	0.000	0.000	0.014
(n = 4)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
*Black Vulture	*Coragyps atratus*	Soaring	0.000	0.000	0.000	0.000	0.006	0.000
(n = 1)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Brown Pelican	*Pelecanus occidentalis*	Aerial Diver	0.054	0.118	0.053	0.125	0.056	0.083
(n = 72)			0.250	0.000	0.000	0.000	0.000	0.000
			0.000	0.944	0.167	0.000	0.333	0.625

Table 2. (Continued) Bird species observed during surveys by reef type. Numbers per species at each reef type: the top number is relative abundance, the middle number is foraging frequency, and the third number is loafing frequency. Relative abundance includes flying; flying frequency is not included separately. Primary foraging style for each species is included, and a total abundance count is found at the bottom of the table. Any species with < five abundance count is annotated with an asterisk. All frequencies are rounded to the thousandths.

Species			Relative Abundance, Foraging, and Loafing					
English Name	Scientific Name	Foraging Style	Restored 2009	Restored 2012	Restored 2015	Restored 2016	Natural	Damaged
Caspian Tern	*Hydroprogne caspia*	Aerial Diver	0.000	0.013	0.062	0.034	0.006	0.010
(n = 16)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.333
Double-crested Cormorant	*Phalacrocorax auritus*	Surface Diver	0.027	0.020	0.027	0.046	0.050	0.059
(n = 37)			0.000	0.000	0.000	0.000	0.000	0.000
			0.500	0.333	0.667	0.000	0.625	0.882
Fish Crow	*Corvus ossifragus*	Ground Forager	0.000	0.000	0.000	0.068	0.025	0.000
(n = 10)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	1.000	0.000	0.000
Forster's Tern	*Sterna forsteri*	Aerial Diver	0.014	0.033	0.071	0.000	0.006	0.007
(n = 17)			0.000	0.000	1.000	0.000	0.000	0.000
			1.000	0.000	0.000	0.000	0.000	0.500
Great Blue Heron	*Ardea herodias*	Stalker	0.027	0.013	0.000	0.011	0.019	0.010
(n = 11)			0.000	0.000	0.000	0.000	0.333	0.000
			0.000	1.000	0.000	0.000	0.000	1.000
Great Egret	*Ardea alba*	Stalker	0.068	0.013	0.018	0.011	0.056	0.010
(n = 22)			0.600	1.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Green Heron	*Butorides virescens*	Stalker	0.000	0.000	0.018	0.057	0.013	0.000
(n = 9)			0.000	0.000	0.000	0.200	0.000	0.000
			0.000	0.000	1.000	0.200	0.000	0.000

Table 2. (Continued) Bird species observed during surveys by reef type. Numbers per species at each reef type: the top number is relative abundance, the middle number is foraging frequency, and the third number is loafing frequency. Relative abundance includes flying; flying frequency is not included separately. Primary foraging style for each species is included, and a total abundance count is found at the bottom of the table. Any species with < five abundance count is annotated with an asterisk. All frequencies are rounded to the thousandths.

Species			Relative Abundance, Foraging, and Loafing					
English Name	Scientific Name	Foraging Style	Restored 2009	Restored 2012	Restored 2015	Restored 2016	Natural	Damaged
Herring Gull	*Larus argentatus*	Ground Forager	0.014	0.033	0.035	0.034	0.044	0.014
(n = 24)			0.000	0.200	0.000	0.000	0.000	0.000
			0.000	0.600	0.250	0.667	0.714	0.750
*Hooded Merganser	*Lophodytes cucullatus*	Surface Diver	0.027	0.000	0.000	0.000	0.000	0.000
(n = 2)			1.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Killdeer	*Charadrius vociferus*	Ground Forager	0.000	0.000	0.044	0.000	0.013	0.007
(n = 9)			0.000	0.000	0.000	0.000	1.000	0.000
			0.000	0.000	0.000	0.000	0.000	1.000
Laughing Gull	*Leucophaeus atricilla*	Ground Forager	0.122	0.190	0.100	0.102	0.106	0.388
(n = 187)			0.000	0.000	0.091	0.000	0.058	0.000
			0.111	0.793	0.000	0.000	0.471	0.964
Least Tern	*Sternula antillarum*	Aerial Diver	0.000	0.026	0.018	0.000	0.000	0.007
(n = 8)			0.000	0.500	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Little Blue Heron	*Egretta caerulea*	Stalker	0.000	0.007	0.009	0.011	0.019	0.000
(n = 6)			0.000	0.000	0.000	0.000	0.667	0.000
			0.000	0.000	0.000	0.000	0.333	0.000
*Mourning Dove	*Zenaida macroura*	Ground Forager	0.000	0.000	0.000	0.000	0.013	0.000
(n = 3)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000

