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## EXPLORING MULTI-SCALE VARIATION OF FISH COMMUNITY DIVERSITY IN A DYNAMIC COASTAL ESTUARY

by

## BRITTANY VIOLA TROAST

### B.S. University of Florida, 2014

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 2019

Major Professor: Geoffrey S. Cook

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#### ABSTRACT

Examining diversity over multiple spatial and temporal scales affords the opportunity to develop a mechanistic understanding of the factors influencing community diversity dynamics, and how these may shift in a changing world. This thesis first examines multi-decadal fish community diversity metrics across a coastal biogeographic transition zone to quantify changes in species assemblages, assess relationships between fish community diversity and the abiotic environment, and capture potential shifts in the location of a putative biogeographic break. Results of this chapter indicate not only a change in fish community composition, but also a shift in the location of the biogeographic transition zone. If these trends continue, a potential 16-62km shift northward by the year 2100 could occur. Understanding the novel species assemblages these shifts could result in is necessary for the future management of this area. Next this thesis examines diversity on a local scale, assessing the response of the fish community to restoration of oyster reefs and coastal wetlands which act as essential fish habitat. Results support the idea that fish community composition at restored oyster reefs is more similar to those of live reefs than dead reefs, however, results of abundance and diversity analyses were equivocal. Living shoreline analyses produced no differences between control and restored sites before or after restoration. Possible explanations for lack of clear trends in the fish community could be explained by the presence of other essential fish habitats in the area, scale of restoration, and length of monitoring. This thesis explores diversity on a multitude of spatial and temporal scales to better understand how fish communities respond to change and generates fundamental knowledge that can improve our ability to conserve and manage coastal communities and better inform the development of ecosystem-based management strategies.

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I dedicate this thesis to my parents for their unconditional love and support. I would not be here without you, I would not be me without you, and I will never be able to thank you enough for the friendship, guidance, and love you have given me.

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#### **CHAPTER 1: INTRODUCTION**

Spatial and temporal patterns of diversity are prevalent at all scales (Mannion et al. 2014). At the broadest scales, terrestrial and marine biodiversity increase as one moves from the poles to the equator creating latitudinal diversity gradients (Fischer 1960; Pianka 1966; Stevens 1989; Rohde 1992; Hillebrand 2004; Mittelbach et al. 2007). Variation in primary productivity, seasonality, and total habitat area are proposed mechanisms explaining these latitudinal trends in diversity (Dobzhansky 1950; Darlington Jr 1959; Gaston 2000; Mannion et al. 2014). Emerging evidence suggests broad-scale patterns in diversity are dynamic; over deep geologic time, peaks in diversity have been shown to cycle between low-latitudes during global cooler periods and temperate regions during warmer periods (Mannion et al. 2014). Understanding diversity dynamics and ensuing patterns of species distribution across multiple scales is critical to understanding and conserving biodiversity (Gray 1997; Gaston 2000; Jackson and Johnson 2001; Olson et al. 2002; Mannion et al. 2014)

Species diversity can be separated into three general scales: alpha, gamma, and beta diversity (Whittaker 1960, 1972). Alpha diversity ( $\alpha$ ) describes species assemblages within a local community or habitat; gamma diversity ( $\gamma$ ) is the total species diversity found within a broader region of interest; and beta-diversity ( $\beta$ ) is the link between local and regional scales as it describes the change in alpha ( $\alpha$ ) diversity as one compares community composition across a region (Whittaker 1960, 1972). The most general form of beta diversity compares the diversity of the region ( $\gamma$ ) to the average diversity of the sites within it ( $\alpha$ ) (Whittaker 1960; Koleff et al. 2003). Additionally beta diversity can be calculated along spatial, temporal, or environmental gradients, described as species turnover, or non-directionally by comparing the variance of

diversity among sampling sites (Legendre and De Cáceres 2013). Further exploration, quantification, and comparison of diversity across a mosaic of ecosystems, both natural and restored, could provide valuable scientific insight and understanding.

This thesis analyzes fish community diversity and composition over broad and narrow temporal and spatial scales to generate a more complete understanding of what factors drive community composition and to make recommendations for managing the fish community in a changing environment. Chapter Two focuses on changes in the fish community in a large estuary spanning Florida's east coast over two decades. In this chapter a biogeographic transition zone between temperate and tropical fish species is examined to quantify potential latitudinal shifts in species assemblages. Changes in the fish community is compared to environmental parameters to better understand the forces driving fish diversity and community composition. Chapter Three examines fish community diversity and composition at the patch reef scale to better understand fine scale changes associated with transformations in essential fish habitat. Fish communities before and after oyster reef and coastal wetland restoration were examined for changes in abundance, diversity, and community composition and to identify species indicative of successful restoration. These findings were compared with environmental metrics to assess the potential factors driving these changes. Considering multiple scales of fish community diversity allows for a better understanding of responses to both global and local change which in turn can more fully inform management practices.

## CHAPTER 2: MULTI-DECADAL SHIFTS IN FISH COMMUNITY DIVERSITY ACROSS A DYNAMIC BIOGEOGRAPHIC TRANSITION ZONE

#### Introduction

Over the past century, increased temperatures have altered sea level, salinity, pH, and dissolved oxygen in the ocean (Rhein et al. 2013; Wong et al. 2014; Breitburg et al. 2018). Changes in the abiotic environment have had known impacts on habitat suitability, resulting in altered geographic ranges, seasonal activities, migration patterns, abundances, and species interactions (McCarty 2001). For many marine species, physiology is one of the primary determinants of habitat suitability; many fish are thermal conformers, relying on water temperature to regulate body temperature and related metabolic rates (Clark et al. 2003). Therefore as environmental conditions change, fish populations have three general responses: 1) species expand their geographic distribution as environmental conditions become more favorable, 2) species move accordingly while retaining a comparable geographic distribution as favorable conditions shift in location, or 3) species' ranges contract and populations decline, potentially leading to extirpation or extinction as favorable conditions contract in area or disappear (Cheung et al. 2009; Perry et al. 2014). Together individual and species-level responses to biotic and abiotic factors result in changing species distributions and community assemblages.

Current trends of species distribution suggest many marine species are moving from the tropics poleward as minimum temperatures increase at higher latitudes turning formerly inhospitable areas into favorable habitat (Horta E Costa et al. 2014). Warm water tropical species are expected to move poleward relatively quickly as most tropical species live close to

their thermal maximum and must respond more rapidly than species residing in cooler climate regimes (Pörtner and Knust 2007; Horta E Costa et al. 2014). However, relative to tropical species, many temperate species have broader tolerance limits to varying environmental conditions which could result in a lower rate of movement in response to a changing environment, influencing local extinction rates (Horta E Costa et al. 2014). Varying rates of colonization should result in an increased proportion of warm water species contributing to diversity within a given region undergoing change (Cheung et al. 2009; Estes et al. 2011; Perry et al. 2014). This process of species turnover has been called "tropicalization" (Cheung et al. 2009; Wernberg et al. 2013; Vergés et al. 2016). Evidence of the process of tropicalization has been documented in birds (Thomas and Lennon 1999), mammals (Hersteinsson and Macdonald 2016), butterflies (Parmesan et al. 1999), freshwater and marine fishes (Cheung et al. 2009; Perry et al. 2014) and mangroves (Cavanaugh et al. 2014). However, many aspects of how tropicalization and its ensuing novel species assemblages may alter community diversity dynamics is still lacking.

Here a 21-year dataset is utilized to explore fish community diversity dynamics through a spatio-temporal lens to gain insight into changes that may be occurring. Aims of this study were to: 1) examine multiple indices of diversity across a latitudinal gradient to quantify how fish community diversity may be changing; 2) better understand how an area of relatively high biotic change could be utilized to track changes in species assemblages; and 3) assess relationships between changes in fish community diversity dynamics and abiotic environment.

#### Methods

#### <u>Study Area</u>

Data utilized in this study were generated from an extensive portion of the Indian River Lagoon, Florida (Figure 1). The Indian River Lagoon (IRL) is one of the largest estuaries in the United States, spanning more than 250km; it is tidally restricted and relatively shallow (average water depth ~1m), being comprised of a mosaic of essential fish habitats including oyster reefs, seagrass beds, mangrove forests, and coastal wetlands (Gilmore, 1977). The IRL is composed of three distinct but connected bodies of water that form the broader lagoon system; Mosquito Lagoon, Banana River, and the Indian River proper. The biotic community found in the lagoon is comprised of many species found off the Eastern continental shelf of Florida due to the exchange of individuals through five inlets connecting the IRL to the Atlantic Ocean, resulting in the IRL being referred to as one of the most diverse estuaries in North America (Gilmore 1977, 1995; Snelson 1983). The gradient of environmental factors resulting from the considerable latitudinal extent of the IRL contributes to the relatively high biological diversity. The latitudinal location of the IRL lies at the transition zone between tropical and subtropical or warm temperate species assemblages constructing a putative biogeographic transition zone at approximately 28°N (Gilmore 1977, 1995; Snelson 1983). Biogeographic transition zones are

areas in which many species are near their physiological limits and a change in climate regimes of the biota appear (Horta E Costa et al. 2014).



*Figure 1:* Indian River Lagoon located on the east coast of Florida. Lines represent boundaries of 5km bins or "groups". Study area represents 130km (latitudinally) of the approximately 250km estuary.

#### Data Collection

Samples were collected, and data generated by the Florida Fish and Wildlife Conservation Commission (FWC) Indian River Field Laboratory as part of the state-wide Fisheries Independent Monitoring (FIM) program. Fish were sampled monthly with bag seines and a large haul seine using a stratified random sampling design. Bag seines were 21.3m long, dragged for 15.5m and used to collect juvenile and small adult fish (typically <10cm) in areas having less than 1.5 m of water. Two implementations of these small seines were used, one where the net was set offshore, and the other set onshore categorized as a beach seine. Haul seines were 183 x 3m, deployed by boat in a rectangular shape along shorelines and on offshore flats, and used to collect larger adult fish (Stevens et al. 2016). Fish were identified and enumerated in the field and released, with a subset of samples returned to the lab to verify accuracy of identification. At the time of collection, related environmental variables were recorded including temperature, dissolved oxygen, salinity, pH, and conductivity using Hydrolab and YSI units.

#### Data Analyses

#### Managing Data

Data for the analyses were provided by FWC. The data were truncated to the years 1997 to 2017 and limited to a geographic range from 27.65°N to 28.81°N latitude (approximately 130 km), to provide a more continuous dataset around the putative 28°N biogeographic break. To simplify analyses, mean monthly abundance counts per groupings (explained in more detail in later sections) were calculated for each year during the study period. Numerical abundance

data were 4<sup>th</sup> root transformed to down-weight highly abundant species, usually schooling fishes, and allow mid-range and relatively rare species to contribute with greater influence on analyses. *Anchoa mitchilli* was by far the most numerically abundant species in the dataset (*A. mitchilli* abundance was roughly five times greater than the second most abundant species *Lucania parva*). This species was excluded from analyses due to the inordinate influence the species' abundance had, hindering data interpretation.

Original data included several gear types including seines, trawls and gill nets. Seines were used for analyses as they had the greatest continuous spatial coverage. The remaining gear types were not included as they were used inconsistently through time and space thereby introducing potential gear biases. Three types of seines were included in analyses, but because larger haul seine catches showed differences in species assemblages when compared to the two small seine catches as well as the physical difference in nets used, these gear types were analyzed separately and referred to as "small" versus "large" seines, moving forward. The study area covers three connected bodies of water, cluster analyses were conducted to determine if those bodies of water accounted for differences in species assemblage. Results of the cluster analyses indicated that the species assemblages in the three basins were similar and therefore could be pooled for subsequent analyses, resulting in a more continuous latitudinal gradient (Figure 30).

#### Spatial Analyses

To analyze the latitudinal gradient, the study area was divided into 29 four and a halfkilometer bins, referred to as "groups" starting from the southernmost point. These groups

were used in determining changes throughout the ~130km latitudinal range under examination. Foundational broad spatial analyses were conducted on these groups pooled into three regions spanning the study area, North, Central, and South. The southern portion contains the first 10 groups, the central portion contains groups 11 through 19, and the northern portion contains groups 20 through 29. The putative biogeographic transition zone of 28°N lies roughly between the southern and central regions.

Cluster analysis was performed by utilizing non-metric multidimensional scaling (NMDS) of species assemblage allowing for visualization of similarity between points represented by distance on a 2D-plane. Data were normalized, and analyses were based on Bray Curtis dissimilarity, which uses abundances of species between sites for differences with chronological clustering (ordering of sites latitudinally). Clusters were constrained to two groups (k=2) to identify where the latitudinal biogeographic transition zone "best derived split" occurred over the 21 year study period. A subset of the total time series was used in analyzing trends in the biogeographic transition zone due to atypical abiotic and biotic conditions such as relatively extreme cold fronts and algal blooms (and superblooms) following 2011 that generated high variability in the signal. Distances of movement in the biogeographic transition zone were quantified by calculating the straight-line latitudinal distance from one group to another. Each group was 4.45km long; this distance was multiplied to change in bins experienced over the sampling period. Indicator species resulted from analyzing the species assemblages north and south of the split each year and determining which species where characteristic of the region in both abundance and exclusiveness using the R package "indicspecies" (Cáceres and Legendre 2009). This package identifies indicator species for the groups of sites being assessed by

producing an "indicator value" (IndVal) derived from the exclusivity to the group of sites analyzed (*A*) and number of sites within a group where the species is present (*B*) (Cáceres and Legendre 2009). Climate regimes for each species or taxa analyzed were assigned using FishBase as it is the most comprehensive source available within the study region.

To understand where the greatest latitudinal change in fish community diversity occurred over time, pairwise beta diversity was calculated using both Jaccard's (presence/absence) and Bray-Curtis (abundance) dissimilarities. Broadly, pairwise beta diversity describes the dissimilarity of communities between a pair of sites, however varying components of beta diversity provide further insight into how communities are different. Presence/absence analysis included overall dissimilarity, turnover defined as species replacement from one site to another, and nestedness defined as species loss or gain between two sites (Baselga 2010; Baselga and Orme 2012). Bray-Curtis beta diversity analysis includes overall dissimilarity as well as species balance and gradient components, these indices are analogous to Jaccard's analysis but take into account abundance when determining differences (Baselga 2013). Examining components of beta diversity provides insight into a dynamic system when combined with measures of the individual site, or alpha diversity.

A series of alpha diversity indices were calculated including species richness, Shannon diversity index (H), Pielou's evenness, and Simpson diversity. Species richness was calculated as the number of species present. The Shannon diversity index takes into consideration number of species and their abundance and is defined as:

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

The term  $p_i$  represents the number of individuals of the *i*th species and *R* is richness, or the total number of species (Shannon 1948). Pielou's evenness ranges from 0 to 1 and is a measure of how similar in abundance species are to each other. It is measured in relation to the Shannon index and defined as:

$$J' = \frac{H'}{H'_{max}}$$

 $H'_{max}$  describes the maximum possible value of H' if all species were equally likely and is defined as:

$$H'_{max} = -\sum_{i=1}^{S} \frac{1}{S} \ln \frac{1}{S} = \ln S$$

*S* here represents the number of species in the dataset (Pielou 1966). Simpson diversity uses the same variables as Shannon diversity and examines richness and abundance, giving greater weight to dominant species in the dataset (Simpson 1949) and is defined as:

$$\lambda = \sum_{i=1}^{R} p_i^2$$

Species richness is the simplest measure of diversity but is informative in the broadest presence/absence sense. Shannon diversity builds upon this by including abundance data to explore species evenness within a community. Simpson diversity provides similar information to

Shannon diversity but by giving greater weight to common species, it de-emphasizes the relative value of rare species. Pielou's evenness focuses on the proportion of the species being examined and not the number of species present. Comparison of these indices can provide insight into how diversity changes spatially and temporally (e.g., are the number of species in the IRL increasing or are the abundances of species already present in the IRL changing).

#### Environmental Analyses

To determine the link between the abiotic and biotic community, Akaike information criterion (AIC) model selection was utilized to determine which environmental variables best explain the trends in diversity indices calculated. A negative binomial distribution was selected when examining species richness since it is comprised of count data and a gaussian distribution was used for continuous Shannon, Simpson, and Pielou's evenness diversity metrics. To further examine environmental variables' relationships to species assemblages an "envfit" test from the R package "vegan" (Oksanen et al. 2018) was performed to visualize which variables accounted for differences in species assemblage.

#### Results

#### Catch and Environmental Statistics

A total of 7,601,946 individuals were collected and 3,280,550 were part of this analysis after excluding *A. mitchilli (bay anchovy,n=4,321,396),* representing 270 taxa. *Lucania parva (rainwater killifish)* was the most abundant species with 803,765 specimens accounting for 24.5% of the catch. The remaining top ten most abundant taxa were *Lagodon rhomboides* (pinfish, n=444,466; 13.6%), *Menidia spp.* (silversides, n=271,659; 8.3%), *Eucinostomus spp.* 

(mojarras, n=163,762; 5.0%), *Leiostomus xanthurus* (spot, n=147,060; 4.5%), *Mugil cephalus* (striped mullet, n=130,035; 4.0%), *Bairdiella chrysoura* (silver perch, n=113,205, 3.5%), *Diapterus auratus* (irish mojarra, n=108,492, 3.3%), *Floridichthys carpio* (goldspotted killifish, n=105,529, 3.2%), and *Mugil curema* (white mullet, n=105,275, 3.2%). The top ten taxa account for 73.0% of the total; the 50 most abundant species account for 98.9% of the total catch (Table 5).

Environmental variables taken at the time of collection include temperature, conductivity, pH, salinity, and dissolved oxygen. Mean monthly temperatures per ~5km bin over sampling period ranged from  $6.3^{\circ}$ C to  $35.9^{\circ}$ C ( $\overline{x}$ =24.99°C; SD=4.91). Conductivity ranged from 3.1 to 73.42 ( $\overline{x}$ =40.42; SD=9.72). Values of pH ranged from 7 to 9.6 ( $\overline{x}$ =8.10; SD=0.25). Salinity(ppt) ranged from 1.5 (ppt) to 44.9 (ppt;  $\overline{x}$ =25.90; SD=6.70), and dissolved oxygen ranged from 1.2 mg/L to 15 mg/L ( $\overline{x}$ =7.29; SD=1.71).

