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Effects of Wave Action on the Structure of Fish Assemblages Across an Exposure Gradient

Lauren Liddon
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EFFECTS OF WAVE ACTION ON THE STRUCTURE OF FISH ASSEMBLAGES
ACROSS AN EXPOSURE GRADIENT

by

Lauren Elizabeth Liddon

A Thesis

Submitted to the Graduate School,
the College of Science and Technology,
and the Department of Biological Sciences
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Master of Science

August 2017

EFFECTS OF WAVE ACTION ON THE STRUCTURE OF FISH ASSEMBLAGES
ACROSS AN EXPOSURE GRADIENT

by Lauren Elizabeth Liddon

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ABSTRACT

EFFECTS OF WAVE ACTION ON THE STRUCTURE OF FISH ASSEMBLAGES ACROSS AN EXPOSURE GRADIENT

by Lauren Elizabeth Liddon

August 2017

Disturbance affects the function and diversity of ecosystems. Increased wave exposure to salt marsh can disturb sediments and cause a loss of habitat. The purpose of this study was to explore the effects of increased wave exposure on diversity, abundance, and functional ecology of estuarine fishes. If increased wave exposure is acting as a disturbance to these habitats, ecological theory (Intermediate Disturbance Hypothesis) predicts that diversity will peak at intermediate frequencies and intensities of disturbance. Fish were sampled from 10 sites monthly for 6 years. The sites were assigned to different exposure categories (Open, Intermediate, and Sheltered) using an exposure assessment method. My results did not support the Intermediate Disturbance Hypothesis. Abundance was highest at the most open sites. No significance functionality difference was found between groups. I used geometric morphometrics to determine if the increased exposure had an effect on the body shape of 4 abundant species. In freshwater studies, patterns of flow have plastic and evolutionary effects on body shape in fishes with individuals caught in faster flow having more streamline bodies and larger fin area. I was curious if the same trends would be observed in estuaries. The shape analysis yielded significant differences between exposure groups; however, not in the way expected when compared to the results from other studies. In conclusion, diversity, abundance, and shape differences were found when comparing exposure groups. However, increased wave

action alone is not the driving factor; therefore I deduce the presences of other stressors and factors in this habitat affecting the dispersal and shape of individuals.

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I would like to thank my committee members, Dr. Mike Davis and Dr. Paul Mickle, for their advice and contributions to my project. I especially thank my major professor, Dr. Jake Schaefer. His knowledge, work ethic, and excellent example has helped drive me to become a better researcher. I would not have achieved this level of success without his guidance. He saw potential in me as a naïve undergraduate and allowed me to grow into a biologist with many tools in my arsenal. I have been inspired ever since our first meeting.

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Finally, I would like to thank my family and friends who have supported me through these years. I could not have made it through without their love and advice. I would like to dedicate this thesis to my grandfather, Flint Liddon, who always instilled the importance of education and value of hard work in me.

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CHAPTER I – EXPOSURE EFFECT ON BIODIVERSITY

Introduction

Disturbances have long been known to play a vital role in regulating ecosystem processes. Disturbances vary in spatial and temporal scales with examples ranging from common everyday agitations (ripples on a pond's surface) to rare catastrophic events (hurricanes or wildfires). Larger and more powerful disturbances cause variations in communities through direct mortality as well as the physical impacts to habitat. While there is a long history to disturbance ecology, formal definitions are any destructive mechanism that limits biomass (Grime 1977). Sousa (1984) added to this definition by stating that openings are created for new individuals and species to establish. Disturbance mediated mortality leaves empty niche space, which provides opportunities for other species to colonize. Disturbance has also been defined as instabilities produced by biotic (predation, grazing, competition, displacement of other organism, etc.) or abiotic (fires, ice storms, floods, droughts, high winds, large waves, loss of land, etc.) processes that result in directional change in a community over time. Collins (2000) observed the response of several prairie communities to different burn frequencies and found the greatest directional community change found in areas of annual burnings. All these definitions have a similar broad theme; disturbance is a physical change to an area that affects resident communities within that area. Disturbance is a major cause of changes in community structure and a driver of natural selection, which prevents the community to ever fully reaching equilibrium (Sousa 1984). Different disturbance conditions will select for different life history traits. Many have hypothesized that some level of disturbance allows for greater diversity through suppression of competitive dominants. The