Table 2. (Continued) Bird species observed during surveys by reef type. Numbers per species at each reef type: the top number is relative abundance, the middle number is foraging frequency, and the third number is loafing frequency. Relative abundance includes flying; flying frequency is not included separately. Primary foraging style for each species is included, and a total abundance count is found at the bottom of the table. Any species with < five abundance count is annotated with an asterisk. All frequencies are rounded to the thousandths.

Species			Relative Abundance, Foraging, and Loafing					
English Name	Scientific Name	Foraging Style	Restored 2009	Restored 2012	Restored 2015	Restored 2016	Natural	Damaged
Osprey	*Pandion haliaetus*	Aerial Diver	0.162	0.033	0.100	0.034	0.156	0.028
(n = 64)			0.417	0.200	0.182	0.000	0.320	0.500
			0.500	0.400	0.091	0.333	0.200	0.000
Red-breasted Merganser	*Mergus serrator*	Surface Diver	0.014	0.013	0.000	0.000	0.031	0.000
(n = 8)			0.000	0.500	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
*Reddish Egret	*Egretta rufescens*	Stalker	0.000	0.000	0.009	0.011	0.000	0.000
(n = 2)			0.000	0.000	1.000	0.000	0.000	0.000
			0.000	0.000	0.000	1.000	0.000	0.000
Red-winged Blackbird	*Agelaius phoeniceus*	Ground forager	0.041	0.026	0.053	0.091	0.019	0.000
(n = 24)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Ring-billed Gull	*Larus delawarensis*	Ground Forager	0.027	0.007	0.018	0.000	0.025	0.017
(n = 14)			0.000	0.000	0.500	0.000	0.000	0.000
			0.000	1.000	0.000	0.000	0.500	1.000
*Roseate Spoonbill	*Platalea ajaja*	Sifter	0.014	0.000	0.000	0.000	0.000	0.000
(n = 1)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Royal Tern	*Thalasseus maximus*	Aerial Diver	0.054	0.105	0.027	0.023	0.006	0.156
(n = 71)			0.250	0.313	0.000	0.000	1.000	0.044
			0.250	0.563	0.333	0.000	0.000	0.889

Table 2. (Continued) Bird species observed during surveys by reef type. Numbers per species at each reef type: the top number is relative abundance, the middle number is foraging frequency, and the third number is loafing frequency. Relative abundance includes flying; flying frequency is not included separately. Primary foraging style for each species is included, and a total abundance count is found at the bottom of the table. Any species with < five abundance count is annotated with an asterisk. All frequencies are rounded to the thousandths.

Species			Relative Abundance, Foraging, and Loafing					
English Name	Scientific Name	Foraging Style	Restored 2009	Restored 2012	Restored 2015	Restored 2016	Natural	Damaged
Ruddy Turnstone	*Arenaria interpres*	Ground Forager	0.014	0.007	0.000	0.011	0.000	0.069
(n = 23)			0.000	1.000	0.000	0.000	0.000	0.950
			1.000	0.000	0.000	1.000	0.000	0.050
Sanderling	*Calidris alba*	Prober	0.000	0.000	0.009	0.011	0.013	0.007
(n = 6)			0.000	0.000	1.000	1.000	1.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
*Semipalmated Plover	*Charadrius semipalmatus*	Ground Forager	0.000	0.007	0.000	0.000	0.000	0.000
(n = 1)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	1.000	0.000	0.000	0.000	0.000
Snowy Egret	*Egretta thula*	Stalker	0.014	0.033	0.027	0.034	0.031	0.000
(n = 17)			1.000	0.400	0.000	0.000	0.800	0.000
			0.000	0.000	0.000	0.333	0.200	0.000
*Spotted Sandpiper	*Actitis macularius*	Prober	0.000	0.000	0.000	0.011	0.000	0.000
(n = 1)			0.000	0.000	0.000	1.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Tree Swallow	*Tachycineta bicolor*	Aerial Forager	0.068	0.013	0.009	0.000	0.013	0.000
(n = 10)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
Tricolored Heron	*Egretta tricolor*	Stalker	0.068	0.007	0.009	0.023	0.000	0.000
(n = 9)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000