#### <u>Spatial Analyses – Broad Scale</u>

Cluster analyses supports the presence of a biogeographic transition zone located within the IRL. Mean species assemblages within the IRL indicate species in the North and Central regions were more similar than the species assemblage of the southern region, the region below the 28°N break (r<sup>2</sup>=0.68, stress=0.12; Figure 2). Regressions of the mean monthly environmental variables indicate that changes in the abiotic data have occurred over the study period with an increase of temperature from 24.52°C (SE=0.34) to 25.44°C (SE=0.34), an increase in salinity from 21.12ppt (SE=0.39) to 30.47ppt (SE=0.39), and a decrease in dissolved oxygen from 7.4mg/L (SE=0.09) to 7.26mg/L (SE=0.09; Figure 3). These data indicate that over the past 20 years there has been an increase in temperature of 0.92°C, an increase of salinity of

9.35ppt, and a decrease in dissolved oxygen of 0.14 mg/L. Combined, these coarse-scale spatial data illustrate both variation of the species assemblages along the latitudinal gradient with a greater difference between the southern and central regions, supporting the presence of a biogeographic break at ~28°N, as well as broad changes in the abiotic environment.



Figure 2: Non-metric multidimensional scaling of mean species assemblage per region in Indian River Lagoon, FL from 1997-2017. Each point represents the species assemblages of a region in one year. Blue squares are the northern third of the study area, green circles represent the middle third, and red triangles represent the southern third. The putative 28°N biogeographic break falls roughly between the central and southern regions. The northern and central sites are more similar than the southern site (r<sup>2</sup>=0.68, stress=0.12).



Figure 3: Temperature, Salinity, and Dissolved Oxygen mean monthly values per region of the Indian River Lagoon, FL. Northern region is represented in blue, central region in green, and southern region in red. Black linear regression line includes 95% confidence intervals in gray.

#### <u>Spatial Analyses – Fine Scale</u>

Large and small seine data showed changes in the best-defined break in species assemblage between the northern and southern region (Figure 4). Small and large seine catch data exhibited shifts toward higher latitudes over thirteen years of the study (small seine 32.86± 21.84 km; large seine 8.51±5.40 km). Large seines had relatively lower latitudinal breaks with all breaks occurring between bins 9 and 13. Small seine catch data produced a stronger northern trend (2.52 km/yr) than large catch data (0.65 km/yr). All changes over the contracted 13 year time period were significant at the 0.1 level (small seines p=0.0905, large seines p=0.0743).



Figure 4: Location of the "best derived break" in species assemblages across a biogeographic transition zone using a) small seine data and b) large seine data. Colors represent the group with warmer red color representing lower latitude breaks and blue cooler colors representing higher latitude breaks. Black dashed line represents linear regression.

Overall pairwise beta-diversity between individual 5km bins was driven by species turnover in presence/absence-based Jaccard's dissimilarity and species balance in abundancebased Bray-Curtis dissimilarity (Figure 5a,c). Species turnover accounted for 72.4% of dissimilarity between 5km bins in small seines and 63.1% in larger seines. The species balance component of the fish community assemblage accounted for 73.6% of dissimilarity between bins from small seine data and 65.7% of large seine data (Figure 5a,c). In addition, pairwise beta diversity between years was attributed predominantly to the turnover and species balance components of dissimilarity. In small seines species turnover accounted for 76.2% of dissimilarity and 7.11% in large seines (Figure 5,d). Species balance accounted for 77% of dissimilarity in small seine catch and 72.5% in large seine catch (Figure 5,d).

Jaccard's beta diversity describing dissimilarity spatially between groups (Figure 5a) peaked in overall and turnover components near group 12, while all three components peaked near groups 18 and 23 tapering down as latitude increased for both small and large seine data. Bray-Curtis beta diversity between groups (Figure 5) showed these same trends. Results of pairwise beta diversity temporally between years also show similar trends when comparing Jaccard's versus Bray-Curtis dissimilarity (Figure 5b,d). Here small and large seine data beta diversity stayed relatively constant with peaks occurring near 2012 followed by a dip and a sequential rise.



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Figure 5: Jaccard's pairwise beta diversity between a) groups and b) years and Bray-Curtis pairwise beta diversity for c) groups and d) years. Jaccard's beta diversity uses presence/absence data and Bray-Curtis beta diversity uses abundance data. Black line is  $\beta_{OVERALL}$ , blue line is  $\beta_{TURNOVER}$  for Jaccard's dissimilarity or  $\beta_{BALANCE}$  for Bray-Curtis dissimilarity, red line is  $\beta_{NESTEDNESS}$  for Jaccard's dissimilarity and  $\beta_{GRADIENT}$  for Bray-Curtis dissimilarity. Small seine data results are delineated with a solid line while large seine data results are delineated with a dashed line.

#### Indicator Species

Cluster analyses identified indicator species for the broad-scale northern and southern groupings described above. *Cyprinodon variegatus* (sheepshead minnow), *Gambusia holbrooki* (eastern mosquitofish), and *Gobiesox strumosus* (skilletfish) were the top three species in small seines representing the area north of the biogeographic break and *Fundulus grandis* (gulf killifish) was the single indicator species identified from the large seine data (Table 1). The region south of the biogeographic break was larger and consequently had a greater number of representative species. The top three indicator species collected from the small seines were Orthopristis chrysoptera (pigfish), Micropogonias undulatus (atlantic croaker), and Lutjanus griseus (mangrove snapper). The top three indicator species of the large seine data were Selene vomer (lookdown), Sphoeroides testudineus (checkered puffer), and Sphyraena barracuda (great barracuda). Small and large seine data shared three indicator species for the southern portion of the biogeographic transition zone, Citharichthys spilopterus (bay whiff), Sphoeroides testudineus (checkered puffer), and Sphyraena barracuda (great barracuda; Table 1). Table 1: Table of indicator species for the northern and southern sites through the 1997-2017 pooled over time. Indval is the "indicator value" of the species. "A" represents exclusivity to a grouping of sites, and "B" represents the proportion of sites the species is found in a radius. All species listed are significant (n=0.001).

Species	Small Seines			Large Seines		
North	IndVal	Α	В	IndVal	Α	В
Cyprinodon variegatus	0.68	0.74	0.62			
Gambusia holbrooki	0.43	0.73	0.25			
Gobiesox strumosus	0.31	0.70	0.14			
Fundulus grandis				0.33	0.86	0.13
South						
Orthopristis chrysoptera	0.82	0.86	0.78			
Micropogonias undulatus	0.80	0.87	0.73			
Lutjanus griseus	0.67	0.85	0.53			
Anchoa hepsetus	0.65	0.76	0.56			
Trachinotus falcatus	0.61	0.87	0.42			
Citharichthys spilopterus	0.60	0.97	0.37	0.58	0.81	0.42
Sphoeroides testudineus	0.59	0.98	0.35	0.66	0.94	0.46
Ctenogobius boleosoma	0.56	0.98	0.32			
Centropomus undecimalis	0.55	0.77	0.40			
Sphyraena barracuda	0.52	0.95	0.28	0.64	0.82	0.50
Selene vomer				0.66	0.85	0.51
Paralichthys albigutta				0.59	0.91	0.38
Synodus foetens				0.47	0.94	0.23
Gerres cinereus				0.46	0.79	0.26
Archosargus rhomboidalis				0.45	0.85	0.23
Caranx latus				0.42	0.80	0.22
Prionotus tribulus				0.41	0.86	0.20

species is found in a region. All species listed are significant (p=0.001).

Examining climate regimes of the species above and below the break in the biogeographic transition zone, with a focus on tropical species assemblage, the northern and southern regions combined gained 3.12 (+/- 0.92) tropical species over the study period (Figure 6). The southern region had higher mean species richness than the north. Additionally, the southern region, defined as the area below the best derived split each year, experienced a faster rate of increase (0.15 species/year) in the number of tropical species inhabiting the region as compared to the northern region (0.03 species/year), and accounted for the majority of increase in tropical species richness over the entire study area (Figure 6).



Figure 6: Species richness of tropical species each year throughout the Indian River Lagoon, FL, and in the northern and southern regions. Total study area is represented in black, northern portion defined as the area above the "best derived split" in blue, and the southern portion below the "best derived split" in red. Regression line and r-squared value provided with line represented by a gray dashed line.

Large seine data have higher mean species richness, Shannon diversity, and Simpson diversity, and lower Pielou's evenness than small seine data, however, both sized seine datasets follow similar trends temporally and spatially (Figure 7). Values from large and small seines at the beginning of the sampling period (1997-2002) are more similar across regions but begin to diverge after 2002 (Figure 7, left sub-panels). When viewed over the 21-year time series, small seine diversity metrics were relatively constant. Large seine diversity metrics showed an increase in species richness, Shannon and Simpson Diversity; species evenness decreased in the large seine catch (Figure 7, left sub-panels). Mean species richness was greatest in 2008, and lowest in 1997 (Figure 7a). When diversity was assessed spatially (by ~5 km bins), maximum species richness, Shannon diversity, and Simpson diversity were located at bins 29, 5, and 5 respectively; diversity minima occurred near bins 12, 12, 13 for small seines and 28 for large seines (Figure 7, right sub-panels). As with the temporal assessment, evenness exhibited the opposite pattern to the other diversity metrics, species evenness was lowest in bins 5, 22, and 29, and greatest near bins 12, 16, and 27 (Figure 7). Broadly speaking, the southern region generally has the highest values of species richness, Shannon diversity, and Simpson diversity, and the lowest values of Pielou's evenness (Figure 7, right sub-panels).


Figure 7: Mean monthly species richness, Shannon diversity, Simpson diversity, Pielou's evenness per year (a,b,c,d) and per group (e,f,g,h). Yearly diversity indices are grouped by overall area in black, area north of the yearly best derived break in blue, and area south of the break in red. Results derived from small seine data are represented by a solid line and a dashed line for large seine data in all plots.

## Environmental Results

Results of AIC model selection for most diversity indices (species richness, Shannon Diversity, and Pielou's evenness) for small and large seine catches revealed the combination of all environmental variables (temperature, salinity, pH, and dissolved oxygen) to be the model that best described the data. Simpson diversity from the large seine data follow suit with the previous metrics however Simpson diversity from the small seine data differs with temperature alone best describing the data ( $\Delta$ AIC=0.1;Table 6). In general, the next best performing models were all closely associated with temperature (temperature, month of year, dissolved oxygen), suggesting temperature had a very large influence on fish diversity within the study region.

The environmental fit test, which determines which environmental variables best describe the species assemblages present, supported the results of AIC model selection. Temperature followed by dissolved oxygen best described the empirical data of the variables selected; dissolved oxygen was inversely related to temperature. Salinity was the next best determinate, and pH was the least informative variable (Figure 8). Conductivity was removed as an explanatory variable, as it was collinear to salinity.



Figure 8: Environmental fit test over NMDS of mean species assemblage per group per year from 1997-2017 in the Indian River Lagoon, FL. Each point represents the species assemblage of a group for a specific year. Environmental variable relationships overlaid in blue, length of arrow represents influence on point placement.

# Discussion

# Biogeographic Transition Zone

Biogeographic transition zones mark the convergence of distinct biota and have been recognized as hotspots where species range shifts occur (Poloczanska et al. 2013; Horta E Costa et al. 2014). The overlap of temperate, subtropical, and tropical species, and their associated environments, can be useful in assessing changes in ecological communities, as many species in these zones of overlap may be close to their upper or lower physiological limits (Horta E Costa et al. 2014). Here the validity of a putative biogeographic transition zone was assessed in a barrier island lagoonal system and was examined for how this area could be utilized to understand the spatial and temporal dynamics of a diverse fish community.

The assumed biogeographic transition zone in the Indian River Lagoon occurs at approximately 28°N (Gilmore 1977, 1995; Snelson 1983). The results from a preliminary analysis pooled across the sampling period supports the existence of a community transition within 5km (~28.05°N) of this area, while the finer spatial scale cluster analysis produced a noisier signal. The finer scale analyses indicated the biogeographic break fluctuated over several kilometers through time for both gear types, confirming how variable and dynamic the environment and associated biota can be. Despite this variation, both gear types exhibit a northern trend in transition zone location, although with varying rates. The differences in these rates were most likely attributed to gear bias with smaller schooling fish more likely to be caught in small seines and larger lower abundance fish caught in large seines. Attributes of these taxa such as mobility and residency, could be responsible for the different rates of northern movement, and could ultimately lead to novel species assemblages. Similar to this study, other researchers have shown a poleward trend in species distribution shifts (Hawkins et al. 2003; Cheung et al. 2009; Perry et al. 2014; Vergés et al. 2014), but there are cases with inconsistent or no responses (Chen et al. 2011; Kuhn et al. 2016). Incorporating species-specific differences in response to climate suggests that instead of identifying a distinct biogeographic break in species assemblages, it may be more accurate to identify and consider broader dynamic transition zones in which the species pool naturally fluctuates. While comparing the trends observed over 13 years of data described in these clustering analyses, it suggests the break between southerly tropical and more northerly subtropical/temperate species has itself

shifted at least 8.51 (±5.41) km to as much as 32 (±21.84) km north since 1997, depending on gear type. While this is a relatively short time series when compared with broad-scale changes in climate, considering a fixed rate of change of diversity from the selected 13 years, and extrapolating the results of the seine catch data through 2100, the best derived break between tropical and subtropical/temperate species assemblages could move northward from 16 (±5.40) km to 62.15 (±21.84 km), or approximately 2 km to 7 km per decade. This value is lower than other studies that have reported marine species expanding their leading range edge by 72 km per decade (Poloczanska et al. 2013). Regardless of the actual distance per unit time, these supporting lines of evidence have very real implications for the fish community and broader marine ecosystem.

The intended purpose of identifying indicator species for the areas above and below the biogeographic break was to find taxa that could serve as tools or "canaries in the coal mine" for managers to more easily identify when change is happening in their system, monitor the break over time, and even as a benchmark for successful mitigation. These species would have the ability to elucidate potential shifts in the biotic or abiotic environment, identify environmental impacts, and indicate the diversity of other species in the area (Cáceres and Legendre 2009). Indicator species of the northern region may have been influenced by the relatively large area of coastal wetland located in the northern Indian River Lagoon and southern Mosquito Lagoon. Habitat in the northern portion of the IRL is located within the boundaries of Merritt Island National Wildlife Refuge and Canaveral National Seashore and contains relatively large areas of undeveloped coastal wetland. In comparison, habitat in the southern portion of the IRL is more developed and has been impacted by human influences including hard armoring. Focusing on

the climate regimes of the fish assemblages above and below the break revealed an overall increase in the mean species richness of tropical species over the study time series, with a faster rate of increase in the southern region than in the north. Tropicalization of the region, in the broad sense of an increase of tropical species, is supported by the results of this study. Further analysis of this trend is beyond the geographic scope of our study as the increase in tropical species may originate from a species pool inhabiting water beyond the study region.

Exploring species assemblages and breaks that occur in the biogeographic transition zone indicate the area has experienced change in the last 21 years, however, there are several factors that could be contributing to a noisier signal. A system with a high degree of habitat heterogeneity may be comprised of microhabitats that allow fish to survive in areas that would be too extreme without the buffering effect of these potential refugia (Scheffers et al. 2014). The Indian river lagoon has shallow impoundments located on the grounds of the Kennedy Space Center that could act as these types of refugia. There is evidence that climatically, Earth's tropical band is widening, and will continue to widen with anthropogenic climate change (Seidel et al. 2008). If this continues, fluctuations and overall change in the fish community assemblage would be expected into the future.

#### Indices of Diversity

Biodiversity is not homogenous across the Earth and variation exists; efforts to understand the mechanisms driving those differences are increasing, especially through the lens of a changing climate (Nekola and White 1999; Koleff et al. 2003; Soininen et al. 2007a, 2007b, Tuomisto 2010a, 2010b; Anderson et al. 2011; Viana et al. 2016; Alahuhta et al. 2017; König et al. 2017). These results show the most important components driving spatial and

temporal dissimilarity are species turnover and species balance (similar abundances). The natural process driving these particular components of diversity was species sorting associated with the physical environment, suggesting that changes in the environment may be responsible for changes in beta diversity (Si et al. 2015). The results of this study further corroborate recent studies that found turnover to be the dominant component driving beta diversity; a metaanalysis assessing the relative importance of beta-diversity components found turnover to be 5 times greater than nestedness (Tisseuil et al. 2012; Viana et al. 2016; Hill et al. 2017; Soininen 2018). In this study, the relative importance of turnover was two to three times greater than nestedness, as was the case when comparing the relative importance of species balance and gradient components of abundance-based diversity metrics. This slightly lower relative importance of turnover (vs nestedness) and species balance (vs gradient) may be representative of ordered extinction and colonization events acting more strongly in this region than other systems.

The trend that beta diversity decreases as latitude increases has been identified in plant and animal communities (Soininen et al. 2007a; Qian 2009; Qian et al. 2009). The consistent beta diversities found throughout the southern portion of the IRL, with heterogeneity and dissimilarity increasing as one moves further north contradicts the expectation of lower beta diversity moving poleward. This unexpected result suggests additional factors were influencing the observed trends. One of these factors could have been the result of our study region spanning <200km, while these broader trends in diversity play out over larger spatial scales. Additionally, as mentioned above, there are habitat differences across the breadth of the study region that may have a greater influence on beta diversity at the local spatial scale, when

compared to broad spatial scale changes in climate. Another possible factor influencing the trends could be the influence of the sub-tropical latitude where the broader trends only present themselves in less speciose temperate systems found at higher latitudes. When considering temporal beta diversity, the trends were more consistent than those of the spatial results. Large seine data beta diversity show decreased dissimilarity after 2010, in which the area experienced a relatively severe cold event (Stevens et al. 2016). The negative trend in dissimilarity could be an artefact of the time it took for the region to recover from both direct and indirect effects of this acute disturbance, creating more similar species assemblages between years. However, many of the years following this extreme cold event were additionally impacted by widespread intense algal blooms, introducing additional confounding disturbance events into the data set.

Examining results of species richness, Shannon diversity, Simpson Diversity, and Pielou's evenness indicated that small and large seine data generally exhibit complimentary trends, suggesting these types of fish were affected similarly by the factors that drive these metrics. Shannon and Simpson diversity exhibit similar trends implying there weren't large changes in common versus rare species, even though the data were transformed to increase the relative weight of rare species. Pielou's evenness values were generally inverse to those of the additional diversity indices; when there was an increase of species it was less likely those species would be of equal abundance. The combination of these results helps to describe the species sorting processes that influence change in the fish community and provide a baseline for further analysis as sampling continues.

## Environmental drivers

Reports from the International Panel on Climate Change determined the upper 75m of the ocean is warming globally at 0.11°C per decade. Within our study system, broad temperature analysis indicated water temperatures had increased more rapidly (by 0.92°C over the past 21 years), setting the stage for continued shifts in the fish community within the IRL ecosystem as the climate continues to warm. The greater increase in water temperature as compared to the global mean increase is most likely attributed to local environmental conditions; the IRL is a relatively shallow body of water, which increases the influence of changes in air temperature. Dissolved oxygen has been decreasing globally since the middle of the 20<sup>th</sup> century and is inversely related to temperature, as well as increasing CO<sub>2</sub> concentrations and nutrient inputs (Breitburg et al. 2018). Low dissolved oxygen events can contribute to direct and indirect effects on species assemblages and can result in fish kills (Breitburg et al. 2008). Many fish kills have been reported recently in the Indian River Lagoon, with exceptionally large kills being documented in March 2016 and August 2018 (Gray 2016, Cook Pers. Obs.). Further investigations into dissolved oxygen and fish community dynamics could produce useful insights into understanding, predicting, and mitigating these events.