Intermediate Disturbance Hypothesis (IDH) posits that diversity will peak at intermediate rates of disturbance (Connell 1978). At a high frequency of disturbance, communities have high mortality rates, which limits the ability of competitive dominants to grow population size and exclude subordinates. In an area of low disturbance, lower diversity results from superior competitors excluding competitive subordinate species. The IDH has been supported in other studies involving marine invertebrates (Osman 1977; Valdiva et al. 2005), algal species (Sousa 1979), fishes (Clark 1997), plants (Townsend et al. 1997), and corals (Aronson and Precht 1995). However, some studies have challenged the validity of the IDH. Schwilk et al. (1997) found the IDH to not apply to diversity of plants in the shrublands of South Africa where fire was the disturbance. They found diversity to peak at high frequencies of fires. Crandall et al. (2003) found evidence that the IDH is rarely supported by mobile invertebrate and vertebrate studies when it comes to flooding events. For this study, the type of disturbance researched is wave disturbance. As exposure increases, wave velocity increases.

Disturbances have long been known to play a vital role in regulating ecosystem processes. Disturbances vary in spatial and temporal scales with examples ranging from common everyday agitations (ripples on a pond's surface) to rare catastrophic events (hurricanes or wildfires). Larger and more powerful disturbances cause variations in communities through direct mortality as well as the physical impacts to habitat. While there is a long history to disturbance ecology, formal definitions are any destructive mechanism that limits biomass (Grime 1977). Sousa (1984) added to this definition by stating that openings are created for new individuals and species to establish. Disturbance mediated mortality leaves empty niche space, which provides opportunities for other

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the IDH is rarely supported by mobile invertebrate and vertebrate studies when it comes to flooding events. For this study, the type of disturbance researched is wave disturbance. As exposure increases, wave velocity increases.

For centuries, humans have settled coastal habitats due to the abundance of natural resources and economic growth potential. Currently, 44% of the global human population lives within 150 km from a coast (Small and Cohen 2004). This is in part due to the large amount of consumable biomass found in marine waters (Costanza et al. 1997). This growing anthropogenic footprint is exerting pressures on local ecosystems and its ability to continue to provide the services that fueled the growth in the first place. Along North America's northern Gulf Coast, the reduction of marsh and wetland habitats is threatening wildlife populations as well as human populations and economies. Most of the natural salt marsh coastlines surrounding the Mississippi Gulf Coast have been modified to sandy beaches for tourism purposes. However, the existence of this dynamic habitat is a crucial part of the health and success of the entire coast.

A major threat to salt marshes, erosion is the cause of about 60% of wetland habitat loss along the Gulf of Mexico at a rate of 0.3 m/year (Phillip 1986; Smith 1990; Kennish 2001; Moody 2013). This can naturally occur as the historic marsh would remain at equilibrium with sediment deposition and erosion rates; however, human impacts have sped up erosion rates while decreased deposition rates leading to, in some locations, complete habitat destruction. Some major factors driving erosion include shoreline modification by anthropogenic structures, rising sea levels, pollution, and increased wave action (Orson et al. 1985; Kennish 2001; Deegan et al. 2012). As coastlines are further developed, erosion rates increase. Humans have tried to decrease

the threat of erosion, usually with armored structures including bulkheads and sea walls; however, this change of the shoreline was found to cause a loss of biodiversity in certain areas and fragmentation of marsh habitats causing a decrease in habitat productivity (Chesney et al. 2000; NRC 2007; Bulleri and Chapman 2010; Chapman and Underwood 2011; Munsch et al. 2017).

Wave energy changes seasonally, maxing out in times of frequent storm events (Sousa 1984). In the Gulf of Mexico, this peak is during the summer months; in 2016 alone, the Atlantic basin was hit by 6 tropical storms, 2 hurricanes, and 2 major hurricanes (NHC 2016). This time of year coincides with the busiest tourist season, and human presence in the water is increased during summer months. Like most coastal areas, the Gulf Coast economy is largely dependent on fishing, shipping, and recreational uses. The working and recreational vessels produce waves as they move through the Mississippi Sound, one driver for wave-induced erosion. As annual demand increases and coastal areas are further developed, anthropogenic pressures on salt marshes will increase as more shipping vessels are commissioned. This rise in ships and boats increases the amount of wave action especially around the marinas and docks. To protect the docked boats from storms, marinas and docks are placed within the bays, which, on the Mississippi coast, are executive salt marsh habitat.