Table 2. (Continued) Bird species observed during surveys by reef type. Numbers per species at each reef type: the top number is relative abundance, the middle number is foraging frequency, and the third number is loafing frequency. Relative abundance includes flying; flying frequency is not included separately. Primary foraging style for each species is included, and a total abundance count is found at the bottom of the table. Any species with < five abundance count is annotated with an asterisk. All frequencies are rounded to the thousandths.

Species			Relative Abundance, Foraging, and Loafing					
English Name	Scientific Name	Foraging Style	Restored 2009	Restored 2012	Restored 2015	Restored 2016	Natural	Damaged
Turkey Vulture	*Cathartes aura*	Soaring	0.014	0.013	0.000	0.000	0.006	0.007
(n = 6)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
White Ibis	*Eudocimus albus*	Prober	0.108	0.065	0.133	0.171	0.088	0.017
(n = 67)			0.750	0.267	0.667	0.467	0.857	0.000
			0.000	0.400	0.000	0.000	0.000	0.400
Willet	*Tringa semipalmata*	Prober	0.041	0.137	0.133	0.057	0.113	0.045
(n = 75)			1.000	0.619	0.800	1.000	0.777	0.154
			0.000	0.238	0.200	0.000	0.056	0.846
*Wilson's Plover	*Charadrius wilsonia*	Prober	0.000	0.000	0.000	0.000	0.006	0.007
(n = 3)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	1.000	1.000
*Wood Stork	*Mycteria americana*	Prober	0.000	0.000	0.000	0.000	0.019	0.000
(n = 1)			0.000	0.000	0.000	0.000	0.000	0.000
			0.000	0.000	0.000	0.000	0.000	0.000
*Yellow-crowned Night	*Nyctanassa violacea*	Stalker	0.014	0.000	0.000	0.000	0.000	0.000
heron			1.000	0.000	0.000	0.000	0.000	0.000
(n = 1)			0.000	0.000	0.000	0.000	0.000	.000
Total Abundance Count			74	153	113	88	160	289

ture differences between reefs was due to differences in species availability at each location rather than habitat selection by the species. The secondary data matrix included the following variables for each reef: 1) reef type, 2) age of reef, 3) reef area, and 4) mean oyster density. Age of reef was determined from the date of oyster reef restoration or the formation of damaged oyster reefs from historical ML maps in ArcGIS (Table 1). Age of natural reefs were considered to be at least as old as the latest maps in ArcGIS (Table 1). Reef area was calculated as total meters squared of restored reef and total area of damaged or natural reef in ArcGIS (Table 1). Mean oyster density was determined by yearly collection of live oyster count data within thirty 0.25 m^2 quadrats on all reefs (Table 1).

Initial analysis used Sorenson (Bray-Curtis) distance measure and 250 runs of real and randomized data with random starting configurations. Stress values were evaluated using guidelines in McCune and Grace (2002, pp. 125-142), with stress values between 10-20 considered common for ecological data and values >20 considered a poor fit for the data. Final configuration was based on a two-dimensional solution and starting configuration from the initial analysis. Correlation coefficients (tau) for each axis were evaluated to identify species and second matrix variables influencing the distribution of communities in the NMS plot. A perMANOVA was conducted to compare similarity of sites based on reef type. A rank-abundance curve was created for each reef type to show species richness (number of species observed) and species evenness (relative abundance of species) utilized in the NMS analysis of the avian communities.