Environmental relationships with biota throughout a biogeographic transition zone like the one studied here are less understood in regard to species distributions (Caselle et al. 2010; Selig et al. 2010). This study corroborates findings of earlier studies that excluding the combination of all possible environmental factors together, temperature, and its associated variables, best describe the diversity of a study region (Clark et al. 2003; Clarke and Gaston 2006; Horta E Costa et al. 2014; James et al. 2016; Woodworth-Jefcoats et al. 2016).

Temperature, and sometimes equally but inversely related parameters such as dissolved oxygen in the coastal environment appear to be the ultimate environmental drivers influencing the long-term distribution and abundance of marine fishes. Understanding changes occurring in species assemblages of marine ecosystems is necessary to develop effective ecosystem-based management strategies of those systems. Connecting said management strategies with community-level response to changes are critical to develop a mechanistic understanding of these processes. Therefore, by providing greater insight into the causes of change in coastal communities managers could thus create better solutions to the challenges facing marine ecosystems.

# CHAPTER 3: PATCH-SCALE DIVERSITY DYNAMICS – HOW DOES FISH COMMUNITY DIVERSITY RESPOND TO RESTORATION OF ESSENTIAL FISH HABITAT?

## Introduction

Traditionally management of fisheries focused on specific species or singular outcomes, with little regard for habitat, species interactions, or ecosystem components (Pikitch et al. 2004). More recently ecosystem-based management (EBM) and ecosystem-based fisheries management (EBFM) approaches have been promoted; these more holistic strategies take a comprehensive approach to managing an ecosystem by attempting to achieve benefits for not only a target species, but the broader ecological community (Pikitch et al. 2004). A primary component of EBM is identifying habitats that support a healthy ecosystem. Essential fish habitat is defined as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity" (*Magnuson-Stevens Fishery Conservation and Management Act* 1996) and are now used, in combination with EBFM, as a tool to protect and improve habitats critical to the survival of fishes.

Over the past several decades coastal habitats such as shellfish reefs and coastal wetlands have experienced losses of approximately 85% and 50%, respectively (Peterson et al. 2003; Dahl 2006; Beck et al. 2011). Both habitats are recognized as essential habitat for an array of taxa including fishes (Coen et al. 2007; Swann 2008). Oyster reefs are known for their many additional ecosystem services including shoreline protection, wave attenuation, improved water clarity, linking energy between trophic levels, and creation of physical structure (Peterson et al. 2003; Coen et al. 2007; Gregalis et al. 2009). Coastal wetlands are comprised of salt marsh plants and mangroves (Boesch et al. 1994), and filter water to combat eutrophication and stabilize the shoreline (Barbier et al. 2011). Together oyster reefs and coastal wetlands help mitigate various problems facing coastal ecosystems, and their restoration can potentially increase fish diversity and abundance (Peterson et al. 2003; Coen et al. 2007; Gittman et al. 2016). Understanding how benthic habitat restoration may increase fish production and diversity will better our understanding of how coastal habitat restoration can be used as a tool to mitigate events that negatively impact fish communities (Peterson et al. 2003).

Much debate has surrounded the link between diversity and factors like ecosystem function, stability, and resilience (Grime 1997; Schwartz et al. 2000; Loreau et al. 2001; Tilman et al. 2014). These linkages between diversity and ecosystem function are being actively explored; experimental studies support a positive relationship between diversity and ecosystem function, but generalities about the role of diversity in ecological communities are few (Purvis and Hector 2000; Balvanera et al. 2006; Tilman et al. 2014). Broadly, community diversity can refer to a variety of characteristics in an ecosystem, ranging from species richness (number of species), to more complex indices incorporating both the number and proportion of species (Gray 1997). However, all measures of diversity have the common goal of quantitatively describing the assortment of species found within a region. Due to the dynamic nature of ecosystems, more knowledge about the ecological role of diversity within communities can be generated by simultaneously quantifying and comparing multiple indices of diversity (Purvis and Hector 2000).

Here fish community data collected from natural and restored oyster and living shoreline sites over two summers were used to explore fish community dynamics in response to restoration. Aims of this study were to 1) quantify how species diversity is impacted by restoration; 2) understand species' associations with natural versus restored habitats; 3) examine the time scale over which the fish community responds to restoration.

## Methods

#### Study Region

Data for this study were collected in Mosquito Lagoon, located in the northernmost portion of the Indian River Lagoon as described in chapter two (Figure 9). It is recognized for its recreational fishing opportunities and regarded as the "Redfish Capital of the World" (Kahn 2012). Within the boundaries of the Mosquito Lagoon are a Florida State Aquatic Preserve, the Merritt Island National Wildlife Refuge, and Canaveral National Seashore, part of the U.S. National Park System, which strives to protect the environment while keeping it open for public use. Its benthic habitats are characterized by intertidal oyster reefs to the north and seagrass beds and salt marshes to the south (Walters et al. 2017). However these critical habitats have declined in recent years; to mitigate these losses, restoration of oyster reefs and living shorelines has occurred within the Mosquito Lagoon to restore these ecosystems and the services they provide (please see below, Dahl 2006; Beck et al. 2011; Birch and Walters 2012).



Figure 9: Mosquito Lagoon, Florida. Points represent sites of before/after control/impact experimental design in both oyster (navy) and living shoreline (green) habitats.

# **Experimental Design**

A before/after control/impact (BACI) design was utilized to examine how fish communities respond to restoration of eight oyster reefs and seven living shoreline sites. The eight restored oyster reefs were compared against four negative controls, referred to as "dead" reefs, and four positive controls, referred to as "live" reefs, resulting in 16 oyster sites. Living shoreline sites were compared to two controls representing natural coastal wetlands for a total of nine living shoreline sites. Of the eight restored oyster reefs, four were restored in June of 2017 (referred to as "2017 Reefs"), and four were restored in June of 2018 (referred to as "2018 Reefs"), when comparing between these sites they are referred to as "restoration sets". Four coastal wetland sites were restored into "living shorelines" in July of 2017 (referred to as "2017 Shorelines"). However, one living shoreline site was destroyed by Hurricane Irma in September of 2017, and therefore was no longer sampled. In lieu of restoring a second set of living shorelines, four previously restored living shoreline sites of varying ages (two, three, five, and seven years old) were sampled beginning in May 2018 (referred to as "2018 Shorelines").

Dead reefs were identified by high vertical profiles above mean water line made up of dead oyster shell. When high energy boat wakes erode relatively soft sediment around live reefs, it results in live oyster clusters breaking off reefs and becoming pushed on top of the reef where they no longer experience intertidal water conditions and die, ultimately creating a dead reef (Wall et al. 2005). Oyster sites were restored by raking down dead shell mounds to intertidal water level. Vexar mesh nets affixed with clean oyster shells, referred to as "oyster mats", were placed on the raked area, secured together, and weighted with concrete weights. This method produces a restored oyster reef by providing intertidal structure for local oyster recruits to settle upon and mature. Live reefs are characterized by mean water level height, low vertical profile and expansive live oysters.

Coastal wetlands are also affected by recreational boat wakes as they facilitate recruitment of non-native plant species by effectively dispersing their seeds and dislodging epifauna, thereby disturbing community composition (Bishop 2005; Gabel et al. 2012; Walters et al. 2017). Coastal wetlands are restored into "living shorelines" by placing bags filled with clean oyster shell, referred to as "oyster bags", along the natural shoreline in order to protect the restored portion of shoreline from high energy waves, followed by inland plantings of

smooth cordgrass (*Spartina alterniflora*), and further inland plantings of a mixture of red and black mangroves (*Rhizophora mangle* and *Avicennia germinans*).

#### Sampling Methods

A combination of three gear types were used to sample the different fishes that utilize benthic habitat in Mosquito Lagoon. Lift nets are deployed on the reef or in the shoreline adjacent to coastal wetlands to target relatively sedentary reef and shoreline habitat residents. Seines sample the water column and benthos directly adjacent to the target habitat. Taxa caught in seines are relatively transient species that utilize the reef or shoreline habitat for foraging, refugia, and other behaviors, but not exclusively as is the case for reef and shoreline residents (Table 7). Trawls sample the water column and benthos in the broader area just offshore of the sampling sites. The species captured in trawls tend to be skewed toward softsediment residents, but also capture "spillover" species that are moving among patches of oyster reef and coastal wetland habitat, thus capturing a subset of resident species captured in lift nets and relatively transient species captured in seine nets.

Lift nets consisted of 0.6m X 0.6m PVC quadrats fitted with 1.5mm 16kg delta netting to form a bag. On oyster reefs, three lift nets were deployed just above the low tide line of the reef and three lift nets were deployed on lower edge of the high tide line on the reef. The high tide line nets were intertidal on live and restored reefs and above the high tide line on dead reefs due to the high vertical profile of that reef type. On living shorelines six lift nets were placed along the mid-water line running the length of the site. Lift nets contained either one oyster mat or one oyster bag, similar to the oyster mats and bags used for restoration, depending on the habitat type being sampled (oyster vs. living shoreline). Nets soaked for

approximately seven days and upon sampling would be picked up swiftly, the mat or bag shaken down in the net to catch organisms hiding in the refugia, and fish identified and enumerated.

Seines were approximately 21 meters long and two meters high with a 2m X 2m center bag. Seine netting was 3.2mm square 16kg delta knotless nylon with floats along the top and leads along the bottom. Nets were dragged the entire length of oyster sites and approximately half the length of living shoreline sites (~35m), and the catches identified and enumerated.

Trawling was done with a 6.1m otter trawl with 0.9m X 0.45 wooden doors, 4.7m main body net constructed from 38mm stretch mesh and a 3.2m cod end made from 3mm delta knotless mesh. The otter trawl was dragged by boat for two minutes at ~3 knots as close to the site as possible with oyster reefs located at the center of distance being trawled. Living shoreline trawls sampled both control and restore sites as part of one trawl due to the close proximity of the sites; control sites were adjacent to living shoreline restoration sites. Therefore, trawl data from living shoreline sites were not included in subsequent analyses. Generally, trawls in this study were used as a broad survey of the adjacent soft-sediment fish community and species moving near study sites rather than targeting oyster reef or living shoreline-specific fish communities.

Sampling frequency varied with gear type, however the second set of living shorelines in which sampling began in May 2018 were sampled monthly for the first three months by all gear types and then every three months thereafter. In summer 2017, lift nets were deployed at oyster and living shoreline sites pre-restoration. Following restoration, lift nets were deployed

at one week, two weeks, one month, two months, three months, and then every three months thereafter. The two week-post restoration sampling was dropped for oyster reefs in summer 2018 as there were no significant differences in catches at one and two weeks post restoration. Seines for the 2017 summer oyster and living shoreline sites were conducted pre-restoration, one day post-restoration, as well as at one week, two weeks, one month, six weeks, two months, three months, and then every three months thereafter. The two-week and six-week time sampling periods were dropped in summer 2018, as catches did not differ from the one week and one month sampling, respectively. Trawls for all sites were performed pre-restoration and monthly thereafter. In total 15 months of post-restoration data were used in these analyses for oyster and living shoreline sites restored in summer 2017 and three months of post-restoration data were used for summer 2018 restoration sites, however sampling is ongoing.

## <u>Data Management</u>

Species community data were square root transformed to allow rarer species to have influence in the statistical tests and to down-weight the effect of more abundant schooling fish. *Anchoa* species including *A. mitchilli, A. lyolepis, A. hepsetus,* and *Anchoa. spp.* were the most numerically abundant species. This species complex was excluded due to their high abundance combined with difficulty in identification, hindering data interpretation. One restored oyster reef (restore 3) was not included in analyses due to low oyster recruitment and subsequent loss of reef profile post restoration. This site was directly adjacent the intracoastal waterway, and was exposed to large boat wakes and hurricane damage shortly after restoration.

## Statistical Methods

All analyses were completed using R statistical software (version 3.4.4). Mean abundance and diversity metrics (species richness, Shannon's diversity, Simpson's diversity, and Pielou's evenness) as described in Chapter two, were quantified for each site and sampling period. A one-way analysis of variance (ANOVA) test was performed followed by a Tukey HSD post-hoc test to determine significant differences (p<0.05) among treatment types. The same tests run on abundance and diversity indices per treatment type were also run grouped by sampling period for a temporal analysis.

Beta diversity of species assemblages were calculated on presence/absence data using Jaccard's dissimilarity and abundance data using Bray-Curtis dissimilarity using the R package "betapart". These analyses assess trends in differences and similarities between species composition at sites; results are presented as similarity (1-β). Beta-diversity analyses presented in this study are used to gain a better understanding of which treatment types are most similar in species assemblages while additional tests help to add significance to these results. Permutational multivariate analysis of variance (PERMANOVA) was utilized to determine significant differences (p<0.05) between abundance and presence/absence community data, and beta dispersion was tested to assess for non-significance of data spread, a critical assumption to run PERMANOVA. Indicator species were determined using the R package "Indicspecies" following the methods described previously and were based on treatment type (Cáceres and Legendre 2009). Trophic levels were examined by acquiring each taxon's trophic value from "FishBase", as it was the most comprehensive database. Distributions of trophic levels across and within each restoration set (2017 reefs/shorelines vs. 2018 reefs/shorelines)

separately for all gear types were explored per treatment type. ANOVAs and Tukey HSD posthoc tests were run on mean trophic level per treatment type to determine significant differences and groupings.

Cluster analyses were completed using the R package "vegan" and utilized non-metric multidimensional scaling (NMDS) which presents species assemblage data on a 2D plane where similar assemblages are placed in closer proximity than those farther apart. Cluster analyses were performed on species abundance data averaged by time period per treatment type then normalized and distances calculated with Bray-Curtis dissimilarity.

Environmental data were explored using the same analyses described in chapter two. In brief, the parameters examined were temperature (°C), salinity (ppt), dissolved oxygen (mg/L), and Secchi depth (m) as a water clarity metric. Temperature and dissolved oxygen were taken with a ProDSS YSI unit, salinity was taken with a refractometer, and water clarity was assessed using a Secchi disk. Akaike information criterion model selection will be used to determine which environmental data best describe trends in diversity, and an "Environmental Fit" test using "envfit" in package "vegan" to explore how environmental variable are associated with overall species assemblages (Oksanen 2008).

# Results

# Catch and Environmental Statistics

A total of 119,606 individuals were captured from May 2017 to October 2018 representing 87 taxa (Table 7). After excluding the *Anchoa* species complex, 48,903 individuals consisting of 83 taxa were used in analyses. Of the remaining taxa, *Eucinostomus spp*.

(mojarras) was the most abundant with 12,645 individuals accounting for 28.9% of the catch. Completing the top ten most abundant taxa are *Menidia spp*. (silversides, n=6,359; 13.0%), *Bairdiella chrysoura* (silver perch, n=4,633; 9.5%), *Diapterus auratus* (irish mojarra, n=4,425; 9.1%), *Lucania parva* (rainwater killifish, n=2.575; 5.3%) *Eucinostomus harengulus* (tidewater mojarra, n=2,362; 4.8), *Lagodon rhomboides* (pinfish, n=2,285; 4.7%), *Harengula jaguana* (scaled sardine, n=2,131; 4.4%), *Microgobius gulosus* (clown goby, n=1,849; 3.8%), and *Eucinostomus gula* (common mojarra, n=1,589; 3.3%). The top ten taxa represent 83.5% of the total catch. Oyster sites had 24,822 individuals representing 75 taxa (Table 8). Living shoreline sites had 24,086 individuals representing 65 taxa. Seines collected the highest number of taxa and individuals (78 taxa, n=44,598) among all gear types. Trawling collected 2,447 individuals representing 44 taxa, while lift nets collected 1,863 individuals representing 33 taxa.

Environmental variables taken at the time of collection consist of temperature, salinity, dissolved oxygen, and Secchi depth. Temperature ranged from 17.4° C to 34.7° C ( $\bar{x}$ = 28.3° C; SD=3.7). Salinity ranged from 25 ppt to 41 ppt ( $\bar{x}$ =34.0 ppt; SD=3.7). Dissolved oxygen ranged from 3.11 mg/L to 9.72 mg/L ( $\bar{x}$ =6.2 mg/L; SD=1.3). Water clarity ranged from 0.24 m to 1.40 m ( $\bar{x}$ =0.63 m; SD=0.2).

#### Oyster Reefs

## Abundance and Diversity

There were few significant differences in catch per unit effort (CPUE), measured as mean abundance per sampling event, when treatment types were compared within and across restoration sets (Figure 10). Abundance among gear types are significantly different (p<0.01),

seines had the highest overall abundance ( $\bar{x}$ =14.48±5.16) followed by trawl ( $\bar{x}$ =4.54±2.99) and lift net catches ( $\bar{x}$ =0.57±0.29). Lift nets at live reefs had significantly greater CPUE than restored and dead oyster reefs, both within restoration set (2017 Reefs: F<sub>2,52</sub>=6.91,p=0.002; 2018 Reefs: F<sub>2,45</sub>=7.915, p=0.001), and across restoration sets (F<sub>2,67</sub>=9.539, p=0.001).





Examining metrics of diversity over the entire study period, seine catches have higher species richness, Shannon diversity, and Simpson diversity than trawl and lift net catches (Figure 11a, b, c). Seine catches did not exhibit any significant differences among treatments. Lift net catches at live reefs had significantly greater species richness ( $F_{2,67}$ =5.832,p=0.004, p<0.05; Figure 11e) and Shannon diversity ( $F_{2,67}$ =6.26, p=0.009; Figure 11f) than dead and restored reefs. Trawl catches at live reefs had significantly greater Simpson diversity (F<sub>2,83</sub>=4.46,p=0.01; Figure 11k) and Pielou's evenness (F<sub>2,70</sub>=4.50,p=0.01; Figure 11l) than at restore reefs.



Figure 11: Species richness, Shannon diversity, Simpson diversity and Pielou's evenness for dead (gray), restore (turquoise), and live (navy) reefs from seine, trawl, and lift net catch data in the Mosquito Lagoon, FL. Error bars represent 95% bootstrapped confidence intervals. Letters represent results of post-hoc Tukey HSD test (p < 0.05). Shared letters represent no significant differences, while different letters represent significant differences.