As sheltered areas erode, they become more open, which exposes salt marsh to more waves. Boesch et al. (1994) reported over 1500 square miles of Louisiana coastal wetlands were lost over a 60-year period and the main cause was erosion. This change in flow regime could affect resident fish assemblages including a possible reduction of diversity as areas become more open and subject to extreme disturbances. This could lead

to a loss of functionality necessary for the health of the ecosystem. Tilman (1997) found this to be true when researching plants species of grasslands, where functional diversity and composition has the greatest effect when explaining plant productivity and found ecosystem stability was correlated with biomass. High diversity gives rise to high stability. McCann (2000) discussed this point in a review article and added to it by saying that diversity is not a driver for stability yet they are correlated. More diverse communities contain more occupied niche space and a greater amount of functionality, which increases communities' resistance to disturbance. The portfolio effect describes situation where highly diverse systems can rebound if a few species are extirpated because another species could fill their functional role (Tilman 1999).

Previous studies have looked at wave action and its effect on fish assemblages, but were located in coral reef (Friedlander et al. 2003) and sandy beach habitat (Clark 1997). Both of these studies found the highest fish diversity rate at moderate levels of wave exposure. However, little has been done with salt marshes of the Gulf of Mexico and the effects of wave action on the fish assemblages. For my study, I would like to better understand the fish responses to large waves as this could help researchers predict how the fish assemblages will change with increased exposure and wave action.

I predicted sites with similar wave exposures would exhibit similar trends in both species richness and abundance and I predict the most diversity will be found at sites with an intermediate exposure to waves, in accordance with the IDH. The purpose of this chapter was to (1) compare the diversity and abundance of fish species between sites with different levels of exposure and (2) determined if there is a change in functional groups between exposure groups. If increasing wave exposure physically affects the habitat, we

would expect different functional groups to be present. For example, low wave action sites will feature more vegetation and different substrate composition, which would favor different functional groups. I will compare the presence and absences of chosen functional groups and the abundances of individuals within those groups across my samples.

Methods

Study Area

The sites used in this study were located along the Mississippi Gulf Coast, which was historically dominated by salt marsh habitat; however a majority of this habitat has been replaced with sandy beaches due to tourism pressures. Smooth cordgrass (*Spartina alterniflora*) and needlerush (*Juncus roemerianus*) dominate the remaining salt marsh habitat found in bays and estuaries (Lowe and Peterson 2014). Two major bays are located along the MS gulf coast including Bay of St. Louis and Biloxi Bay. The MS sound is enclosed by 4 barrier islands (Cat, Ship, Horn, and Petit Bois), and waters of the MS sound are influenced by freshwater output from the Pascagoula, Pearl, and Mississippi Rivers.

Sampling Effort and Habitat Selection

A portion of the data used in this study was historical data from a completed study (Schaefer et al. 2016) (here after referred to as the historic project). In this study, fish assemblages were sampled by seine and trawl monthly over a 4-year (2011-2015) period. Sites were within brackish or marine waters along the Mississippi coast. From the historic project, I included only the seining data obtained during the summer months (April - October) in my study. To continue my study, I selected 10 sites from the original historic

sites to sample for two more summers (2015 & 2016) mimicking the sampling effort from the historic project. The sampling effort included two pulls with a 1 by 15 meter bag seine with 1/8th mesh used to thoroughly sample fish assemblages. As with any sampling method, seining comes with bias (some areas are easier to move through than others) and errors (bottom snags, seine rolling and twisting, human error, etc.), which could reduce capture rate. Despite the caveats listed above, seining is the fastest and most efficient way to sample estuarine habitat (Clark et al. 1994). The fish were fixed in 10% buffered formalin, and later transferred to 70% ethanol before being identified and enumerated in the lab. The species and number of individuals was recorded and entered into a database. In addition to the computer database, the specimens are vouchered in the USM Ichthyological Collection at Lake Thoreau Environmental Center.