Behavioral analyses

Birds in direct contact with oyster reefs exhibited two primary behaviors, loafing and foraging. To compare frequencies of foraging and loafing between reef types, we calculated the proportion of observed foraging and loafing behaviors for each reef for all species combined. Differences in proportion of foraging behaviors observed at restored and damaged reef types compared to natural reefs was conducted using analysis of deviance for proportion data with quasi-binomial distribution (R Core Team 2017). Observed species with a total abundance between all reef types of less than five were excluded from the behavioral analyses.

Results

Abundance and diversity

In total, we observed 877 birds, representing 41 species, at all oyster reef types in ML: 74 birds at reefs restored in 2009, 153 at reefs restored in 2012, 113 at reefs restored in 2015, 88 at reefs restored in 2016, 160 at natural reefs, and 289 at damaged reefs (Table 2). The two-dimensional NMS plot of bird communities (Fig. 2a) had a final stress of 16.8 and final instability of less than 0.0001. This stress value is considered "fair" for ecological data (McCune and Grace 2002, pp. 125-142) and the rank-abundance curves are included to provide additional evaluation of the community structure.

Spatially, there was overlap in all reef types and there was no significant variation between reef type (Fig. 2a; perMANOVA p = 0.074). In the NMS plot (Fig. 2a), the distribution of communities was most strongly correlated with commonly observed species. Axis one was negatively correlated with Willets (*Tringa semipalmata*; tau=