## Community Composition

Beta diversity is shown as similarity  $(1-\beta)$  for greater ease in discerning trends in species assemblages; higher values of 1-beta-diversity show a higher similarity of species assemblages than lower values. Comparing beta diversity using presence/absence data in 2017 reefs, (Figure

12a) dead vs. live reefs and dead vs. restore reefs have the same similarity (1- $\beta$ =0.65), while live versus restore reefs have lower similarity (1- $\beta$ =0.57). In 2018 reefs (Figure 12b), dead vs. live reefs have the highest similarity (1- $\beta$ =0.68). Beta diversity of seine catches from abundance data shows equal similarity between dead and live reef community composition, and dead and restore reefs in 2017 reefs (1- $\beta$ =0.76) with slightly lower similarity between live and restore reefs (1- $\beta$ =0.71; Figure 12c ). 2018 reefs differ from 2017 reefs in seine catch beta diversity with live and restore reefs species composition being more similar (1- $\beta$ =0.73) than dead vs. live, and dead vs. restore reefs (Figure 12d).



Figure 12: Beta similarity (1-B) for seine catches based on presence/absence data (a,b) and abundance data (c,d). 2017 reefs are shown in graphs a and c, and 2018 reefs are shown in figures b and d. Increasing size and depth of color indicate greater similarity between treatment types. Higher values of 1-beta-diversity indicate higher similarity between treatment types than lower values.

Presence/absence data from lift net catches in 2017 reefs (Figure 13a) indicate dead and restore reefs were more similar (1- $\beta$ =0.44) than restore vs. live reefs and dead vs. live reefs (1- $\beta$ =0.41, 0.40). In 2018 reefs (Figure 13b) the same trends continue with dead vs. restore reefs being most similar (1- $\beta$ =0.53), followed by restore vs. live and dead vs. live (1- $\beta$ =0.5.0.45). Using abundance data, 2017 reefs' lift net catches show greatest similarity between restored and live reefs (1- $\beta$ =0.66), and lowest similarity between dead and live reefs (1- $\beta$ =0.58;Figure 13c). In 2018 reefs' abundance data from lift nets suggest greatest similarity between dead and restore reefs (1- $\beta$ =0.67; Figure 13d), and lowest community composition similarity between dead and live reefs.



Figure 13: Beta similarity (1-B) for lift net catches based on presence/absence data (a,b) and abundance data (c,d). 2017 reefs are shown in graphs a and c, and 2018 reefs are shown in figures b and d. Increasing size and depth of color indicate greater similarity between treatment types. Higher values of 1-beta-diversity indicate higher similarity between treatment types than lower values.

Presence\absence beta-diversity from trawl catches in 2017 reefs (Figure 14a) show live vs. restore reefs having the lowest similarity (1- $\beta$ =0.50), and dead vs. restore reefs and dead vs. live reefs having alike similarities (1- $\beta$ =0.58,0.56). In 2018 reefs (Figure 14b), dead vs. restore have the smallest similarity buy a considerable amount (1- $\beta$ =0.25) compare to dead vs. live (1- $\beta$ =0.5), with restore vs. live reefs closer to dead vs. live (1- $\beta$ =0.33). Abundance trawl catch beta-diversity has the greatest similarity between dead and restore in 2017 reefs (1- $\beta$ =0.72), and between dead and live treatment types in 2018 reefs (1- $\beta$ =0.65, Figure 14c). Of note, 2018 reefs' trawl data show very little similarity between dead and restore reefs (1- $\beta$ =0.38; Figure 14d).



Figure 14: Beta similarity (1-B) for trawl catches based on presence/absence data (a,b) and abundance data (c,d). 2017 reefs are shown in graphs a and c, and 2018 reefs are shown in figures b and d. Increasing size and depth of color indicate greater similarity between treatment types. Higher values of 1-beta-diversity indicate higher similarity between treatment types than lower values.

Zeroes in trawl catch data precluded PERMANOVA analyses. For seine and lift net catches, beta dispersion was checked for all combinations of data groupings and there were no significant differences in spread (Table 2). There were no significant differences in presence/absence seine catch data in 2017 reefs. However, in 2018 reefs, dead and live reefs were significantly different (p=0.04). In lift net catches, dead and restore reefs were not significantly different in both restoration sets. In seine-derived abundance data for 2017 reefs, only dead and live reefs were significantly different (p = 0.02). In 2018 reefs, both dead vs. restore and dead vs. live reefs were significantly different (p=0.03,0.02). Restore and live reefs species assemblages were not significantly different. In lift net catches, for 2017 and 2018 reefs separately, dead vs. restore was the only grouping that did not have significant differences in species assemblages.

Table 2: PERMANOVA results table of presence/absence and abundance data. Beta-dispersion tested for each data set for no

	Seine			Lift Net			
	Beta			Beta			
	Dispersion	p-value	Sig.	Dispersion	p-value	Sig.	
Presence/Absence							
2017 Reefs	0.99			0.10			
Dead vs. Restore	-	0.77			0.33		
Dead vs. Live		0.22			<0.01	*	
Restore vs. Live		0.37			<0.01	*	
2018 Reefs	0.64			0.14			
Dead vs. Restore	-	0.04	*		0.40		
Dead vs. Live		0.23			0.01	*	
Restore vs. Live		0.38			<0.01	*	
Abundance							
2017 Reefs	0.99			0.31			
Dead vs. Restore	_	0.65			0.46		
Dead vs. Live		0.02	*		<0.01	*	
Restore vs. Live		0.13			<0.01	*	
2018 Reefs	0.53			0.09			
Dead vs. Restore	_	0.03	*		0.41		
Dead vs. Live		0.02	*		<0.01	*	
Restore vs. Live		0.29			<0.01	*	

significant difference in spread (p>0.05). Significance for paired treatments tested at p<0.05.

Indicator species were determined to examine what species were representative of the various treatment types (Table 3). Seine catches had one indicator species per treatment type: *Chilomycterus schoepfi* (striped burrfish) represented dead reefs, *Citharichthys spilopterus* (bay whiff) represented live reefs, and *Lutjanus synagris* (lane snapper) represented restore reefs. Of these three indicator species, *L. synagris* has the highest trophic level (3.8). Seine catch species' "indval" statistic was dominated by exclusivity to the treatment type. Lift nets found indicator species only at live reefs and consisted of *Gobiosoma bosc (naked goby)*, *Eucinostomus spp*.

(mojarras), *Ctenogobius boleosoma* (darter goby), and *Bairdiella chrysoura* (silver perch). Trawl catches did not have any significant indicator species.

Table 3: Table of indicator species per treatment type for seine and lift net gear types. "IndVal" is the "indicator value" of the species which is based on "A" and "B" statistics. "A" represents exclusivity to a grouping of sites, and "B" represents the proportion of sites the species is found within a treatment type. All species listed are significant (p<0.05).

Species			Seine		Lift Nets			
	Trophic	IndVal	Α	В	IndVal	Α	В	
Dead	_							
Chilomycterus schoepfi	3.5	0.31	1.00	0.10				
Live	-							
Citharichthys spilopterus	3.6	0.38	0.76	0.19				
Gobiosoma bosc	3.2				0.57	0.60	0.54	
Eucinostomus spp.	3				0.47	0.90	0.25	
Ctenogobius boleosoma	3.3				0.39	0.72	0.21	
Bairdiella chrysoura	3.2				0.39	0.70	0.21	
Restore								
Lutjanus synagris	3.8	0.38	0.76	0.19				

There were no significant differences in species' mean trophic level per sampling event across treatment types, however some trends do appear (Figure 15). Across all gear types, restored and live reefs have the highest trophic maxima at 4.4 while dead reef trophic level maximum was 4.2. Dead reefs also possessed the lowest minimum trophic level at 2.5; lower than restored reefs (2.77), and live reefs (2.8). Median trophic level of species across all gear types were similar, 3.36 for dead reefs, 3.33 for restored reefs, and 3.31 for live reefs. Comparing trophic level of the species caught using various gear types, lift net catches had the highest mean trophic level (3.56±0.36), followed by trawl catches (3.40±0.48), and seine catches (3.30±0.24). Lift nets and trawls have higher maxima trophic levels (4.4) than seines (4.0). Seine catches had a lower minimum mean trophic level (2.5) than trawls (2.7) and lift nets (3.04).



Figure 15: Boxplot showing distribution of mean trophic level per treatment for all gear types for combined restoration sets and restoration sets separately. White diamond represents the mean. Error bars are 95% bootstrapped confidence intervals.

# Temporal Analysis of Restoration Effects on Abundance and Diversity

Following restoration there were no significant differences among treatment types in seine catches (Figure 16). Trends show seasonal differences with lower values of diversity indices (except evenness) and abundance six months post restoration (winter months). Prior to restoration, live reefs had higher mean abundance, species richness, and Shannon diversity compared to dead and pre-restoration reefs. In 2018 reefs, restored reefs were more similar to dead reefs pre-restoration. At one week and two months post-restoration, restored reefs' diversity values were equal to or greater than live reefs' values (inverse for evenness). However, at three months post-restoration, restored reefs diversity values fell between those of dead and live reefs.



Figure 16: Mean seine catch fish abundance, species richness, Shannon diversity, Simpson diversity, and Pielou's evenness across selected sampling periods for all treatment types for both the first and second set of restoration. Error bars represent 95% bootstrapped confidence intervals.

Lift net catches on live reefs have the highest diversity metrics in both restoration sets (Figure 17). Restore sites in general have similar to lower values of diversity than dead and live

sites in 2017 reefs, with the exception of the seven-month sampling period, occurring in January, where no organisms were found at dead reefs and there were relatively low catches at live reefs. Significant differences in abundance and diversity metrics are exhibited in lift net catches. However, all significant differences occur only during the pre-restoration sampling events (Figure 17). In 2017 reefs, all metrics except Simpson diversity show significant differences between restore and live reefs; dead reefs have intermediate diversity values. In 2018 reefs' lift net catch abundance, species richness, Shannon diversity and Pielou's evenness are significantly greater at live reefs than dead and/or restore reefs, with dead reef of intermediate significance in abundance.





Cluster analyses were used to visualize species assemblage groupings of treatment type and sampling period. In seine collected samples there were no significant trends in species assemblages. However, 2018 reefs' species assemblage results suggest some differences between restore and live sites before and one month after restoration (Figure 18)



Figure 18: Non-metric multidimensional scaling with seine catch data of selected sampling periods per treatment type for 2017 reefs (a), and 2018 reefs (b). Black ellipses represent best clustering from cluster analysis.

Lift nets also do not show significant differences in species assemblage from cluster analyses (Figure 19). Tests representing clustering based on differences in fish community could not find differences in species assemblage and are presented with one ellipse (Figure 19).





# **Environmental Analyses**

Secchi depth, a proxy for water clarity, best described species richness capture from seines, followed by temperature and all environmental variables combined (Table 9). Shannon diversity, Simpson diversity, and Pielou's evenness were best described by temperature followed by the sum of all environmental variables (Table 9). An environmental fit test on seine catch corroborated the results of AIC model selection. Based on factor loadings, Secchi depth and temperature were found to be the strongest predictors of species assemblage. Secchi depth had a stronger influence on seine catches than temperature. These variables were not correlated but they acted similarly when describing species assemblages. Dissolved oxygen was inversely related to temperature, but its loading was slightly greater than temperature. Salinity only had a minor effect on species assemblage (Figure 20).


Figure 20: Environmental fit plot for seine catches. Blue dots represent species assemblages. Arrows represent environmental variables in regard to species assemblages.

#### Living Shoreline

### Abundance and Diversity

Catch per unit effort, defined as mean abundance per sampling event, did not differ significantly between control and restored living shoreline sites for seine and lift net catches (Figure 21), but gear types means were significantly different (One Way ANOVA:  $F_{2,174}$ =107; p<0.01). Control shoreline had marginally higher mean abundance than restored sites across sampling combinations. Seine had higher CPUE ( $\bar{x}$ =24.62±21.29) than lift nets ( $\bar{x}$ =1.56±1.9). As mentioned in the Methods above, trawl data were not included in this analysis as two-minute trawls span across adjacent treatment types.



Figure 21: Mean abundance per gear type for both restoration sets combined and 2017 and 2018 shorelines separately. Error

bars represent 95% bootstrapped confidence intervals.

There were no significant differences in living shoreline diversity metric values between

treatment types, but restored sites had marginally higher values diversity across the four

diversity metrics (Figure 22). Comparing gear types, seine catches had the highest species

richness, Shannon diversity, Simpson diversity, and lowest Pielou's evenness.



Figure 22: Species richness, Shannon diversity, Simpson diversity and Pielou's evenness for control (navy) and restored (turquoise) shorelines from seine, and lift net catch data in the Mosquito Lagoon, FL. Error bars represent 95% bootstrapped confidence intervals.

## Community Composition

PERMANOVA analysis on both seine and lift net catch data did not produce any

significant differences in presence/absence or abundance species composition (Table 4).

Indicator species testing was conducted; however, no indicator species were identified for living

shoreline sites.

Table 4: PERMANOVA table for living shoreline seine and lift net catches for both restoration sets combined and 2018 and 2018

shorelines separately.

	Sein	е	Lift N	let
	Beta		Beta	
	Dispersion	p-value Sig.	Dispersion	p-value Sig.
Presence/Absence				
2017 Shorelines	0.77		0.34	
Control vs. Restore	-	0.90		0.58
2018 Shorelines	0.23		0.40	
Control vs. Restore	_	0.28		0.44
Abundance				
2017 Shorelines	0.56		0.98	
Control vs. Restore		0.76		0.33
2018 Shorelines	0.18		0.44	
Control vs. Restore	_	0.29		0.46

Analysis of mean trophic levels of species captured in seines and lift nets show the majority of trophic levels ranged between 3.0 and 3.5 (Figure 23). Species captured in lift nets have a larger range in trophic level (2.2) than species captured in seines (0.5).



Figure 23: Boxplot showing distribution of mean trophic level per treatment for seine (a,b,c) and lift net (d,e,f) catches for combined restoration sets (a,b), 2017 shorelines (b,e), and 2018 shorelines (c,f) separately in living shoreline habitat. White diamond represents the mean. Error bars are 95% bootstrapped confidence intervals.

### Temporal Analysis of Restoration Effects on Abundance and Diversity

Following restoration there were no significant differences in seine catches between treatment types. In 2017 shorelines, control shorelines had greater diversity than restored shorelines except at six months post-restoration (winter months). 2018 shorelines' results differ in that there are no restoration control sites for the shorelines restored years prior. All reefs restored more than two years ago had similar diversity, but the three-year post-restoration site had relatively low diversity (Figure 24).





Temporal analysis of the living shoreline lift net catch data show values of diversity at control and restoration sites are similar after one year. However, restored sites have slightly higher values of abundance, species richness, Shannon diversity, and Simpson diversity (Figure 25). Restoration sites that were restored five and seven years ago have lower lift net catch diversity than sites that were restored two and three years ago.





Cluster analyses performed on living shoreline sites from 2017 begin to show changes following restoration, however all sites are a part of all groupings showing a seasonal trend. There were no distinct species assemblages comparing sites restored two, three, five, and seven years ago (Figure 26).



Figure 26: NMDS of living shoreline species assemblages of seine catches between treatment types and sampling periods of 2017 shorelines (a), and past restored 2018 shorelines (b). Ellipses show 95% clusters based on ideal number of clusters.

Cluster analysis on lift net catches produce no clustering between control types in 2017 shorelines or among reefs restored two, three, five, and seven years prior (Figure 27)



Figure 27: NMDS of living shoreline species assemblages of seine catches between treatment types and sampling periods of 2017 shorelines (a), and past restored sites in 2018 shorelines (b). Ellipses show 95% clusters based on ideal number of clusters.

Assessing seine and lift net catch abundance and diversity metrics over annual timescales (one to seven years post restoration), there were no significant differences (Figure 28). However, seine catches show all metrics of diversity (except for evenness) falling from one-year post-restoration until three years and then rising until seven years post-restoration. Lift net data trends are more variable; trends show a decrease in abundance, species richness, and Shannon diversity over time and an increase in Simpson diversity.



Figure 28: Abundance (a,f), species richness (b,g), Shannon diversity (c,h), Simpson diversity (d,i), and Pielou's evenness (e,j) of living shoreline sites 1, 2,3,5, and 7 years post restoration from seine (a-e) and lift net (f-j) catches. Error bars represent 95% bootstrapped confidence intervals. Color darkens as time from restoration increases.

Temperature best describes all metrics of diversity examined: species richness, Shannon diversity, Simpson diversity and Pielou's evenness (Table 10). Temperature was followed by the combination of all environmental variables (Figure 29). These results were supported by the environmental fit test on seine catch data, which suggests temperature and salinity were the most strongly associated environmental variables to species assemblage, followed by dissolved oxygen and Secchi depth (Figure 29).



Figure 29: Environmental fit plot for seine catches. Blue dots represent species assemblages. Arrows represent environmental variable loadings in regard to species assemblages.

#### Discussion

Oyster reefs and coastal wetlands are essential fish habitats and a critical component of the estuarine landscape. However, estuaries and coastal systems are vulnerable to multiple anthropogenic stressors due to their proximity to human development, and as such their abundant natural resources have been degraded over time (Teichert et al. 2016). Restoration is ongoing in many of these systems to mitigate losses or maintain levels of ecological functions and ecosystem services. Examining the effects of habitat restoration throughout all aspects of the ecosystem, including fishes, is critical to assessing benefits to the entire ecosystem (Grabowski et al. 2005; Baggett et al. 2015; Humphries and Peyre 2015; Valesini et al. 2017; Gilby et al. 2018). Fishes can good indicators of estuarine health due to their sensitivity to disturbance and ability to elucidate aspects of how restoration enhances the broader estuarine system (Pérez-Domínguez et al. 2012). This study examined the effect of oyster reef and coastal wetland restoration on abundance, diversity, and species composition of estuarine fish communities. Interpreting significant differences among treatment types in this study reveal how habitat restoration is beginning to impact the fish community. However, at this relatively early stage following restoration, a lack of significant differences among treatment types suggests additional monitoring and further investigations into the potential mechanisms influencing the success of restoration are required. This knowledge can inform the development of management strategies that may better enhance the efficacy of habitat restoration with respect to the fish community.