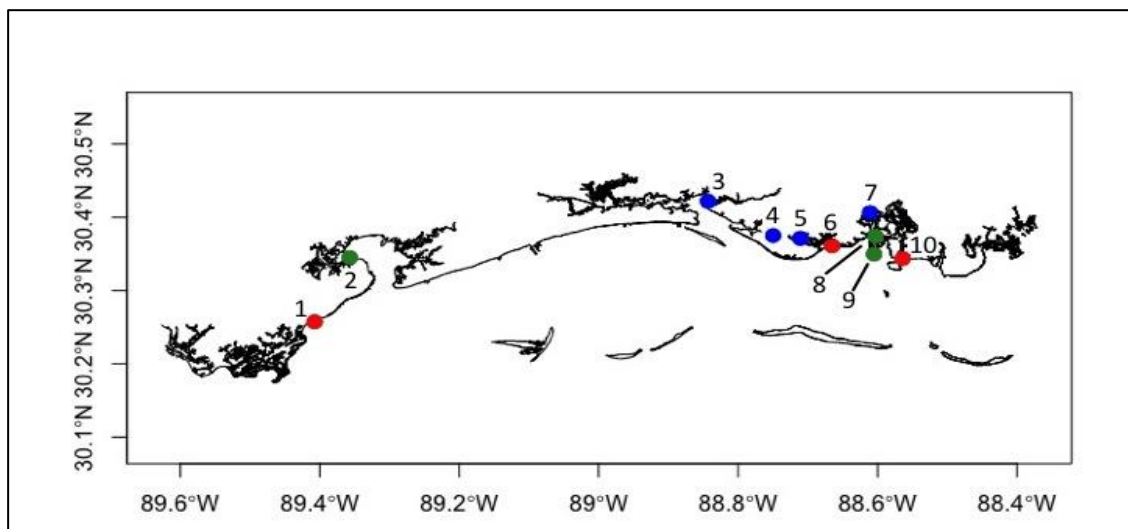


Figure 1. Map of Sites along Mississippi Coastline.

Note, Sites sampled in this study are colored by exposure type: Open sites are red (n=3), Intermediate sites are green (n=3), and Sheltered sites are blue (n=4). Each site is numbered from west to east, which correspond to site descriptions in Appendix A.

Biodiversity Data Analysis

The 10 sites were divided into three categories of exposure: Open (n=3 sites), Intermediate (n=3 sites), and Sheltered (n=4 sites) (Fig 1). All sites were assigned to the categories qualitatively based on visual assessment of wave exposure and distance from the open water. To verify the classifications, I used a quantitative method of assessing wave exposure by measure erosion rates (See Wave Assessment Method section). For all analyses, rare species (less than 2 occurrences in the dataset) were eliminated. For each sample, I calculated metrics of alpha diversity (Rarefied diversity, Shannon's diversity, and species richness) and individual abundance. Rarefied diversity uses a random subset from each sample in the community and controls for differences in abundance among samples. The constant number used in rarefied diversity should be set to the smallest observed abundance across the dataset, which was 17 individuals for my dataset. I believed this number to be too low and would not accurately describe the diversity at my sites; therefore the constant number of individuals was set at 100 per sample. Shannon's Diversity is a measure of species richness that accounts for both abundance and evenness (in abundance) of present species in an area (Shannon 1948). Species richness was the untransformed number of species in each sample. The abundance measure for this study consists of the log-transformed sum of all individuals (pooling among species) in each sample. This measure is an assay of biomass. 4 two-way ANOVA tests were performed with fixed factors of exposure and site nested within exposure to compare measures of alpha diversity and abundance between the three exposure categories.