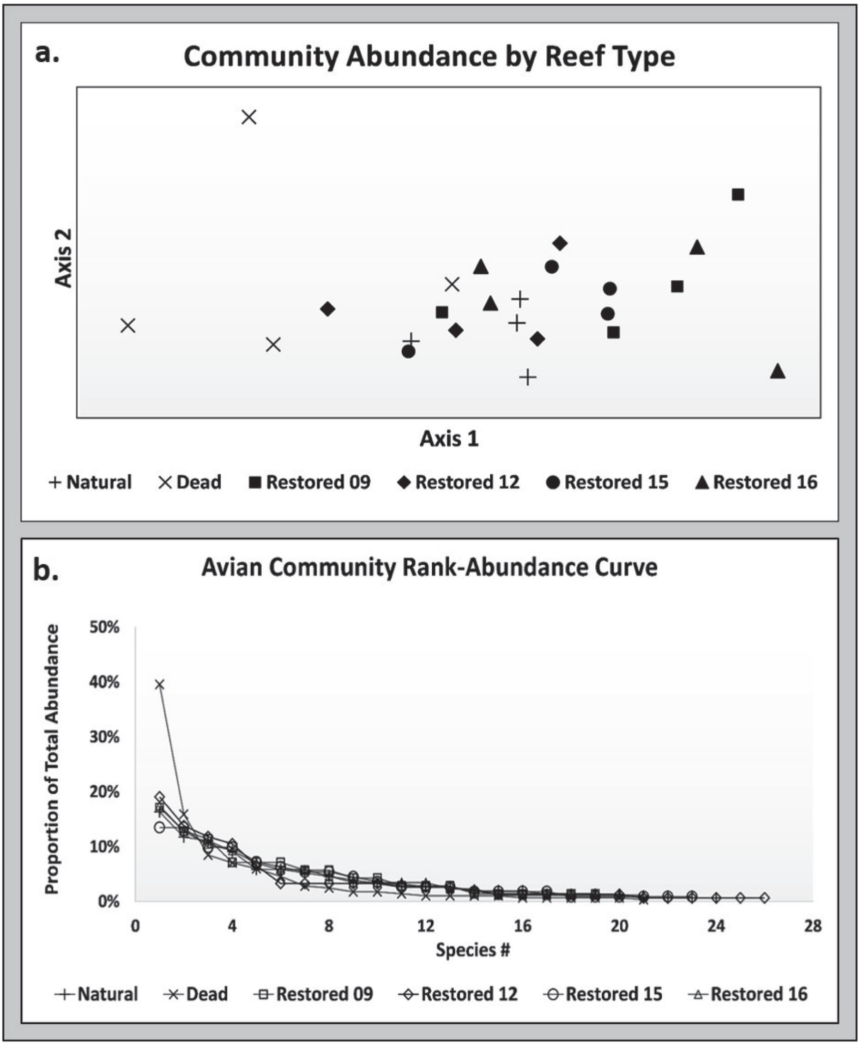

Figure 2. a) Non-metric multidimensional scaling plot of community structure comparing natural, damaged, and restored reefs (final stress: 16.82; instability: 0.00; perMANOVA [reef type: p = 0.074]. b) Rank-abundance curve for proportion of total abundance in avian community with proportions of total abundance between reef types natural, damaged, and restored with year class included.

-0.55) and Brown Pelicans (*Pelecanus occidentalis*; tau= -0.63). Willets were commonly observed on natural reefs and Brown Pelicans were commonly observed on damaged reefs. Variations in abundances of these two species helps to explain the distribution of sites along axis one in the NMS plot. Axis two was negatively correlated with Laughing

Gulls (*Leucophaeus atricilla*; tau= -0.41) and American Oystercatchers (tau= -0.49), with both of these species observed primarily on damaged and natural reefs. Variation in communities of individual sites was also negatively correlated with reef area (tau= -0.34) along axis one and axis two, and was negatively correlated with oyster density (tau= -0.24).

Oyster reefs used in this study varied in area, influencing the available space for bird usage (Table 1). Mean oyster densities per 0.25 m^2 (± SE) on restored reefs was 85.6 ± 9.1, 171.4 ± 48.2 on natural reefs, and 3.1 ± 2.4 oysters on damaged reefs (Table 1). Thus, differences in live oyster cover may have influenced habitat selection of species searching for food resources (greater on natural and restored reefs) or area for loafing (greater on damaged reefs).

Excluding the species less than five in abundance, the combined species richness at restored reefs was 30, at natural reefs was 25, and at damaged reefs was 21 (Table 2). Comparing all six reef types (natural, damaged, restored 2009, restored 2012, restored 2015, restored 2016), species richness was highest at the 2012 restored reefs (n = 26) and lowest at the 2009 restored reefs (n = 19) (Table 2).

The rank-abundance curve (Fig. 2b) shows that avian communities on damaged reefs had less species evenness than restored and natural reefs, with five species (Laughing Gulls; Royal Terns, *Thalasseus maximus*; Brown Pelicans; Ruddy Turnstones, *Arenaria interpres*; and Double-Crested Cormorants, *Phalacrocorax auritus*) dominating the community and making up 77% of the total relative abundance of 21 total species on damaged reefs (Fig. 2b; Table 2). The remaining 16 species found on damaged reefs were in very low abundance, resulting in a steep, L-shaped curve (Fig. 2b). The natural and restored reef avian communities' curves were similar to each other in slope and species abundances were more evenly distributed among all species in the community, resulting in low-sloping curves. On natural reefs, the five most abundant species (Ospreys, *Pandion haliaetus*; Willets; Laughing Gulls; White Ibis, *Eudocimus albus*; and Great Egrets, Ardea alba) were 54.2% of the total relative abundance of 25 total species. All year classes within the restored reefs were similar to natural reef communities, with the five most common species accounting for between 54.1% and 61.8% of total relative abundance of between 19 and 26 total species (Fig. 2b; Table 2).