#### Community Responses to Oyster Restoration

Utilization of several gear types helped to understand how different components of the fish community, resident versus transient fishes, shifted following restoration. Differences in mean abundance of oyster sites occurred only in lift net catches and results to date suggest live reefs differ from both dead and restore reefs. Changes in lift nets indicate reef residents like gobies, are impacted by the characteristics of reef type. The lack of response in abundance of fishes caught in all gear types at restored reefs compared to dead reefs suggests the basic structure created through relatively short-term habitat restoration may not be sufficient to produce the same quality fish habitat as natural reefs; rather a more complex mature reef structure may be needed before benefits are realized by the fish community. Divergence of diversity indices occurred among oyster reef treatment types in both lift net and trawl data. Lift net data indicate live reefs were different in species richness and Shannon diversity from dead and restore reefs. Differences in these empirical metrics specifically indicate live reefs tend to have a greater number of relatively rare species driving diversity, than either dead or restore reefs. Conversely, variance in trawl catch data in both Simpson diversity and Pielou's evenness indicate species composition of dead reefs is intermediate to restore and live reefs. These metrics indicate differences in common higher abundance species in the transient fish community compared to resident fishes caught in lift nets. Diversity trends in trawl catch data are indicative of common schooling fish utilizing restored reefs similarly to dead reefs, but differently than live reefs. These results suggest with additional time and increased habitat complexity, the fish community on restored reefs may begin to accumulate rare species, and with respect to diversity, ultimately resemble more complex live oyster reefs.

Beta-diversity following restoration had confounding results. Values of beta diversity varied depending on temporal scale and gear type. In 2017 reefs, seine data at restored reefs were least similar to live reefs representing positive controls, suggesting restored reefs were utilized by transient fish caught in seines differently than at dead and live reefs, but generally, there were not large differences in values of beta diversity. To complicate data interpretation, 2018 reefs did not generate the same set of results as 2017 reefs. In 2018 reefs, live and restore reefs have more similar species composition, in presence/absence and abundance data. This implies dead reefs have different transient species than restore and live reefs. Lift nets however, which target relatively small and sedentary reef residents, like gobies, tell a different story. Lift net data suggest dead and live reefs have the lowest similarity in both restoration sets for abundance and presence/absence data; restore reefs have an intermediate species composition. In lift net sampling, which captured reef residents, dead and live reef species compositions were distinct, while the species composition of restore reefs were intermediate to the communities found at dead and live reefs. Compared to seines and lift nets, trawls generally capture demersal fishes inhabiting soft-bottom areas adjacent to reefs and relatively mobile fishes moving among patches of hard bottom habitat. Catch data show in 2017 reefs dead and restore species composition are most similar, and restore and live sites least similar. However, in 2018 reefs, dead and restore sites are least similar. Shifts in community composition between the first and second year of restoration and ensuing results could in part be due to annual variability in recruitment driving overall changes in species abundances lagoon wide. For example, in the first summer of sampling, grey snapper (L. griseus) was relatively common and lane snapper (L. synagris) was relatively uncommon, but in the second summer of

our study, this pattern was reversed (Table 7). Inherent variability in recruitment between years can result in different assemblages of species colonizing sites following restoration. If annual variability in the species assemblage varied with respect to treatment types due to temporal variability in colonization and recruitment, this could explain the differences observed comparing 2017 and 2018 reefs, and the ultimate assessment of how habitat restoration influences the fish community.

Mosquito Lagoon oyster reefs are being lost to wave energy and sedimentation caused by recreational boat wakes (Wall et al. 2005). If more live oyster reefs are converted to dead reefs due to anthropogenic stressors, these results predict shifts in the species composition of fish would ensue in the broader study region. Transient fish species compositions are responding to oyster reef restoration partially in 2017 reefs and more fully in 2018 reefs, possibly due to differences in species assemblages or physical arrangement of reef restoration. Species composition of reef residents at restored reefs differ from those at dead reefs, but after two years post-restoration, do not yet resemble those collected at live reefs.

Examining indicator species at oyster reef treatment types informs how specific fish are using the reefs. Dead reefs found in the lagoon are made up of dead shell and have high vertical profiles and low habitat complexity (Wall et al. 2005). Striped burrfish was identified as an indicator species for dead reefs as they high vertical profile of this habitat provides substrate valued by gastropods and crabs in which this species prey upon (Motta et al. 1995). Lane snapper, an indicator species for restored reefs, is a transient reef-associated sportfish. Less mature oyster reefs may provide relatively good habitat in which many prey fish come for structure, however the lower complexity of the habitat (relative to a fully developed live oyster

reef) can also provide good foraging grounds for the snapper (Flynn and Ritz 1999; Coen et al. 2007). Indicator species in seine nets were selected due to their high exclusivity to each treatment type. Several taxa were identified as indicator species for live reefs, many of which are known as oyster reef residents (Tolley and Volety 2005). Compared to transient species, reef resident indicator species appeared more consistently throughout all sites within a treatment type which supports reef residents relying on the more complex live oyster reefs. The higher trophic level indicator species from trawl catches was the bay whiff, a flat fish that inhabits soft sediment bottoms, like those surrounding healthy live oyster reefs (Moles and Norcross 1995; Chambers et al. 2018). Presence of the bay whiff may help to indicate complexity of a reef as the fine sediment accrues with maturity of the reef over time (Chambers et al. 2018). Identifying indicator species for the various treatment types can act as a diagnostic tool for identifying the stage of restoration or reef quality as it proceeds along its developmental trajectory following restoration (Bergquist et al. 2006); more clearly identifying indicator species of restoration success should be possible by comparing putative indicator species with specific oyster reef metrics including abundance and length. As resource managers assess various strategies to benefit multiple species of fish, these findings can help guide the decision-making process by informing if and where habitat restoration should be considered throughout an ecosystem.

Analyzing trophic levels (excluding outliers) indicate the fish community had smaller trophic ranges at live reefs and larger trophic ranges at restored reefs, these results corroborate other studies analyzing trophic range (Rezek et al. 2017). One possibility for this finding is that live reefs are healthy relatively stable habitats, while restored reefs have

undergone a recent substantial disturbance (restoration), and dead reefs are characterized as a reef that no longer functions as a live oyster reef. A large proportion of fishes at live oyster reefs are reef residents that reside entirely on the reef, as compared to dead and restored reefs that tend to support more transient species. Therefore, as fishes forage at live reefs, they tend to consume a relatively narrow range of prey, namely reef residents, as compared to the prey base available at recently restored and dead oyster reefs. Further stable isotopic analyses could provide additional support for these findings, and studies including dead, live, and restored reefs reefs will allow us to better understand the trophic transition of the fish communities utilizing oyster reefs (Abeels et al. 2012; Rezek et al. 2017).

Examining temporal shifts in abundance and diversity allows for a better understanding of the restoration timeline and differences in seasonality that may occur. Restored oyster reefs have lower diversity values than live reefs for both transient and reef resident species, except during winter sampling when all treatments had relatively low diversity. Overall lower abundances of fish is expected during winter months (there is lower overall diversity in winter catches when water temperatures are relatively low, and fishes are not as active), therefore documenting higher abundances at restored than live reefs is interesting (Tremain and Adams 1995). This same unexpected pattern was observed at living shoreline sites, but only for transient species. Characteristics of restored reefs and living shorelines may provide a different type of refugia during relatively cold-water winter months. Seasonal trends in fish species occur (tropical and warm temperate species shift distributions by migrating to more southerly waters), resulting in changes to the relative proportion of more cold-tolerant species in the study region within years (Rooker and Dennis 1991; Barletta et al. 2008). This shift in winter

composition of the fish community may result in there being additional temperate species that find the restored reefs and living shorelines more habitable than other potential habitats in the study region, further skewing the relative abundance of these more cold-tolerant species at restoration sites; an interesting trend to explore in future studies. A priori hypotheses would suggest evidence for success of oyster restoration in regard to the fish community should show dead reefs and live reefs species assemblages cluster separately prior to restoration, with restore reefs initially clustering with dead reefs. However, the species assemblage at restoration sites should shift from the dead reef cluster toward the live reef cluster over time. In this study, due to inherent variability in the data, and overlap in the fish community among sites and treatments, there was not a clear enough separation between dead and live reefs at the onset of the study to make strong conclusions on community-wide shifts following restoration.

Environmental parameters are driving forces of fish diversity across habitats (Cheung et al. 2009; Horta E Costa et al. 2014; Perry et al. 2014; Vergés et al. 2014). Environmental analyses correlating diversity metrics to water parameters indicate temperature, water clarity, and dissolved oxygen best describe fish community composition. Secchi depth, as a proxy for water clarity, is assumed to be driven by oysters filtering water in the lagoon resulting in overall improvement in water quality and clarity near oyster reefs. Greater water clarity, generated by a higher abundance of oysters filtering the water column could influence the fish community by increasing the ability of foraging predators to visually locate prey, or conversely for prey to visually avoid predators, resulting in an overall increase in diversity, especially species richness as shown in this study. At broader scales, changes in oyster reef abundance could have a strong

effect on water quality, clarity, and generally habitat availability (as forage habitat for predators or refugia for prey), ultimately resulting in positive shifts in fish community diversity.

#### Community Responses to Coastal Wetland Restoration

Differential response of oyster reef and living shoreline fish communities may be due to the physical arrangements of the habitat itself (Grabowski et al. 2005; Meynecke et al. 2008). Oyster reefs are patch habitats physically separated from other reefs by an uninhabited softbottom habitat spanning meters to 100s of meters. By comparison, living shoreline restoration sites are long continuous stretches of shorelines with little to no spatial separation among sites, providing a constant corridor along which fish may disperse between control and restoration treatments. Increased habitat connectivity, in combination with the relatively lower number of shoreline specific resident species, may drive the general trend of few significant differences among restoration and control sites. Since restoration sites were always physically connected to control sites in this study, differences among control and restore sites were generally not significant; this also held true when considering the lack of significant differences in species composition between sites.

Salinity was the most important variable in determining species assemblages at living shoreline habitat, and could relate to the critical role of salt-tolerant marsh vegetation in coastal wetlands acting as essential fish habitat. Secchi depth was least important, implying that clarity of the water, as it relates to the absence of oysters, and their role in filtering water was not as influential in the maturation of the wetland vegetation and its impact on species assemblages.

#### Management Lessons

After almost two years of monitoring in the Mosquito Lagoon, the effects of oyster reef and coastal wetland restoration on the fish community were only starting to emerge. A lack of clear response from the fish community suggests monitoring will be necessary to more fully assess responses to restoration, and if over time the diversity and composition of the fish community begins to resemble natural oyster reefs and healthy salt marsh ecosystems. Gittman et al. (2016) saw greater abundances and diversity of fish at restored shorelines when compared to natural and hardened shorelines in Pine Knoll Shores, North Carolina, however these differences did not occur until 3 years post-restoration. It has been shown that adult fishes may utilize the habitat instantly and increasingly in the months after restoration, but trends may be different in juvenile fishes (Davis et al. 2006). In oyster reefs in other systems with comparable fish assemblages in the southeastern United States, it has been shown that the structure created by restoration can be enough to see significant enhancement of the fish community and does not necessarily progress with complexity (Lehnert and Allen 2002; Gregalis et al. 2009; Humphries et al. 2011).

There are several potential explanations to account for why marked quantifiable differences in diversity were not observed over the course of this study. The first is a function of study length; that is, the time series post-restoration may not be sufficient to capture changes in fish community diversity, but with additional monitoring differences may emerge. Another explanation for the relatively slow response of the fish community to restoration could be the habitat surrounding the experimental sites. Studies have shown that habitat types adjacent to reefs is vital in determining how and if fish use a given reef (Grabowski et al. 2005; Geraldi et al.

2009; Baggett et al. 2015). Fish communities respond to restoration of oyster reefs in areas of bare soft-bottom habitat more clearly than restoration of reefs located next to marsh or seagrass habitat, as these are alternative forms of essential fish habitat (Grabowski et al. 2005). Many of the restoration sites in this study were located in close proximity to mangroves, other oyster reefs, and in some instances seagrass beds, all of which are essential fish habitats that may provide three-dimensional structure and complex habitat necessary for various life stages of fishes. This understanding of neighboring habitats when combined with the results of the present study indicates the response of the fish community to restoration may not be as easily discernable in complex mosaics of essential fish habitats as compared to restoration occurring in regions surrounded predominately by bare soft-bottom habitat. Furthermore, functional redundancy can occur when other essential fish habitats are readily available (Gittman et al. 2016). In the Mosquito Lagoon there are large expanses of oyster reef and mangroves that the fish community is able to utilize. These habitats may be functionally redundant in terms of fish habitat use, however they do not necessarily provide the same environmental services as oyster reefs. Results of indicator species analyses suggest certain species have an affinity for particular habitat types, and the greater the number of habitat types available leads to higher alpha diversity within a system. More diverse mosaics of essential fish habitat-types should also lead to greater regional diversity by providing multiple areas inhabited by different assemblages of fish, while simultaneously producing a greater suite of ecosystem services.

Two of the many possible benefits of oyster reef restoration are to improve water quality via oyster filtration and to increase the area of essential fish habitat to benefit the fish community. However, these ecosystem services may be achieved to varying degrees as

restoration can provide asymmetric benefits, with marginal improvements for the fish community and large improvements in water quality. Gaining a better understanding of what characteristics of restoration result in improved ecosystem function and the production of associated ecosystem services will enable resource managers to tailor habitat restoration through an ecosystem-based framework for the needs and desired outcomes of a given region (Gilby et al. 2018).

Living shoreline habitats and controls did not have great differences in fish communities. However, as was mentioned earlier, this may be a result of the close proximity of restoration sites with adjacent controls effectively functioning as one contiguous stretch of shoreline habitat. An additional factor to consider was that shoreline sites restored in this study were not devoid of mangroves. They were degraded when compared to the more densely vegetated control sites, but still contained slopes and patchy vegetation. The habitat present at restoration sites, before or after restoration, still provides more complex essential fish habitat than areas in which shoreline hardening has occurred (Peters et al. 2015). Potential benefits of restoration depends on the habitat being replaced and restored, which can increase difficulty when analyzing overall benefits of coastal wetland restoration (Bilkovic et al. 2016). Results presented in this study are similar to those found in Peters et al. (2015) where higher fish diversity was found at restored rip-rap mangrove sites than natural sites. Future studies exploring the role of fish habitat complexity in relatively degraded coastal wetlands versus natural and hardened shoreline, or hardened shoreline with living shoreline enhancements, in this area would provide insight into the role the spectrum of natural and artificial shoreline

types have on supporting fish populations and help quantify the relative importance of these habitat types on fish community diversity (Toft et al. 2013; Gittman et al. 2016).

Scale of restoration is another factor that may influence the response of the fish community (Grabowski et al. 2005). Live reefs in Mosquito Lagoon are often located in expansive areas surrounded by and in relatively close proximity to other live oyster reefs, as compare to restored reefs which are chosen based on need of restoration, are often patchy, and in areas of high boat traffic that resulted in the initial degradation and destruction of the reef (Wall et al. 2005; Garvis et al. 2015). If large areas of reef, or a network of smaller reefs were to be restored at once, a greater response in larger relatively transient fish may be detected (Grabowski et al. 2005). Each year as reefs are selected for restoration, benefits to the fish community may accrue more rapidly if many reefs in relatively close proximity were to be restored to generate a stronger localized increase in reef habitat as opposed to spreading reefs out across a broader geographic region. In the present study, positive effects occurred in the second set of restoration sites, when three out of four of these restored reefs were relatively close in proximity. This restoration design could have passed an unknown threshold generating a larger local impact. Testing how patchiness and spatial configuration of restoration sites impacts outcomes at the level of the fish community could help increase the efficacy of future restoration designs and strategically guide the application of restoration resources. Additionally, mitigating the predominant factor causing death of reefs, in this case boat wakes, would help restored reefs mature more rapidly (Wall et al. 2005).

Distinct differences existed between restoration outcomes over time. Annual variability in the fish community is a well-known phenomenon but considering these shifts in the fish

community in regard to the spatial and temporal scale of restoration, is an area in need of further investigation. The results of this study suggest that two years of monitoring is not enough time to fully understand the effects of oyster restoration on the fish community, related changes in the biotic and abiotic environment, and the effects these may have on human communities, which in turn have reciprocal impacts on the environment. Increasing the replicates of large-scale oyster restoration and exploring annual differences, as compared with strategically selected control sites, could allow for better understanding of the most opportune times and locations to implement oyster restoration that will achieve the greatest benefits for both the human and natural components of the ecosystem.

There has recently been a call for larger regional-scale studies exploring the role of natural versus restored habitat types to inform, assess, and develop more effective ecosystembased management strategies (Baggett et al. 2015; Gittman et al. 2016). This study is part of a broader project incorporating oyster reef dynamics, hydrology, biogeochemistry, infaunal and macroinvertebrate communities, shorebirds, and their linkages to human communities. Integrating the results of this study with the complementary components of the larger project will allow for a more holistic understanding of the natural and human factors influencing the success of restoration. The next clear collaboration will be to compare fish community dynamics with oyster reef metrics to help reduce the noise in temporal sampling and produce more fine-scale results. Basin-wide manipulations, similar to those being conducted in terrestrial and aquatic environments (e.g. Hubbard Brook Experimental Forest or International Institute for Sustainable Development Experimental Lakes Area), have also been suggested to enable regional-scale experiments and manipulations of coastal estuaries, providing the ability

to develop a more fundamental and mechanistic understanding of restoration on estuarine ecosystem structure and function (Grabowski et al. 2005). Large research projects like these can be logistically daunting, however as oyster restoration programs continue to restore habitat at the local scale, the effects and benefits may begin to accrue at the regional scale. The goal of comparing results from complementary restoration programs across large spatial scales may become a reality, thereby providing novel insight regarding the role of habitat restoration in a changing world. The results of this study build upon the existing body of knowledge in this field and has begun to illustrate the effects of restoring oyster and coastal wetland habitat within a broader estuarine ecosystem. Combining and comparing these results with studies from other coastal communities, restoration types, or ecosystems, can enable us to develop more effective strategies to restore coastal habitats in a manner that will ultimately benefit the broader environment, and the human communities reliant on these natural systems.

## **APPENDIX: CHAPTER 2 SUPPLEMENTARY FIGURES AND TABLES**



Figure 30: NMDS of mean group per year for each basin. This NMDS shows how the basins greatly overlap in similarity and that I can use these data together during analyses. These results differ from those of Adams and Paperno (2012), however this could be due to the extended 21-year dataset used in this study as compared to the four-month dataset used in Adams and Paperno (2012).