I calculated beta diversity for each site as the mean Raup-Crick similarity among all pairwise samples through time (Chase et al. 2011). The Raup-Crick metric assesses

rates of turnover while controlling for differences in alpha diversity among sites. Pooling values for sites assessed beta diversity for exposure categories. Beta diversity is a measure of the difference in species composition. I visualized and tested for community structure within each exposure type through non-metric multidimensional scaling (NMDS, K=3) of a Bray-Curtis similarity matrix along with a permutational multivariate analysis of variances using distance matrices to test the significance. The permutational MANOVA was used to look for variation within the groups using month, year, exposure, and site nested within exposure as factors. The species data was analyzed with an indicator species analysis to determine representative species of each exposure category. Each species is assigned an indicator value from 0 to 1 (where 0 indicates no increase in abundance or occurrence among groups and 1 being a perfect indicator that is exclusive to one group), and through permutations, significance values are assessed.

Functional Groups

I chose functional traits related to habitat (benthic versus surface; structure versus water column; marine versus euryhaline), as well as caudal fin aspect ratio (height of caudal fin/width from insertion of caudal peduncle to fork). The final functional trait was trophic level, obtained from FishBase.org (Froese and Pauly 2017). They determined the value based on the mean trophic level of the prey items of the species in question. This assigns each species a number that correlates with its placement in the trophic hierarchy. The larger the number is, the higher trophic level that species is assigned. To assess functionality, I used the FD package in R, which measures functional diversity from multiple traits. The response variable was obtained by using the dbFD function, which calculates various functional diversity indices. For my study, I used the index for

functional richness (FRic in R code) (Villegger et al. 2008). Functional richness is the amount of functional space filled by a community. A mixed model ANOVA with site and year as random effects and exposure as the fixed factor was used. A principle component analysis (PCA) plot was created to reduce the data and visualize any trends.

Wave Assessment Method

In addition to qualitatively assessing exposure, a quantitative method was needed to verify assigning of exposure type to each site. Wave action at a site is due to multiple factors (i.e. wind speed, water depth, shelf incline, etc.) and can be difficult to quantify over meaningful time periods (i.e. not a single measurement). Using plaster spheres, Muus (1968) described a technique of measuring mass loss (plaster dissolved) and showed a strong correlation with wave intensity. I used a modified version of this technique described by Fulton and Bellwood (2005). The modified version consists of deploying multiple standardized plaster balls at different sites. The weights of plaster balls were recorded before and after a 24-hr soak in the field (Fig 2).

To form the balls, I mixed a ratio of 200 g of plaster of Paris and 150 mL of water, and the molds were clear plastic fillable Christmas DIY craft spherical ornaments (70mm in diameter). Using a dremel, a hole was drilled into the top of each sphere so that the plaster mixture could be poured in. For an attachment point, a piece of galvanized wire was inserted into the balls, which was bent into a spiral for better hold on the plaster. The weights of the wire were recorded separately. After 2 hours, I removed the balls from their mold and let them air dry for another 6 days until a stable weight was recorded (i.e. diminishing weigh loss due to drying). To anchor the balls in the field, the attachment wire secured each ball through a hole drilled into the side of a 1 1/8 x 48 inch wooden

dowel, which was driven into the sediment until the ball was around 6 cm above the bottom. Two plaster balls were deployed at each site set 3m apart pointed towards the oncoming waves. I deployed them in June and September of 2016.

Wave Assessment Data Analysis

The weights before deployment were subtracted from the weights after deployment. The wire weight was subtracted from that number, to negate the weight of the wire, obtaining the weight loss of each ball. A two-way ANOVA test with exposure and site nested within exposure as the fixed factors was performed to compare the weight loss from the different exposure categories.

Marsh Profile

Another indicator of physical impacts of wave action is the slope of the shore incline. To account for this change, a marsh depth profile was recorded at each site. At the beginning of the summer and again at the end of each sampling season (2015 & 2016), I measured depth every meter for 7 meters from the shore out, and a slope was calculated for each site. I predicted the slopes of the coastline at the open sites would be steeper than those found at the other sites due the higher velocity of waves found at those sites. An ANOVA performed on the slopes with fixed factors of exposure type and site nested within exposure was used to test this prediction.

Results

Wave Assessment Method

The results from the ANOVA yielded a significant effect of exposure type (d.f. = 2, $F=14.08$, $P< 0.001$). I used Tukey's HSD test for pairwise tests among treatments. Average weight loss of balls from the Open, Intermediate, and Sheltered sites were

26.22g, 16.54g, and 11g respectively. The Tukey's HSD test revealed a significant difference between open and intermediate sites ($P = 0.01$) and open and sheltered sites ($P < 0.001$). The difference between the intermediate and sheltered sites was not significant ($P = 0.14$).