Behaviors

Out of 41 total species observed at one or more of the three reef types (including those < five in abundance), 31 species used at least one of the reef types for foraging or loafing, while the remaining species were observed in flyovers only (Table 2). Ten species observed flying over reefs included species not typically associated with oyster reefs as part of their ecological niche, such as Red-winged Blackbirds (*Agelaius phoeniceus*) and Tree Swallows (*Tachycineta bicolor*), as well as some species that occasionally land on oyster reefs (e.g. Osprey). Natural and restored reefs had higher foraging rates than damaged reefs, whereas birds using damaged reefs were observed primarily loafing (Fig. 3a). Mean percentage of foraging (± SE) on natural reefs was 70.0 ± 8.5% of behaviors and was not significantly different from foraging on restored reefs (64.9 ± 8.3%; $p = 0.32$) (Fig. 3a). Mean percentage of foraging on damaged reefs was 6.6 ± 4.2%; this was significantly lower than foraging on natural reefs ($p < 0.001$; Fig. 3a). Natural and restored reefs were dominated by birds probing the sediment, while damaged reefs were dominated by ground-foraging birds (Fig. 3b). On natural reefs, 62.3% of the birds foraged by means of sediment probing, with Willets and White Ibis as the dominant probers (Fig. 3b, Table 2). On restored reefs, 59% of the birds foraged by means of sediment probing by the same species as on natural reefs (Fig. 3b). On damaged reefs, the few observations of foraging were primarily ground-foraging by Laughing Gulls and Ruddy Turnstones (Fig. 3b, Table 2).

Discussion

The goal of this study was to compare avian community structure and foraging behavior between restored, damaged, and natural intertidal oyster reefs in Mosquito Lagoon to better understand ecosystem effects of restoration and the ecological drivers behind these patterns. We found that overall community structure was not distinct between reef types; however, restored and natural reef types were similar to each other and different from damaged reefs in species evenness and behaviors. We found the highest proportions of foraging behavior on natural and restored reefs, with more frequent observations of loafing behavior on damaged reefs. This suggests that restored reefs provide similar foraging opportunities as natural reefs, whereas foraging options for estuarine bird species were limited on damaged reefs. This is supported by the prevalence of probing for food on both natural and restored reefs compared to damaged reefs with observations of foraging primarily occurring by ground foragers. Combined, this suggests oyster reef restoration was successful in creating foraging habitat for estuarine birds in addition to increasing oyster numbers in ML.

After one year of surveying avian communities on ML intertidal oyster reefs, distinct differences in community structure between reef types were equivocal. Our community analysis included both birds flying over and directly using the reef for foraging or loafing to identify