Creation	Total	Percent	Creation	Total	Percent	Canalan	Total	Percent
Species	Abundance	Abundance	Species	Abundance	Abundance	Species	Abundance	Abundance
Lucania parva	803,765	24.50%	Anchoa hepsetus	14,064	0.43%	Chloroscombrus chrysurus	838	0.03%
Lagodon rhomboides	444,466	13.55%	Elops saurus	13,177	0.40%	Eugerres plumieri	818	0.02%
Menidia spp.	271,659	8.28%	Strongylura notata	11,891	0.36%	Sardinella aurita	793	0.02%
Eucinostomus spp.	163,762	4.99%	Menticirrhus americanus	8,130	0.25%	Haemulon parra	686	0.02%
Leiostomus xanthurus	147,060	4.48%	Oligoplites saurus	7,072	0.22%	Lutjanus analis	674	0.02%
Mugil cephalus	130,035	3.96%	Centropomus undecimalis	5,962	0.18%	Gymnura micrura	649	0.02%
Bairdiella chrysoura	113,205	3.45%	Pogonias cromis	4,628	0.14%	Strongylura marina	648	0.02%
Diapterus auratus	108,492	3.31%	Caranx hippos	4,300	0.13%	Hyporhamphus meeki	597	0.02%
Floridichthys carpio	105,529	3.22%	Chilomycterus schoepfii	4,076	0.12%	Sarotherodon melanotheron	546	0.02%
Mugil curema	105,275	3.21%	Lutjanus griseus	3,647	0.11%	Lutjanus synagris	541	0.02%
Brevoortia spp.	85,311	2.60%	Gambusia holbrooki	3,002	0.09%	Microgobius thalassinus	483	0.01%
Microgobius gulosus	84,075	2.56%	Fundulus grandis	2,882	0.09%	Hippocampus erectus	442	0.01%
Eucinostomus harengulus	64,683	1.97%	Anchoa lyolepis	2,851	0.09%	Opsanus tau	436	0.01%
Harengula jaguana	60,621	1.85%	Chasmodes saburrae	2,844	0.09%	Hippocampus zosterae	421	0.01%
Eucinostomus gula	44,265	1.35%	Dasyatis say	2,520	0.08%	Gerres cinereus	416	0.01%
Gobiosoma robustum	43,784	1.33%	Achirus lineatus	2,462	0.08%	Synodus foetens	403	0.01%
Orthopristis chrysoptera	43,632	1.33%	Ctenogobius boleosoma	2,407	0.07%	Prionotus scitulus	402	0.01%
Ariopsis felis	40,920	1.25%	Selene vomer	2,369	0.07%	Strongylura timucu	381	0.01%
Micropogonias undulatus	38,164	1.16%	Trachinotus falcatus	2,323	0.07%	Fundulus similis	377	0.01%
Cyprinodon variegatus	37,101	1.13%	Chaetodipterus faber	2,300	0.07%	Stephanolepis hispidus	373	0.01%
Poecilia latipinna	24,222	0.74%	Cynoscion complex	2,272	0.07%	Albula vulpes	371	0.01%
Opisthonema oglinum	23,296	0.71%	Sphoeroides testudineus	2,248	0.07%	Mugil spp.	364	0.01%
Membras martinica	22,076	0.67%	Anchoa cubana	1,714	0.05%	Trachinotus carolinus	341	0.01%
Archosargus probatocephalus	21,959	0.67%	Anchoa spp.	1,682	0.05%	Bagre marinus	332	0.01%
Sciaenops ocellatus	20,709	0.63%	Syngnathus Iouisianae	1,479	0.05%	Gobiosoma bosc	308	0.01%
Gobiosoma spp.	20,687	0.63%	Citharichthys spilopterus	1,289	0.04%	Strongylura spp.	285	0.01%
Sphoeroides nephelus	19,782	0.60%	Archosargus rhomboidalis	1,251	0.04%	Eucinostomus argenteus	262	0.01%
Syngnathus scovelli	19,753	0.60%	Eucinostomus jonesii	1,091	0.03%	Sphoeroides spengleri	244	0.01%
Dasyatis sabina	18,897	0.58%	Paralichthys albigutta	923	0.03%	Caranx latus	236	0.01%
Cynoscion nebulosus	17,474	0.53%	Sphyraena barracuda	846	0.03%	Prionotus tribulus	220	0.01%

Table 5: Total abundance and percent abundance of all species used in analysis (A. mitchilli excluded, n=4,321,396).

Emocios	Total Percent		Enocios	Total	Percent	Emosion	Total	Percent
Species	Abundance	Abundance	Species	Abundance	Abundance	Species	Abundance	Abundance
Gobionellus oceanicus	211	0.01%	Anchoa lamprotaenia	37	0.00%	Caranx crysos	10	0.00%
Clupeidae spp.	202	0.01%	Acanthostracion quadricornis	36	0.00%	Labrisomus nuchipinnis	9	0.00%
Diapterus spp.	196	0.01%	Sphyrna tiburo	36	0.00%	Lepisosteus platyrhincus	9	0.00%
Mugil rubrioculus	189	0.01%	Myrophis punctatus	33	0.00%	Agonostomus monticola	8	0.00%
Oreochromis/Sarotherodon spp.	177	0.01%	Aluterus schoepfii	32	0.00%	Citharichthys macrops	8	0.00%
Scomberomorus maculatus	166	0.01%	Eucinostomus lefroyi	32	0.00%	Lachnolaimus maximus	8	0.00%
Microgobius microlepis	155	0.00%	Calamus arctifrons	31	0.00%	Sphoeroides spp.	8	0.00%
Hyporhamphus unifasciatus	153	0.00%	Scomberomorus regalis	30	0.00%	Aetobatus narinari	7	0.00%
Pomatomus saltatrix	141	0.00%	Eucinostomus melanopterus	27	0.00%	Chasmodes bosquianus	7	0.00%
Hyporhamphus spp.	132	0.00%	Etropus crossotus	24	0.00%	Echeneis naucrates	7	0.00%
Symphurus plagiusa	132	0.00%	Elops smithi	22	0.00%	Lophogobius cyprinoides	7	0.00%
Mycteroperca microlepis	124	0.00%	Lobotes surinamensis	22	0.00%	Carcharhinus leucas	6	0.00%
Diplodus holbrookii	121	0.00%	Monacanthus ciliatus	21	0.00%	Epinephelus itajara	6	0.00%
Paralichthys lethostigma	115	0.00%	Sparisoma radians	21	0.00%	Gobionellus spp.	6	0.00%
Gobiesox strumosus	99	0.00%	Tylosurus crocodilus	21	0.00%	Lepomis macrochirus	6	0.00%
Gerreidae spp.	95	0.00%	Ctenogobius shufeldti	20	0.00%	Mycteroperca bonaci	6	0.00%
Ctenogobius smaragdus	84	0.00%	Halichoeres radiatus	20	0.00%	Sphyraena guachancho	6	0.00%
Corvula sanctaeluciae	83	0.00%	Anisotremus virginicus	19	0.00%	Centropristis striata	5	0.00%
Megalops atlanticus	78	0.00%	Scorpaena grandicornis	19	0.00%	Ctenogobius stigmaturus	5	0.00%
Bathygobius soporator	73	0.00%	Ocyurus chrysurus	18	0.00%	Halichoeres spp.	5	0.00%
Trinectes maculatus	72	0.00%	Dorosoma petenense	13	0.00%	Lutjanus jocu	5	0.00%
Archosargus spp.	68	0.00%	Dormitator maculatus	12	0.00%	Scorpaena brasiliensis	5	0.00%
Rhinoptera bonasus	67	0.00%	Mugil trichodon	12	0.00%	Anisotremus surinamensis	4	0.00%
Evorthodus lyricus	66	0.00%	Sphyraena borealis	12	0.00%	Bathygobius spp.	4	0.00%
Jordanella floridae	64	0.00%	Diapterus rhombeus	11	0.00%	Caranx spp.	4	0.00%
Fundulus majalis	61	0.00%	Elops spp.	11	0.00%	Centropomus spp.	4	0.00%
Nicholsina usta	56	0.00%	Haemulon sciurus	11	0.00%	Cichlasoma urophthalmus	4	0.00%
Dorosoma cepedianum	54	0.00%	Ostraciidae spp.	11	0.00%	Ctenogobius spp.	4	0.00%
Lactophrys trigonus	54	0.00%	Sciaenidae spp.	11	0.00%	Echeneis neucratoides	4	0.00%
Haemulon plumierii	49	0.00%	Scorpaena plumieri	11	0.00%	Engraulidae spp.	4	0.00%

Canadian	Total	Percent	Creation	Total	Percent	Charles	Total	Percent
Species	Abundance	Abundance	Species	Abundance	Abundance	Species	Abundance	Abundance
Gobiomorus dormitor	4	0.00%	Microgobius spp.	2	0.00%	Hoplosternum littorale	1	0.00%
Lutjanus apodus	4	0.00%	Micropterus salmoides	2	0.00%	Hypleurochilus geminatus	1	0.00%
Lutjanus spp.	4	0.00%	Opistognathus robinsi	2	0.00%	Kyphosus incisor	1	0.00%
Menticirrhus saxatilis	4	0.00%	Scomberomorus spp.	2	0.00%	Labridae spp. (parrotfishes)	1	0.00%
Selar crumenophthalmus	4	0.00%	Stephanolepis setifer	2	0.00%	Lupinoblennius nicholsi	1	0.00%
Abudefduf saxatilis	3	0.00%	Syngnathus spp.	2	0.00%	Lutjanidae spp.	1	0.00%
Calamus penna	3	0.00%	Acanthostracion spp.	1	0.00%	Lutjanus cyanopterus	1	0.00%
Calamus spp.	3	0.00%	Acanthurus chirurgus	1	0.00%	Microphis brachyurus	1	0.00%
Centropomus parallelus	3	0.00%	Aluterus monoceros	1	0.00%	Monacanthus spp.	1	0.00%
Fundulus confluentus	3	0.00%	Ancylopsetta quadrocellata	1	0.00%	Mycteroperca spp.	1	0.00%
Fundulus seminolis	3	0.00%	Atherinidae spp.	1	0.00%	Myliobatis freminvillii	1	0.00%
Histrio histrio	3	0.00%	Bairdiella spp.	1	0.00%	Negaprion brevirostris	1	0.00%
Lactophrys triqueter	3	0.00%	Balistes spp.	1	0.00%	Oreochromis spp.	1	0.00%
Menticirrhus littoralis	3	0.00%	Bothus robinsi	1	0.00%	Paraclinus fasciatus	1	0.00%
Prionotus spp.	3	0.00%	Canthidermis maculata	1	0.00%	Paraclinus marmoratus	1	0.00%
Pseudupeneus maculatus	3	0.00%	Carcharhinus brevipinna	1	0.00%	Paralichthys spp.	1	0.00%
Sparisoma rubripinne	3	0.00%	Centropristis spp.	1	0.00%	Prionotus rubio	1	0.00%
Anguilla rostrata	2	0.00%	Chriodorus atherinoides	1	0.00%	Pterygoplichthys spp.	1	0.00%
Astroscopus y-graecum	2	0.00%	Citharichthys spp.	1	0.00%	Rachycentron canadum	1	0.00%
Caranx bartholomaei	2	0.00%	Coryphaena hippurus	1	0.00%	Scomberomorus cavalla	1	0.00%
Centropomus pectinatus	2	0.00%	Cynoscion nothus	1	0.00%	Selene setapinnis	1	0.00%
Chilomycterus spp.	2	0.00%	Dasyatis americana	1	0.00%	Seriola fasciata	1	0.00%
Cichlidae spp.	2	0.00%	Dasyatis spp.	1	0.00%	Seriola rivoliana	1	0.00%
Ctenogobius stigmaticus	2	0.00%	Dorosoma spp.	1	0.00%	Sparidae spp.	1	0.00%
Fundulus spp.	2	0.00%	Engraulis eurystole	1	0.00%	Syngnathus fuscus	1	0.00%
Gobiosoma ginsburgi	2	0.00%	Epinephelus morio	1	0.00%	Tetraodontidae spp.	1	0.00%
Haemulon aurolineatum	2	0.00%	Fundulus chrysotus	1	0.00%	Trichiurus lepturus	1	0.00%
Haemulon spp.	2	0.00%	Gobiidae spp.	1	0.00%	Tylosurus acus	1	0.00%
Kyphosus saltatrix	2	0.00%	Haemulon flavolineatum	1	0.00%	Tylosurus spp.	1	0.00%
Lactophrys spp.	2	0.00%	Harengula humeralis	1	0.00%	Urophycis floridana	1	0.00%

# Table 6: AIC table of environmental variables for response variables of species richness, Shannon diversity, Simpson diversity, and Pielou's evenness. AIC $_{o}$ delta AIC $_{o}$ , degrees offreedom and the weight of the AIC $_{c}$ score are presented.

Variables								Small Se	eine Data							
	Species Richness				Shannon Diversity				Simpson Diversity			Pielou's Evenness				
	AIC	ΔAIC,	df	AIC, Weight	AIC,	ΔAIC <sub>c</sub>	df	AIC, Weight	AIC	ΔAIC,	df	AIC, Weight	AIC	ΔAIC <sub>c</sub>	df	AIC, Weight
Temperature	27735.5	5.8	3	0.051	8538.8	5.6	3	0.057	-3915.3	0	3	0.56	-11203.1	2.9	3	0.19
Salinity	28060.8	331.2	3	<0.001	8834.5	301.3	3	<0.001	-3741.5	173.7	3	<0.001	-11076.8	129.2	3	< 0.001
DO	27994.7	265.1	3	< 0.001	8763.7	230.5	3	< 0.001	-3784.9	130.4	3	<0.001	-11102.8	103.2	3	< 0.001
pH	28071.5	341.8	3	<0.001	8844.2	311	з	<0.001	-3737.7	177.5	з	<0.001	-11066.2	139.8	3	< 0.001
Conductivity	28052.9	323.3	3	<0.001	8824.7	291.5	з	<0.001	-3747.5	167.8	з	<0.001	-11079.8	126.2	з	< 0.001
Month	27921.9	192.2	3	< 0.001	8729.3	196.1	3	<0.001	-3782.5	132.7	3	<0.001	-11154	52	3	< 0.001
Year	28033.5	303.9	3	<0.001	8803.1	269.9	3	<0.001	-3768.8	146.4	3	<0.001	-11089	117	3	< 0.001
Group	28051.5	321.9	3	<0.001	8838.7	305.6	3	<0.001	-3737.8	177.5	3	<0.001	-11071.3	134.7	3	< 0.001
Year+Month	27888.3	158.7	4	< 0.001	8690.9	157.7	4	<0.001	-3811	104.3	4	<0.001	-11174.2	31.8	4	< 0.001
Temperature+Salinity+DO+pH	27729.6	0	6	0.949	8533.2	0	6	0.943	-3914.8	0.5	6	0.44	-11206	0	6	0.81

		Large Seine Data														
	Species Richness				Sha Dive	nnon ersity	47% 	Simpson Diversity				Pielou's Evenness				
	AIC,	ΔAIC <sub>c</sub>	df	AIC, Weight	AIC	DAIC,	df	AIC, Weight	AIC	AAIC,	df	AIC, Weight	AIC,	ΔAIC <sub>c</sub>	df	AIC, Weight
Temperature	20012.5	62.1	3	< 0.001	4630.7	56.6	3	<0.001	-6701.7	39.8	3	<0.001	-9148.7	54.8	3	< 0.001
Salinity	20327.6	377.2	3	< 0.001	5007.5	433.3	3	<0.001	-6431.4	310.1	3	<0.001	-8811.9	391.5	3	< 0.001
DO	20280.5	330.1	3	< 0.001	4926.1	352	3	<0.001	-6511	230.5	3	<0.001	-8861.5	341.9	3	< 0.001
pH	20392.7	442.3	3	< 0.001	5055.6	481.5	3	< 0.001	-6416.8	324.7	3	<0.001	-8752.3	451.1	3	< 0.001
Conductivity	20295.9	345.5	3	< 0.001	4973.9	399.7	3	< 0.001	-6452.3	289.2	3	<0.001	-8846.8	356.6	3	< 0.001
Month	20197.4	247	3	<0.001	4865	290.9	3	<0.001	-6521.3	220.2	з	<0.001	-8962.9	240.5	3	< 0.001
Year	20295.7	345.3	3	<0.001	4968.2	394.1	з	<0.001	-6451.8	289.8	3	<0.001	-8848.7	354.7	3	< 0.001
Group	20266.1	315.7	3	< 0.001	4972.4	398.3	3	<0.001	-6438.2	303.3	3	<0.001	-8824.5	378.9	3	< 0.001
Year+Month	20088.1	137.7	4	< 0.001	4759.7	185.6	4	<0.001	-6572.9	168.6	4	<0.001	-9074.7	128.8	4	< 0.001
Temperature+Salinity+DO+pH	19950.4	0	6	1	4574.1	0	6	1	-6741.5	0	6	1	-9203.4	0	6	1

# **APPENDIX: CHAPTER 3 SUPPLEMENTARY TABLES**

# Table 7: Species abundance and percent total abundance per gear type and overall catch (Anchoa species complex excluded, n=70,703).