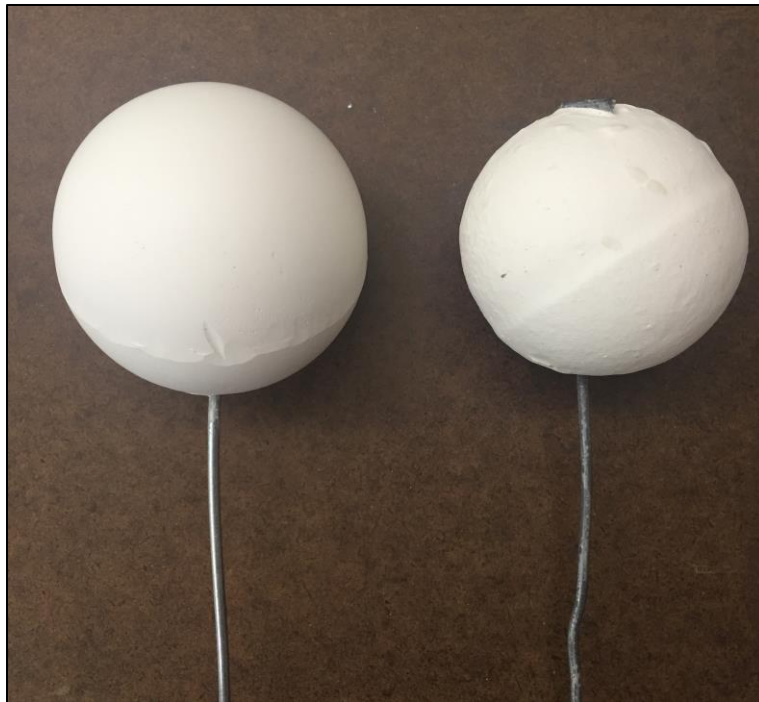


Figure 2. Plaster Balls Before and After Deployment.

Note. The plaster ball on the left is photographed before deployment, while the plaster ball on the right is photographed after being retrieved from a 24-hour soak in an Open site.

Marsh Profile

The ANOVA resulted in a significant effect of exposure ($F=3.87$, $P=0.03$) and a highly significant interaction effect between exposure and site ($F=19.20$, $P<0.001$). The majority of variation comes from between site differences (See Appendix A). The mean

slopes for each exposure type are as follows: Open - 0.0577, Intermediate - 0.0585, and Sheltered - 0.0736.

Biodiversity

After elimination of rare species ($n < 2$ occurrences), the complete dataset consisted of 347 samples with 77 species and a total of 296,750 individuals. The most abundant species was *Anchoa mitchilli* (made up 46% of all individuals in the dataset). All species caught in this study as well as their abundances and number of occurrences are listed in Appendix B.

Table 1

ANOVA Results on Measure of Diversity and Abundance

Source	d.f.	<i>F</i>	<i>P</i>
<i>Rarefied Diversity</i>			
Exposure	2	19.30	< 0.001*
Exposure × Site	7	2.30	0.03*
<i>Shannon's Diversity</i>			
Exposure	2	12.75	< 0.001*
Exposure × Site	7	4.07	< 0.001*
<i>Species Richness</i>			
Exposure	2	10.11	< 0.001*
Exposure × Site	7	1.99	0.06
<i>Abundance</i>			
Exposure	2	2.92	0.06
Exposure × Site	7	3.77	< 0.001*

Note. Asterisks emphasize significant P values

Rarefied Diversity The ANOVA resulted in a significant effect of exposure and a significant interaction effect of exposure and site (Table 1). A Tukey's HSD test was used to further explain the significant differences between the three exposure categories.

All exposure types were significantly different from each other (Open vs. Intermediate: $P < 0.001$; Intermediate vs. Sheltered: $P < 0.001$; Open vs. Sheltered: $P = 0.02$). Looking at the mean rarefied diversity values between the categories, Sheltered sites had the highest (8.31 ± 0.44). Open sites followed (7.37 ± 0.52) and then Intermediate sites (6.18 ± 0.44).