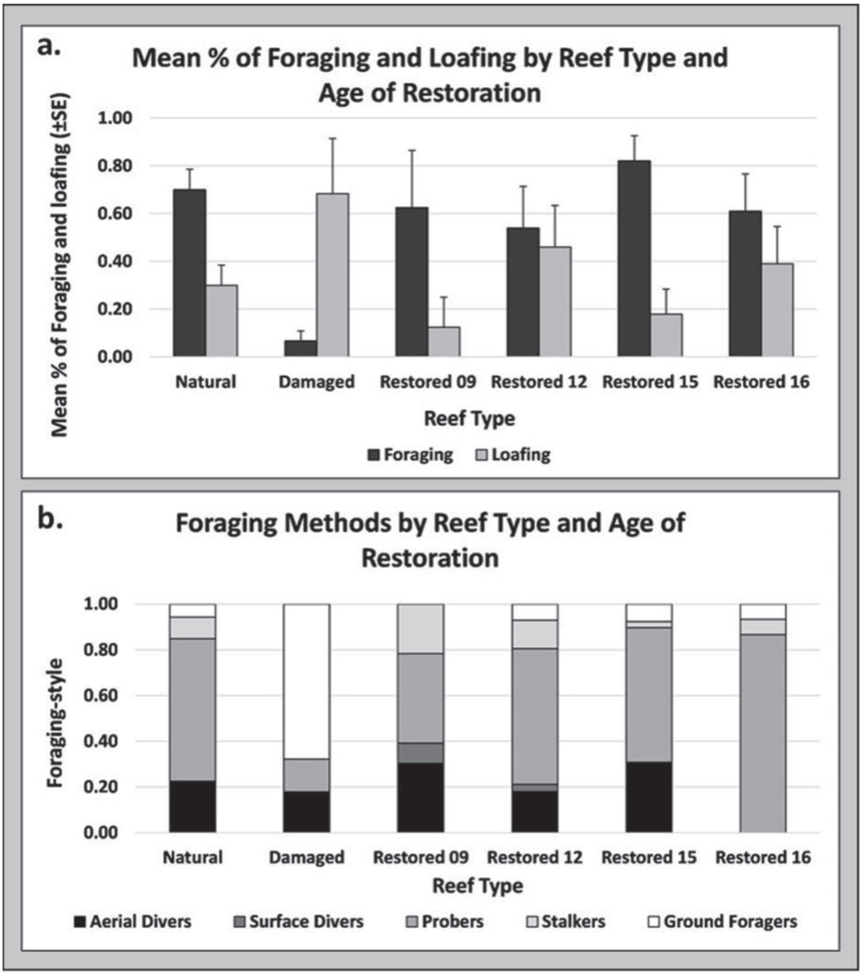

Figure 3. a) Proportion of foraging and loafing at each reef type for natural, damaged, and restored reefs with year class included. Significant difference between natural and damaged reefs ($p < 0.001$); no significant difference between natural and restored reefs ($p = 0.32$). b) Proportion of five foraging styles by reef type with year class included. The five styles are 1) aerial divers (dives from air into water for food), 2) surface divers (dives at surface of water into water column for food), 3) probers (probes into sediment for food), 4) stalkers (stalks prey on ground then attacks rapidly), and 5) ground foragers (sifts through ground debris for food).

all potential users of oyster reefs based on presence in the area. In ML, oyster reefs exist as one habitat within a mosaic of connecting habitats, including mangrove wetlands, seagrass beds, sand bars, and mudflats, with many bird species utilizing multiple habitats for different purposes. It is difficult to determine if the similarities in bird communities are an artifact of this estuarine mosaic condition, or solely driven by the properties of the oyster reefs. Gain et al. (2017) found that habitat linkages in estuarine mosaics in Texas were a major driver of macrofauna communities on intertidal oyster reefs. Macrofaunal communities like those studied by Gain et al. (2017) provide food sources for avian communities in estuaries, potentially resulting in an indirect influence of habitat linkages on these avian communities. Viewing avian communities on a larger spatial scale within multiple habitat types may provide insight into the relation between habitat linkages and community structure in ML.

Large-scale habitat selection within the estuarine mosaics is also important to consider. Along the Big Bend coast of Florida, Frederick et al. (2016) found that avian communities frequently selected sand bars over intertidal oyster reefs during low tide. Our study observed avian communities on oyster reefs only during morning low tides, resulting in the availability of other adjacent habitat types, such as sandbars, for avian communities to utilize during these surveys. During these morning low tides, the main species foraging on natural reefs were probing species such as Willets and White Ibis. Our sampling design focusing only on morning low tides may have biased our observations towards birds preferring specific conditions and excluded species preferring other habitat types during low tides (Schikorr and Swain 1995). Furthermore, *Tringa semipalmata* was found to be a major driver of trends in axis one of the NMS, potentially due to this high rate of foraging during morning low tides. Evaluating bird abundance and behaviors over an entire tide cycle, and in comparison to other habitat types within the estuarine mosaic is needed to better understand bird habitat preferences under different environmental conditions.

Community effects are further influenced by traits of the dominant species (Hillebrand et al. 2008). The most common species on damaged reefs were Laughing Gulls and Brown Pelicans. Burger et al. (2007) found Laughing Gulls showed high levels of food aggression toward other shoreline birds. Since most Laughing Gulls on damaged reefs were not displaying foraging behaviors, these damaged reefs may function as resting areas while the Laughing Gulls wait for food opportunities in adjacent habitats. Schnell et al (1983) found that Laughing Gull kleptoparasitism on Brown Pelicans was extremely common during Brown Pelican foraging, and that Laughing Gull aggression increased during foraging events. Their aggressive behavior may potentially reduce the diversity and abundance of other species using this area for both loafing and foraging. In addition, aggressive species like the Laughing Gull may become strong food competitors on adjacent restored and natural oyster reefs, potentially impacting bird utilization in neighboring habitats. To understand these potential consequences, more research is needed to evaluate species-specific interactions within bird communities.