	Sei	ne Catch	Lift	Net Catch	Tra	wl Catch	То	Total Catch		
Species List	Count	% of Gear Total	Count	% of Gear Total	Count	% of Gear Total	Count	% of Overall Total		
Eucinostomus spp.	12341	25.24%	43	0.09%	261	0.53%	12645	25.86%		
Menidia spp.	6334	12.95%		0.00%	25	0.05%	6359	13.00%		
Bairdiella chrysoura	4403	9.00%	56	0.11%	174	0.36%	4633	9.47%		
Diapterus auratus	4280	8.75%	7	0.01%	138	0.28%	4425	9.05%		
Lucania parva	2389	4.89%	15	0.03%	171	0.35%	2575	5.27%		
Eucinostomus harengulus	2245	4.59%		0.00%	117	0.24%	2362	4.83%		
Lagodon rhomboides	2113	4.32%	29	0.06%	143	0.29%	2285	4.67%		
Harengula jaguana	1385	2.83%		0.00%	746	1.53%	2131	4.36%		
Microgobius gulosus	1806	3.69%	40	0.08%	3	0.01%	1849	3.78%		
Eucinostomus gula	1532	3.13%	2	0.00%	55	0.11%	1589	3.25%		
Gobiosoma spp.	555	1.13%	646	1.32%	15	0.03%	1216	2.49%		
Clupeidae spp.	849	1.74%		0.00%	13	0.03%	862	1.76%		
Cynoscion nebulosus	849	1.74%	1	0.00%	1	0.00%	851	1.74%		
Orthopristis chrysoptera	556	1.14%	13	0.03%	157	0.32%	726	1.48%		
Leiostomus xanthurus	600	1.23%		0.00%	102	0.21%	702	1.44%		
Gobiosoma robostum	52	0.11%	343	0.70%	31	0.06%	426	0.87%		
Lutjanus griseus	230	0.47%	146	0.30%	8	0.02%	384	0.79%		
Micropogonias undulatus	180	0.37%		0.00%	126	0.26%	306	0.63%		
Strongylura notata	295	0.60%	1	0.00%		0.00%	296	0.61%		
Mugil curema	199	0.41%	10	0.02%		0.00%	209	0.43%		
Oligoplites saurus	172	0.35%		0.00%	2	0.00%	174	0.36%		
Elops saurus	151	0.31%		0.00%	19	0.04%	170	0.35%		
Gobiosoma bosc	23	0.05%	138	0.28%		0.00%	161	0.33%		
Archosargus probatocephalus	94	0.19%	33	0.07%	12	0.02%	139	0.28%		
Ctenogobius boleosoma	36	0.07%	103	0.21%		0.00%	139	0.28%		
Syngnathus scovelli	60	0.12%	4	0.01%	61	0.12%	125	0.26%		
Brevoortia spp.	107	0.22%		0.00%		0.00%	107	0.22%		
Membras martinica	92	0.19%		0.00%	5	0.01%	97	0.20%		
Citharichthys spilopterus	76	0.16%		0.00%	2	0.00%	78	0.16%		
Lutjanus synagris	67	0.14%	2	0.00%	2	0.00%	71	0.15%		
Floridichthys carpio	67	0.14%	1	0.00%		0.00%	68	0.14%		
Mugil cephalus	65	0.13%		0.00%		0.00%	65	0.13%		
Opisthonema oglinum	51	0.10%		0.00%	12	0.02%	63	0.13%		
Gobiesox strumosus		0.00%	56	0.11%		0.00%	56	0.11%		
Strongylura marina	53	0.11%		0.00%		0.00%	53	0.11%		
Chasmodes saburrae	1	0.00%	47	0.10%		0.00%	48	0.10%		

Os sailis Intininas	2	0.010/	40	0.00%		0.00%	40	0.000/
Poecilla latipinna Preslichthus elleieutte	3	0.01%	43	0.09%	7	0.00%	46	0.09%
Paralichtnys albigutta	21	0.04%	2	0.00%	7	0.01%	30	0.06%
Achirus lineatus	27	0.06%	10	0.00%	Z	0.00%	29	0.06%
Fundulus granais	15	0.03%	13	0.03%	4	0.00%	28	0.06%
Lutjanus spp.	27	0.06%	-	0.00%	1	0.00%	28	0.06%
Cyprinodon variegatus	20	0.04%	5	0.01%	4	0.00%	25	0.05%
Synodus foetens	23	0.05%		0.00%	1	0.00%	24	0.05%
Syngnathus Iouisianae	14	0.03%	1	0.00%	8	0.02%	23	0.05%
Opsanus tau	4	0.01%	18	0.04%		0.00%	22	0.04%
Bathygobius soporator		0.00%	21	0.04%		0.00%	21	0.04%
Centropomus undecilmalis	19	0.04%	4.0	0.00%		0.00%	19	0.04%
Fundulus majalis	3	0.01%	12	0.02%		0.00%	15	0.03%
Eucinostomus jonesii	11	0.02%		0.00%	_	0.00%	11	0.02%
Sphoeroides nephalus	9	0.02%		0.00%	2	0.00%	11	0.02%
Ariopsis felis	7	0.01%		0.00%	3	0.01%	10	0.02%
Dasyatis sabina	10	0.02%		0.00%		0.00%	10	0.02%
Symphurus plagiusa	10	0.02%		0.00%		0.00%	10	0.02%
Gambusia holbrooki	1	0.00%	8	0.02%		0.00%	9	0.02%
Trachinotus falcatus	9	0.02%		0.00%		0.00%	9	0.02%
Chilomycterus schoepfi	7	0.01%		0.00%		0.00%	7	0.01%
Pogonias cromis	6	0.01%		0.00%	1	0.00%	7	0.01%
Prionotus tribulus	4	0.01%		0.00%	3	0.01%	7	0.01%
Chaetodipterus faber	1	0.00%		0.00%	4	0.01%	5	0.01%
Fundulus spp.	2	0.00%		0.00%	3	0.01%	5	0.01%
Microgobius thalassinus	5	0.01%		0.00%		0.00%	5	0.01%
Myrophis punctatus	1	0.00%	3	0.01%		0.00%	4	0.01%
Sciaenops ocellatus	2	0.00%		0.00%	2	0.00%	4	0.01%
Stephanolepis hispidus	2	0.00%		0.00%	2	0.00%	4	0.01%
Chlorscombrus chrysurus	3	0.01%		0.00%		0.00%	3	0.01%
Cynoscion arenarius		0.00%		0.00%	3	0.01%	3	0.01%
Scomberomorus cavalla	3	0.01%		0.00%		0.00%	3	0.01%
Syngnathidae spp.	2	0.00%		0.00%	1	0.00%	3	0.01%
Albula vulpes	2	0.00%		0.00%		0.00%	2	0.00%
Caranx latus	2	0.00%		0.00%		0.00%	2	0.00%
Selene vomer	2	0.00%		0.00%		0.00%	2	0.00%
Sphyraena barracuda	2	0.00%		0.00%		0.00%	2	0.00%
Ancylopsetta ommata		0.00%		0.00%	1	0.00%	1	0.00%
Carangidae spp.	1	0.00%		0.00%		0.00%	1	0.00%
Caranx hippos	1	0.00%		0.00%		0.00%	1	0.00%
Ctenogobius smaragdus		0.00%		0.00%	1	0.00%	1	0.00%
Dasyatis say	1	0.00%		0.00%		0.00%	1	0.00%
Haemulon spp.	1	0.00%		0.00%		0.00%	1	0.00%
Megalops atlanticus	1	0.00%		0.00%		0.00%	1	0.00%
Acanthostracion quadricornis	1	0.00%		0.00%		0.00%	1	0.00%
Scianediae spp.	1	0.00%		0.00%		0.00%	1	0.00%
Strongylura timucu	1	0.00%		0.00%		0.00%	1	0.00%
Grand Total	44595	91.19%	1862	3.81%	2446	5.00%	48903	100.00%

Table 8: Species abundance list per habitat and treatment type (Anchoa species complex excluded, n=70,703).

		Living Shoreline					
Species List	Control	Restore	Totals	Dead	Restore	Live	Totals
Acanthostracion quadricornis				1			1
Achirus lineatus	13	12	25	3		1	4
Albula vulpes						1	1
Ancylopsetta ommata					1		1
Archosargus probatocephalus	39	39	78	10	12	38	60
Ariopsis felis	2	2	4			4	4
Bairdiella chrysoura	2415	1863	4278	125	53	177	355
Bathygobius soporator				13	1	5	19
Brevoortia spp.	46	59	105	2			2
Carangidae spp.					1		1
Caranx hippos						1	1
Caranx latus	1		1			1	1
Centropomus undecilmalis	4	11	15	1	2	1	4
Chaetodipterus faber	3		3		1	1	2
Chasmodes saburrae	15	26	41	3	2	2	7
Chilomycterus schoepfi	1	1	2	5			5
Chlorscombrus chrysurus					1	2	3
Citharichthys spilopterus	23	10	33	3	1	41	45
Clupeidae spp.	83	247	330	102	174	160	436
Ctenogobius boleosoma				2	19	118	139
Ctenogobius smaragdus						1	1
Cynoscion arenarius		2	2	1			1
Cynoscion nebulosus	541	293	834		15	2	17
Cyprinodon variegatus	15	10	25				
Dasyatis say						1	1
Dasyatis sabina	3	3	6	1	1	2	4
Diapterus auratus	1065	1752	2817	292	323	956	1571
Elops saurus	22	20	42	20	54	22	96
Eucinostomus gula	29	67	96	357	512	575	1444
Eucinostomus harengulus	103	170	273	705	609	659	1973
Eucinostomus jonesii				5	6		11
Eucinostomus spp.	1036	1228	2264	1829	2256	4096	8181
Floridichthys carpio	22	45	67	1			1
Fundulus grandis	6	11	17	3	2	6	11
Fundulus majalis	1	10	11	3		1	4
Fundulus spp.	2	2	4		1		1
Gamhusia holbrooki	2	5	7		1	1	2
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Gobiesox strumosus	1	52	53	2	-	1	3
Gobiosoma bosc	43	45	88	9	7	53	69
Gobiosoma robostum	156	116	272	35	10	108	153
Gobiosoma spp.	454	498	952	56	50	149	255
Haemulon spp.		1	1				
Harengula jaguana	60	376	436	772	752	160	1684
Lagodon rhomboides	225	181	406	465	300	1090	1855
Leiostomus xanthurus	142	108	250	178	47	215	440
Lucania parva	1007	1030	2037	27		510	537
Lutjanus griseus	43	91	134	52	109	80	241
Lutjanus spp.	12	15	27				
Lutjanus synagris				6	51	14	71
Megalops atlanticus				1			1
Membras martinica	22	75	97				
Menidia spp.	1745	3462	5207	771	65	307	1143
Microgobius gulosus	1041	623	1664	24	66	94	184
Microgobius thalassinus	4	1	5				
Micropogonias undulatus	30	68	98	22	48	137	207
Mugil cephalus	16	36	52	2	4	6	12
Mugil curema	54	76	130	22	21	28	71
Myrophis punctatus					1	2	3
Oligoplites saurus	26	113	139	9	17	7	33
Opisthonema oglinum				15	13	35	63
Opsanus tau	1	6	7	1	6	6	13
Orthopristis chrysoptera	68	89	157	280	38	238	556
Paralichthys albigutta	3	2	5	8	7	10	25
Poecilia latipinna	5	41	46				
Pogonias cromis	2	4	6		1		1
Prionotus tribulus	5	1	6		1		1
Sciaenops ocellatus	1		1	1	2		3
Scianediae spp.		1	1				
Scomberomorus cavalla				2	1		3
Selene vomer				1		1	2
Sphoeroides nephalus	3	2	5	3	2	1	6
Sphyraena barracuda	1		1		1		1
Stephanolepis hispidus			0.5	1	2	1	4
Strongylura marina	4	31	35	4	8	6	18
Strongylura notata	104	150	254	12	11	19	42
Strongylura timucu		1	1			2	2
Symphurus plagiusa	4	3	2			3	3
synynauniaae spp.	2 10	c	۲ 10	2	1	1	Ţ
Syngnathus iouisianae	12	0 21	00 20	2	L C	1 26	4 25
Synghuchus SCOVEIII	29	51	90 6	6	3	20	35 19
Trachinotus folcatus	T	د م	٥	Ø	Э	3	Δ
Grand Total	10010	9 12727	ש זעונעב	6202	5702	10197	22171
	10040	1972/	24000	0202	5702	10191	221/1

 Table 9: AIC table of environmental variables for response variables of species richness, Shannon diversity, Simpson diversity, and Pielou's evenness for oyster sites. AIC<sub>c</sub>, delta

 AIC<sub>c</sub>, degrees of freedom and the weight of the AIC<sub>c</sub> score are presented.

Variables	Species				Sha	on		Sim	pso	on	Pielou's					
	AIC <sub>c</sub>	$\Delta AIC_{c}$	df A	IC <sub>c</sub> Weight	AIC <sub>c</sub>	ΔAIC	df	AIC <sub>c</sub> Weight	AIC <sub>c</sub>	$\Delta AIC_{c}$	df	$AIC_{c}Weight$	AIC <sub>c</sub>	∆AIC <sub>c</sub>	df A	AIC <sub>c</sub> Weight
Temperature	925.00	0.00	3	0.40	240.10	0.00	3	0.56	-275.30	0.00	3	0.59	-600.80	0.00	3	0.71
Salinity	931.90	6.90	3	0.01	251.10	11.00	3	<0.01	-265.20	10.10	3	0.00	-595.30	5.50	3	0.05
DO	932.40	7.40	3	0.01	251.40	11.40	3	<0.01	-265.20	10.20	3	0.00	-593.30	7.50	3	0.02
Secchi	925.50	0.50	3	0.31	243.70	3.60	3	0.09	-272.20	3.20	3	0.12	-596.20	4.60	3	0.07
Temperature+Salinity+DO+Secchi	925.80	0.70	6	0.27	241.10	1.00	6	0.34	-276.80	1.50	6	0.28	-597.80	3.00	6	0.16

 Table 10: AIC table of environmental variables for response variables of species richness, Shannon diversity, Simpson diversity, and Pielou's evenness for living shoreline sites. AIC<sub>c</sub>, degrees of freedom and the weight of the AIC<sub>c</sub> score are presented.

Variables	Species				Sha	on		Sim	pso	n	Pielou's					
	AIC <sub>c</sub>	∆AIC <sub>c</sub>	df A	AIC <sub>c</sub> Weight	AIC <sub>c</sub>	$\Delta AIC_{c}$	df	$AIC_{c}Weight$	AIC <sub>c</sub>	$\Delta AIC_{c}$	df	$AIC_{c}Weight$	AIC <sub>c</sub>	∆AIC <sub>c</sub>	df	AIC <sub>c</sub> Weight
Temperature	353.50	0.00	3	0.92	28.50	0.00	3	0.87	-252.50	0.00	3	0.84	-245.90	0.00	3	0.75
Salinity	369.50	16.00	3	<0.001	42.80	14.30	3	<0.001	-240.90	11.60	3	0.00	-231.60	14.30	3	<0.001
DO	373.60	20.10	3	<0.001	45.80	45.80	3	<0.001	-239.70	12.80	3	0.00	-227.10	18.80	3	<0.001
Secchi	370.30	16.90	3	<0.001	42.40	13.90	3	<0.001	-242.40	10.10	3	0.01	-232.70	13.10	3	0.00
Temperature+Salinity+DO+Secchi	358.30	4.80	6	0.08	32.30	3.80	6	0.13	-249.00	3.50	6	0.15	-243.70	2.20	6	0.25

## REFERENCES

- Abeels, H. A., A. N. Loh, and A. K. Volety. 2012. Trophic transfer and habitat use of oyster Crassostrea virginica reefs in southwest Florida , identified by stable isotope analysis 462:125–142.
- Adams, D. H., and R. Paperno. 2012. Stable isotopes and mercury in a model estuarine fish: Multibasin comparisons with water quality, community structure, and available prey base. Science of the Total Environment 414:445–455. Elsevier B.V.
- Alahuhta, J., S. Kosten, M. Akasaka, D. Auderset, M. M. Azzella, R. Bolpagni, C. P. Bove, P. A. Chambers, E. Chappuis, and J. Clayton. 2017. Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude. Journal of Biogeography 44(8):1758–1769. Wiley Online Library.
- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders,
  H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G.
  Swenson. 2011. Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. Ecology Letters 14(1):19–28.
- Baggett, L. P., S. P. Powers, R. D. Brumbaugh, L. D. Coen, B. M. Deangelis, J. K. Greene, B. T.
  Hancock, S. M. Morlock, B. L. Allen, D. L. Breitburg, D. Bushek, J. H. Grabowski, R. E. Grizzle,
  E. D. Grosholz, M. K. La Peyre, M. W. Luckenbach, K. A. Mcgraw, M. F. Piehler, S. R.
  Westby, and P. S. E. zu Ermgassen. 2015. Guidelines for evaluating performance of oyster
  habitat restoration. Restoration Ecology 23(6):737–745.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid.
  2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9(10):1146–1156.
- Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Kock, and A. Stier. 2011. The value of estuarine and coastal ecosystem services. Ecological Monographs 81(2):169–193.

- Barletta, M., C. S. Amaral, M. F. M. Correa, F. Guebert, D. V. Dantas, L. Lorenzi, and U. Saint-Paul. 2008. Factors affecting seasonal variations in demersal fish assemblages at an ecocline in a tropical – subtropical estuary. Journal of Fish Biology 73:1314–1336.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity:134– 143.
- Baselga, A. 2013. Separating the two components of abundance-based dissimilarity : balanced changes in abundance vs . abundance gradients. Methods in Ecology and Evolution 4:552–557.
- Baselga, A., and C. D. L. Orme. 2012. Betapart: An R package for the study of beta diversity. Methods in Ecology and Evolution 3(5):808–812.
- Beck, M. W., R. D. Brumbaugh, L. Airoldi, A. Carranza, L. D. Coen, C. Crawford, O. Defeo, G. J.
  Edgar, B. Hancock, M. C. Kay, H. S. Lenihan, M. W. Luckenbach, C. L. Toropova, G. Zhang, and X. Guo. 2011. Oyster Reefs at Risk and Recommendations for Conservation, Restoration, and Management. BioScience 61(2):107–116.
- Bergquist, D. C., J. A. Hale, P. Baker, and S. M. Baker. 2006. Development of Ecosystem Indicators for the Suwannee River Estuary : Oyster Reef Habitat Quality along a Salinity Gradient. Estuaries and Coasts 29(3):353–360.
- Bilkovic, D. M., M. Mitchell, P. Mason, K. Duhring, D. Marie, M. Mitchell, P. Mason, K. Duhring,
  D. M. Bilkovic, M. Mitchell, P. Mason, and K. Duhring. 2016. The Role of Living Shorelines as Estuarine Habitat Conservation Strategies The Role of Living Shorelines as Estuarine Habitat Conservation Strategies. Coastal Management 44(3):161–174. Taylor & Francis.
- Birch, A. P., and Walters. 2012. Restoring intertidal oyster reefs in Mosquito Lagoon: the evolution of a successful model. Page Final Report, TNC\_NOAA Community-Based Restoration Partnership #NA10NMF4630081. Orlando, FL.
- Bishop, M. J. 2005. Compensatory Effects of Boat Wake and Dredge Spoil Disposal on Assemblages of Macroinvertebrates. Estuaries 28(4):510–518.

- Boesch, D. ., N. Josselyn, M, A. J. Mehta, J. T. Morris, W. . Nuttle, C. A. Simenstad, and D. J. .
   Swift. 1994. Scientific Assessment of Coastal Wetland Loss, Restoration, and Management in Louisiana. Journal of Coastal Research (20):1–103.
- Breitburg, D. L., D. W. Hondorp, L. A. Davias, and R. J. Diaz. 2008. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. Annual Reviews.
- Breitburg, D., L. A. Levin, A. Oschlies, M. Grégoire, F. P. Chavez, D. J. Conley, V. Garçon, D.
  Gilbert, D. Gutiérrez, K. Isensee, G. S. Jacinto, K. E. Limburg, I. Montes, S. W. A. Naqvi, G. C.
  Pitcher, N. N. Rabalais, M. R. Roman, K. A. Rose, B. A. Seibel, M. Telszewski, M. Yasuhara, and J. Zhang. 2018. Declining oxygen in the global ocean and coastal waters. Science 359(6371).
- Cáceres, M. De, and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90(12):3566–3574.
- Caselle, J. E., B. P. Kinlan, and R. R. Warner. 2010. Temporal and spatial scales of influence on nearshore fish settlement in the Southern California Bight. Bulletin of Marine Science 86(2):355–385. University of Miami-Rosenstiel School of Marine and Atmospheric Science.
- Cavanaugh, K. C., J. R. Kellner, A. J. Forde, D. S. Gruner, J. D. Parker, W. Rodriguez, and I. C. Feller. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proceedings of the National Academy of Sciences of the United States of America 111(2):723–7.
- Chambers, L. G., S. A. Gaspar, C. J. Pilato, H. E. Steinmuller, K. J. McCarthy, P. E. Sacks, and L. J.
   Walters. 2018. How Well Do Restored Intertidal Oyster Reefs Support Key Biogeochemical
   Properties in a Coastal Lagoon? Estuaries and Coasts 41(3):784–799. Estuaries and Coasts.
- Chen, I.-C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333(6045):1024–1026.