Shannon's Diversity The ANOVA resulted in a significant effect of exposure and a significant interaction effect of exposure and site (Table 1). Sheltered sites were significantly different from the other exposure types (Intermediate vs. Sheltered: $P < 0.001$; Open vs. Sheltered: $P < 0.001$). The other two categories are not significantly different from each other ($P = 0.09$). The mean Shannon diversity values mimic the results from rarefied diversity. The highest mean value was from Sheltered sites (1.28 ± 0.08), followed by the Open sites (1.10 ± 0.09), and lastly Intermediate sites (0.96 ± 0.09).

Species Richness The ANOVA resulted in a significant effect of exposure and a significant interaction effect of exposure and site (Table 1). Sheltered sites were significantly different from the other exposure types (Intermediate vs. Sheltered: $P < 0.001$; Open vs. Sheltered: $P < 0.001$). The other two categories are not significantly different from each other ($P = 0.09$). The mean Shannon diversity values mimic the results from rarefied diversity. The highest mean value was from Sheltered sites (1.28 ± 0.08), followed by the Open sites (1.10 ± 0.09), and lastly Intermediate sites (0.96 ± 0.09).

Abundance The ANOVA resulted in a significant interaction effect of exposure and site, but a non-significant effect of exposure (Table 1). The mean log transformed values at each exposure type are as follows: Open – 6.13 ± 0.25 , Intermediate – $6.08 \pm$

0.24, and Sheltered – 5.81 ± 0.19 . Unlike the others, there is a gradient of decreasing abundance when moving from Open to Sheltered sites.

Beta Diversity and NMDS When analyzing beta diversity, Intermediate sites had the lowest turnover rate (mean Raup-Crick similarity) (0.051), and Open sites had the highest (0.155)(Figure 3). Using a NMDS, the trends in the community structure of each site within the difference exposures were visualized (Figure 4). Site points from the Sheltered exposures are separated from site points from the Open exposure on the first axis. The stress value was 0.202. The permutational MANOVA resulted in a highly significant effect of month along with a significant effect of exposure and year (Table 2).

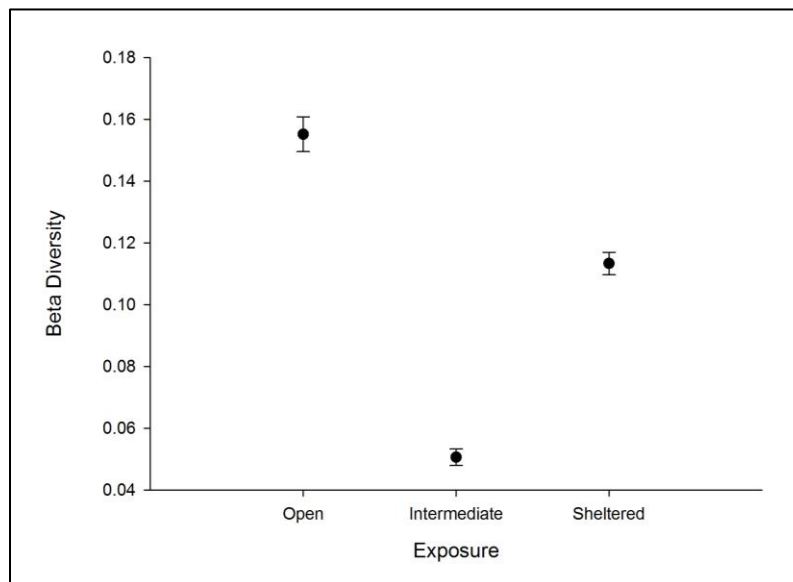


Figure 3. Beta Diversity

Note: Beta diversity is the measure of differences in species composition. For each exposure group, beta diversity \pm 95% confidence intervals are graphed; Open: 0.156 ± 0.006 ; Intermediate: 0.051 ± 0.003 ; Sheltered: 0.113 ± 0.004