Oyster reef restoration has been shown to restore ecosystem services lost with habitat degradation. Previous research documented that restored and natural oyster reefs support biogeochemical properties not found at damaged reefs, with several of these properties, such as sequestration of suspended biomass, increasing rapidly within one year of restoration (Chambers et al. 2018). In our study, age of reef was not a significant factor and suggests habitat use by birds begins soon after restoration occurs, potentially supported by the return of biogeochemical properties (Chambers et al. 2018). Restored and natural oyster reefs create a chemical environment that supports a thriving microbial community, coupling benthic and pelagic food webs (Chambers et al. 2018). We found foraging activity in avian communities to be highest at restored and natural oyster reefs, suggesting that the biogeochemical and structural properties of these oyster reefs may be providing a larger abundance and array of infaunal prey options (Harris 2018). This would also help explain the evenness found on restored and natural reefs, as a greater variety in food options would increase ecological niches and attract birds with a range of foraging styles.

The availability of a greater variety in benthic food sources on restored and natural oyster reefs is also supported by the avian foraging styles exhibited on these reefs. Of the birds observed foraging on these reefs, the most common avian species were those that probe the sediment for prey. These main probing species were Willets, White Ibis, and American Oystercatchers. This is significant as American Oystercatchers are listed as a species of high conservation concern in the U.S. Shorebird Conservation Plan (Brush et al. 2017). Restored and natural oyster reefs also attracted avian species such as Great Egrets and Snowy Egrets (*Egretta thula*) that must stalk their prey, including fishes and crabs. These stalker species were not observed foraging on or adjacent to damaged reefs, suggesting an inability of damaged oyster reefs to support a variety of food options or appropriate vantage points for stalking.

Reefs restored in 2016 did not have aerial divers foraging on them between September 2016 and August 2017. While the reasons for this were unclear, Gregalis et. al. (2009) found that responses by resident and transient fishes (the prey items of aerial divers) to oyster reef restoration in Mobile Bay, Alabama were highly variable due to location-specific biophysical characteristics. There may be similar location-specific biophysical characteristics in ML that are driving foraging site selection by aerial divers, something that was not evaluated in this study. This may also be influenced by the methodology of our study, as bird surveys were conducted only during low tide when there is less water for aerial divers to forage in. Ruddy Turnstones were the dominant species observed foraging on damaged oyster reefs, as they are ground foragers that rely on prey items near the surface of foraging substrate. It is likely that the turnstones were foraging on terrestrial insects on the damaged reefs that are above mean high water.

Restored and natural reefs had higher species evenness than damaged reefs, with five species making up almost the entirety of the observations on damaged reefs. The Brown Pelican was one of these five common species on damaged reefs and strongly correlated with axis one in the NMS. This suggests that loafing by Brown Pelicans on damaged reefs occurred in such large numbers that it had a strong influence on the overall avian community structure found in the NMS. The effects of dominance of a few species within a community can impact species interactions, ecosystem processes, and ecosystem stability (Hillebrand et al. 2008). Low species evenness within a community has shown to decrease productivity and adaptability to new environmental constraints (Hillebrand et al. 2008). Higher bird diversity and evenness observed on natural and restored oyster reefs in ML supports the need for conservation and restoration of oyster reef habitat to increase resilience of bird communities with changing environments. Based on our observations at damaged reefs, continued loss and degradation of oyster reefs will limit available habitat and reduce the diversity and abundance of avian communities within ML. This is a major concern for the near future as coastal ecosystems experience a wide variety of anthropogenic and ecological pressures, including rising temperatures and sea levels from global climate change (Harley et al. 2006).

Our study provides evidence of similarities in avian communities using restored intertidal oyster reefs and natural reefs. Food options are likely a major driver of avian community structure on these reefs. Habitat linkages and habitat selection preferences on a larger spatial scale may be an important driver of observed patterns and future research. Results from this study provide information that supports environmental management plans designed to conserve Florida's unique coastal bird life and its associated prey communities. Overall, the variety of avian life on restored reefs in ML supports a positive connection between intertidal oyster reef restoration and avian communities, emphasizing the importance of habitat restoration for aquatic bird conservation.

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