- Cheung, W. W. L., V. W. Y. Lam, J. L. Sarmiento, K. Kearney, R. Watson, and D. Pauly. 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries 10(3):235–251.
- Clark, R., C. J. Fox, D. Viner, and M. Livermore. 2003. North Sea cod and climate change modelling the effects of temperature on population dynamics. Global Change Biology 9(11):1669–1680.
- Clarke, A., and K. J. Gaston. 2006. Climate, energy and diversity. Proceedings of the Royal Society of London B: Biological Sciences 273(1599):2257–2266. The Royal Society.
- Coen, L. D., R. D. Brumbaugh, D. Bushek, R. Grizzle, M. W. Luckenbach, M. H. Posey, S. P.
   Powers, and S. G. Tolley. 2007. Ecosystem services related to oyster restoration. Marine
   Ecology Progress Series 341:303–307.
- Dahl, T. E. 2006. Status and trends of wetlands in the conterminous United States 1998 to 2004. Washington, DC: US Department of the Interior, Fish and Wildlife Service.
- Darlington Jr, P. J. 1959. Area, climate, and evolution. Society for the Study of Evolution 13(4):488–510.
- Davis, J. L., R. L. Takacs, and R. Schnabel. 2006. Evaluating ecological impacts of living shorelines and shoreline habitat elements: An example from the upper wester Chesapeake Bay.
  Pages 55–61 Management, Policy, Science, and Engineering of Nonstructural Erosion Control in the Chesapeake Bay.

Dobzhansky, T. 1950. Evolution in the tropics. American Scientist 38:209–211.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E.
Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oskanen, T. Oskanen, R. T. Paine, E.
K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E.
Sinclair, M. E. Soule, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet
earth. Science 333 (6040), 301-306. Science 333(July):301–307.

Fischer, A. G. 1960. Latitudinal variations in organic diversity. Evolution 14:64–81.

- Flynn, A. J., and D. A. Ritz. 1999. Effect of habitat complexity and predatory style on the capture success of fish feeding on aggregated prey. Journal of the Marine Biological Association of the United Kingdom 79(1999):487–494. University of Central Florida.
- Gabel, F., X. F. Garcia, I. Schnauder, and M. T. Pusch. 2012. Effects of ship-induced waves on littoral benthic invertebrates:2425–2435.
- Garvis, S. K., P. E. Sacks, and L. J. Walters. 2015. Formation, Movement, and Restoration of Dead Intertidal Oyster Reefs in Canaveral National Seashore and Mosquito Lagoon, Florida. Journal of Shellfish Research 34(2):251–258.
- Gaston, K. J. 2000. Global patterns in biodiversity 405(6783):220–227.
- Geraldi, N. R., S. P. Powers, K. L. Heck, and J. Cebrian. 2009. Can habitat restoration be redundant? Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks. Marine Ecology Progress Series 389:171–180.
- Gilby, B. L., A. D. Olds, C. H. Peterson, R. M. Connolly, C. M. Voss, M. J. Bishop, M. Elliott, J. H. Grabowski, N. L. Ortodossi, and T. A. Schlacher. 2018. Maximizing the benefits of oyster reef restoration for finfish and their fisheries (May):931–947.
- Gilmore, R. G. 1995. Environmental and biogeographic factors. Bulletin of Marine Science 57(1):153–170.
- Gilmore, R. G. J. 1977. Fishes of the Indian River Lagoon and Adjacent Waters, Florida. Bulletin of Florida State Museum, Biological Sciences 22(3):101–148.
- Gittman, R. K., C. H. Peterson, C. A. Currin, F. Joel Fodrie, M. F. Piehler, and J. F. Bruno. 2016. Living shorelines can enhance the nursery role of threatened estuarine habitats. Ecological Applications 26(1):249–263.
- Grabowski, J. H., A. R. Hughes, D. L. Kimbro, and M. A. Dolan. 2005. How habitat setting influences restored oyster reef communities. Ecology 86(7):1926–1935.

Gray, J. 2016. Fish kill in Florida: "Heartbreaking images" seen for miles. CNN.

- Gray, J. S. 1997. Marine biodiversity : patterns , threats and conservation needs. Biodiversity Conservation 175:153–175.
- Gregalis, K. C., M. W. Johnson, and S. P. Powers. 2009. Restored Oyster Reef Location and Design Affect Responses of Resident and Transient Fish, Crab, and Shellfish Species in Mobile Bay, Alabama. Transactions of the American Fisheries Society 138(2):314–327.
- Grime, J. P. 1997. Biodiversity and ecosystem function: The debate deepens. Science 277(5330):1260–1261.
- Hawkins, S. J., A. J. Southward, and M. J. Genner. 2003. Detection of environmental change in a marine ecosystem evidence from the western English Channel. Science of the Total Environment 310(1–3):245–256.
- Hersteinsson, P., and D. W. Macdonald. 2016. Interspecific competition and the geographical distribution of red and arctic foxes Vulpes vulpes and Alopex lagopus. Nordic Society Oikos 64(3):505–515.
- Hill, M. J., J. Heino, I. Thornhill, D. B. Ryves, and P. J. Wood. 2017. Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. Oikos 126(11):1575–1585. Wiley Online Library.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient 163(2):192–211.

- Horta E Costa, B., J. Assis, G. Franco, K. Erzini, M. Henriques, E. J. Gonçalves, and J. E. Caselle.
  2014. Tropicalization of fish assemblages in temperate biogeographic transition zones.
  Marine Ecology Progress Series 504:241–252.
- Humphries, A. T., M. K. La, M. E. Kimball, and L. P. Rozas. 2011. Journal of Experimental Marine
   Biology and Ecology Testing the effect of habitat structure and complexity on nekton
   assemblages using experimental oyster reefs. Journal of Experimental Marine Biology and
   Ecology 409(1–2):172–179. Elsevier B.V.

Humphries, A. T., and M. K. La Peyre. 2015. Oyster reef restoration supports increased nekton biomass and potential commercial fishery value.

Jackson, J. B., and K. G. Johnson. 2001. Measuring past biodiversity. Science 293(5539):2401–4.

- James, N. C., A. K. Whitfield, and T. D. Harrison. 2016. Grey mullet (Mugilidae) as possible indicators of global warming in South African estuaries and coastal waters. Marine Environmental Research 122:188–195.
- Kahn, J. 2012. Florida increasing redfish bag limit in top part of state. The Daytona Beach News-Journal.
- Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence absence data. Journal of Animal Ecology 72:367–382.
- König, C., P. Weigelt, and H. Kreft. 2017. Dissecting global turnover in vascular plants. Global Ecology and Biogeography 26(2):228–242. Wiley Online Library.
- Kuhn, E., J. Lenoir, C. Piedallu, and J. . Gegout. 2016. Early signs of range disjunction of submountainous plant species: an unexplored consequence of future and contemporary climate changes. Global Change Biology (22):2094–2105.
- Legendre, P., and M. De Cáceres. 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecology Letters 16(8):951–963.
- Lehnert, R. L., and D. M. Allen. 2002. Nekton Use of Subtidal Oyster Shell Habitat in a Southeastern. Estuaries 25(5):1015–1024.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294(5543):804– 808.
- Magnuson-Stevens Fishery Conservation and Management Act. 1996. .

- Mannion, P. D., P. Upchurch, R. B. J. Benson, and A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. Trends in Ecology and Evolution 29(1):42–50. Elsevier Ltd.
- McCarty, J. P. 2001. Ecological consequences of recent climate change. Conservation Biology 15(2):320–331.
- Meynecke, J., S. Y. Lee, and N. C. Duke. 2008. Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. Biological Conservation 141:981–996.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P.
  Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A.
  McDade, M. A. McPeek, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J.
  M. Sobel, and M. Turelli. 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. Ecology Letters 10(4):315–331.
- Moles, A., and B. L. Norcross. 1995. Sediment preference in juvenile pacific flatfishes 34:177– 182.
- Motta, P. J., K. B. Clifton, P. Hernandez, B. T. Eggold, S. D. Giordano, R. Wilcox, and S. Jenny. 1995. Feeding relationships among nine species of seagrass fishes of Tampa Bay, Florida. Bulletin of Marine Science 56(1):185–200.
- Nekola, J. C., and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography 26(4):867–878. Wiley Online Library.

Oksanen, J. 2008. Vegan: an introduction to ordination. Management 1:1–10.

- Oksanen, J., F. Guillaume Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin,R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2018.Community Ecology Package.
- Olson, D. M., E. Dinerstien, G. V. M. Powell, and E. D. Wikramanayake. 2002. Conservation biology for the biodiverstiy crisis. Conservation Biology 16(1):1–3.

- Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. a Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399(June):579–583.
- Pérez-Domínguez, R., S. Maci, A. Courrat, M. Lepage, A. Borja, A. Uriarte, J. M. Neto, H. Cabral,
  V. St, A. Franco, M. C. Alvarez, and M. Elliott. 2012. Current developments on fish-based indices to assess ecological-quality status of estuaries and lagoons. Ecological Indicators 23:34–45. Elsevier Ltd.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2014. Climate change and distribution shifts in marine fishes. Science 308(5730):1912–1915.
- Peters, J. R., L. A. Yeager, and C. A. Layman. 2015. Comparison of fish assemblages in restored and natural mangrove habitats along an urban shoreline 91(2):125–139.
- Peterson, C. H., J. H. Grabowski, and S. P. Powers. 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: Quantitative valuation. Marine Ecology Progress Series 264:249–264.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity : A review of concepts. The American Naturalist 100(910):33–46.
- Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13:131–144. Academic Press.
- Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. Dayton, P.
   Doukakis, D. Fluharty, B. Heneman, E. D. Houde, and J. Link. 2004. Ecosystem-Based
   Fishery Management (July):346–348.

- Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K.
  Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, C. M. Duarte, B. S. Halpern, J. Holding, C.
  V. Kappel, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. Schwing, S. A. Thompson, and A.
  J. Richardson. 2013. Global imprint of climate change on marine life. Nature Climate
  Change 3(10):919–925.
- Pörtner, H. O., and R. Knust. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 95(January):95–98.
- Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. Nature Insight Biodiversity 405(May):vol 405 no. 6783.
- Qian, H. 2009. Beta diversity in relation to dispersal ability for vascular plants in North America. Global Ecology and Biogeography 18(3):327–332. Wiley Online Library.
- Qian, H., C. Badgley, and D. L. Fox. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. Global Ecology and Biogeography 18(1):111–122. Wiley Online Library.
- Rezek, R. J., B. Lebreton, E. B. Roark, T. A. Palmer, and J. B. Pollack. 2017. How does a restored oyster reef develop ? An assessment based on stable isotopes and community metrics.
  Marine Biology 164(3):1–17. Springer Berlin Heidelberg.
- Rhein, M., S. R. Rintoul, S. Aoki, E. Campos, D. Chambers, R. A. Feely, S. Gulev, G. C. Johnson, S.
  A. Josey, A. Kostianoy, C. Mauritzen, D. Roemmich, L. D. Talley, and F. Wang. 2013.
  Observations: Ocean. Climate Change 2013: The Physical Science Basis. Contribution of
  Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on
  Climate Change:255–315.
- Rohde, K. 1992. Latitudinal gradients in species diversity : The search for the primary cause. Nordic Society Oikos 65(3):514–527.
- Rooker, R., and G. D. Dennis. 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. Bulletin of Marine Science 49(3):684–698.

- Scheffers, B. R., D. P. Edwards, A. Diesmos, S. E. Williams, and T. A. Evans. 2014. Microhabitats reduce animal's exposure to climate extremes. Global Change Biology 20(495–503).
- Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. Van Mantgem.
  2000. Linking biodiversity to ecosystem function: Implications for conservation ecology.
  Oecologia 122(3):297–305.
- Seidel, D. J., Q. Fu, W. J. Randel, and T. J. Reichler. 2008. Widening of the tropical belt in a changing climate. Nature Geoscience 1:21–24.
- Selig, E. R., K. S. Casey, and J. F. Bruno. 2010. New insights into global patterns of ocean temperature anomalies: implications for coral reef health and management. Global Ecology and Biogeography 19(3):397–411. Wiley Online Library.
- Shannon, C. E. 1948. A mathematical theory of communication. The Bell System Technical Journal 27(July 1928):379–423.
- Si, X., A. Baselga, and P. Ding. 2015. Revealing beta-diversity patterns of breeding bird and lizard communities on inundated land-bridge islands by separating the turnover and nestedness components. PLOS ONE 10(5):e0127692. Public Library of Science.
- Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.
- Snelson, F. F. J. 1983. Ichthyofauna of the northern part of the Indian River Lagoon system, Florida. Florida Scientist 46(3/4):187–206.
- Soininen, J. 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems (May 2017):96–109.
- Soininen, J., J. J. Lennon, and H. Hillebrand. 2007a. A multivariate analysis of beta diversity across organisms and environments. Ecology 88(11):2830–2838. Wiley Online Library.
- Soininen, J., R. McDonald, and H. Hillebrand. 2007b. The distance decay of similarity in ecological communities. Ecography 30(1):3–12. Wiley Online Library.

- Stevens, G. C. 1989. The latitudinal gradient in geographical range : How so many species coexist in the tropics. The American Naturalist 133(2):240–256.
- Stevens, P. W., D. A. Blewett, R. E. Boucek, J. S. Rehage, B. L. Winner, J. M. Young, J. A.
  Whittington, and R. Paperno. 2016. Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in Southern Florida. Ecosphere 7(8):1–13.
- Swann, L. 2008. The Use of Living Shorelines to Mitigate the Effects of Storm Events on Dauphin Island , Alabama , USA. Amedrican Fisheries Society Symposium 64:11pp.
- Teichert, N., A. Borja, G. Chust, A. Uriarte, and M. Lepage. 2016. Science of the Total Environment Restoring fi sh ecological quality in estuaries : Implication of interactive and cumulative effects among anthropogenic stressors. Science of the Total Environment, The 542:383–393. Elsevier B.V.
- Thomas, C. D., and J. J. Lennon. 1999. Birds extend their ranges northwards. Nature 399(6733):213.
- Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and Ecosystem Functioning. Annual Review of Ecology, Evolution, and Systematics 45(1):471–493.
- Tisseuil, C., F. Leprieur, G. Grenouillet, M. Vrac, and S. Lek. 2012. Projected impacts of climate change on spatio-temporal patterns of freshwater fish beta diversity: a deconstructing approach. Global Ecology and Biogeography 21(12):1213–1222. Wiley Online Library.
- Toft, J. D., A. S. Ogston, S. M. Heerhartz, J. R. Cordell, and E. E. Flemer. 2013. Ecological response and physical stability of habitat enhancements along an urban armored shoreline. Ecological Engineering 57:97–108. Elsevier B.V.
- Tolley, S. G., and A. K. A. Volety. 2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. Journal of Shellfish Research 24(2):1007–1012.
- Tremain, D. M., and D. H. Adams. 1995. Seasonal variation in species diversity, abundance and composition of fish communities in the northern indian river lagoon, florida.

- Tuomisto, H. 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part
  1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33(1):2–
  22. Wiley Online Library.
- Tuomisto, H. 2010b. A diversity of beta diversities: straightening up a concept gone awry. Part
  Quantifying beta diversity and related phenomena. Ecography 33(1):23–45. Wiley
  Online Library.
- Valesini, F. J., A. Cottingham, C. S. Hallett, and K. R. Clarke. 2017. Interdecadal changes in the community , population and individual levels of the fish fauna of an extensively modified. Journal of Fish Biology 90:1734–1767.
- Vergés, A., C. Doropoulos, H. A. Malcolm, M. Skye, M. Garcia-Pizá, E. M. Marzinelli, A. H.
  Campbell, E. Ballesteros, A. S. Hoey, A. Vila-Concejo, Y.-M. Bozec, and P. D. Steinberg.
  2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. Proceedings of the National Academy of Sciences 113(48):13791–13796.
- Vergés, A., P. D. Steinberg, M. E. Hay, A. G. B. Poore, A. H. Campbell, E. Ballesteros, K. L. Heck,
  D. J. Booth, M. A. Coleman, D. A. Feary, W. Figueira, T. Langlois, E. M. Marzinelli, T.
  Mizerek, P. J. Mumby, Y. Nakamura, M. Roughan, E. van Sebille, A. Sen Gupta, D. A. Smale,
  F. Tomas, T. Wernberg, and S. K. Wilson. 2014. The tropicalization of temperate marine
  ecosystems: climate-mediated changes in herbivory and community phase shifts.
  Proceedings of the Royal Society B: Biological Sciences 281(1789):1–10.
- Viana, D. S., J. Figuerola, K. Schwenk, M. Manca, A. Hobæk, M. Mjelde, C. D. Preston, R. J. Gornall, J. M. Croft, and R. A. King. 2016. Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. Ecography 39(3):281–288. Wiley Online Library.
- Wall, A. L. M., L. J. Walters, R. E. Grizzle, and E. Paul. 2005. Recreational boating activity and its impact on the recruitment and survival of the oyster Crassostrea virginica on intertidal reefs in Mosquito Lagoon, Florida. Journal of Shellfish Research 24(4):965–9733.

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- Walters, L., M. Donnelly, P. Sacks, and D. Campbell. 2017. Lessons Learned from Living Shoreline Stabilization in Popular Tourist Areas. Living Shorelines: The Science and Management of Nature-Based Coastal Protection (May):235–248.
- Wernberg, T., D. A. Smale, F. Tuya, M. S. Thomsen, T. J. Langlois, T. De Bettignies, S. Bennett, and C. S. Rousseaux. 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nature Climate Change 3(1):78–82. Nature Publishing Group.
- Whittaker. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30(3):279–338.
- Whittaker, R. H. 1972. Evolution and Measurement of Species Diversity. International Association for Plant Taxonomy (IAPT) 21(2/3):213–251.
- Wong, P. P., I. J. Losada, J.-P. Gattuso, J. Hinkel, A. Khattabi, K. L. McInnes, Y. Saito, and A. Sallenger. 2014. Coastal Systems and Low-Lying areas. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change:361–409.
- Woodworth-Jefcoats, P. A., J. J. Polovina, and J. C. Drazen. 2016. Climate change is projected to reduce carrying capacity and redistribute species richness in North Pacific pelagic marine ecosystems. Global Change Biology:1000–1008.