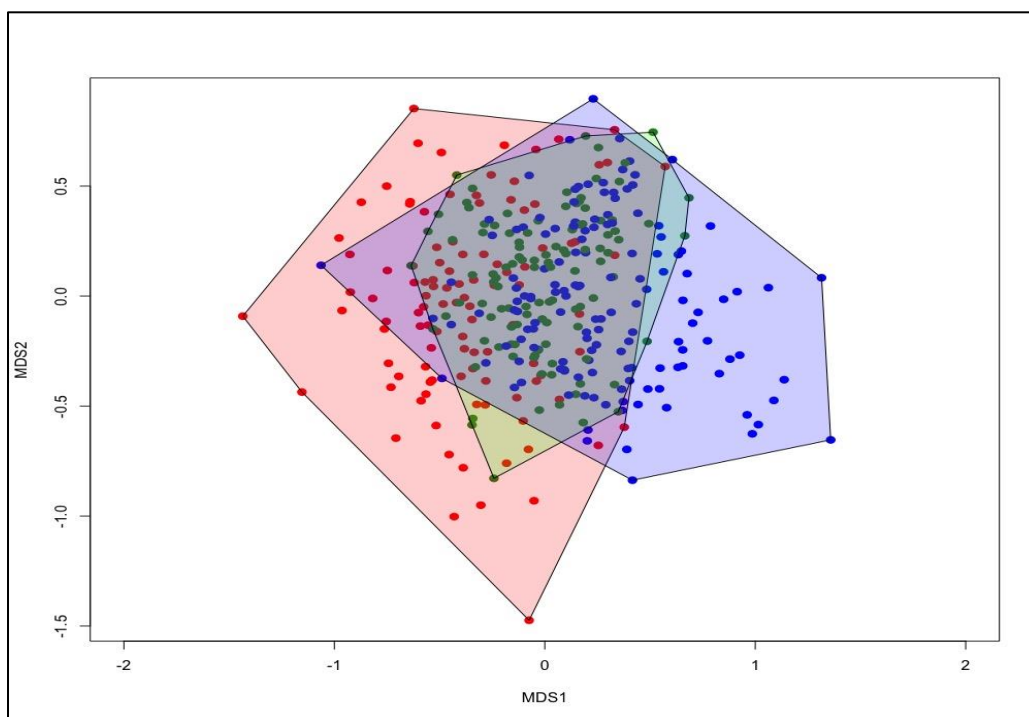


Figure 4. NMDS Plot on Species Composition.

Note. Distances are Bray Curtis distances. The open sites (n=3) are represented by red circles. The intermediate sites (n=3) are represented by green circles. The sheltered sites (n=4) are represented by blue circles. Stress value is 0.202.

Table 2

Permutational MANOVA Results

Source	d.f.	<i>F</i>	<i>P</i>
Exposure	2	20.30	<0.001*
Year	1	12.78	<0.001*
Month	1	40.34	<0.001*
Exposure × Year	2	2.16	0.001*
Exposure × Month	2	3.38	<0.001*
Year × Month	1	4.42	<0.001*
Exposure × Year × Month	2	1.41	0.174
Exposure × Year × Month × Site	7	10.16	<0.001*

Note. NMDS scores based on Bray Curtis distances. Asterisks emphasize significant *P* values

Indicator Species Analysis The indicator species analysis found 23 of the 77 species to be significantly associated with Open sites, 1 species with Intermediate sites, and 21 species with Sheltered sites. For Open sites, *Membras martinica* (Atherinopsidae), *Harengula jaguana* (Clupidae), and *Trachinotus carolinus* (Carangidae) were the top three species that was most significant and had the highest abundance, while *Bairdiella chrysoura* (Sciaenidae), *Lucania parva* (Fundulidae), and *Syngnathus scovelli* (Syngnathidae) were the major indicator species for the Sheltered sites. The only significant indicator species for the Intermediate sites was *Menidia beryllina* (Atherinopsidae) (Appendix B).

Functional Groups

The ANOVA resulted in a non-significant effect of exposure on functional richness (P=0.344). When graphed, the mean PCA scores showed slight trends by exposure type (Figure 5). The standard error scores were also added to the graph. The salinity level and habitat functional groups separated out on the x-axis. Location in the water column separated on the y-axis. Some sheltered sites are separated from the other sites on the y-axis, but there is not complete separation of any group (Table 3). Neither tropic level nor aspect ratio separated out on either axes

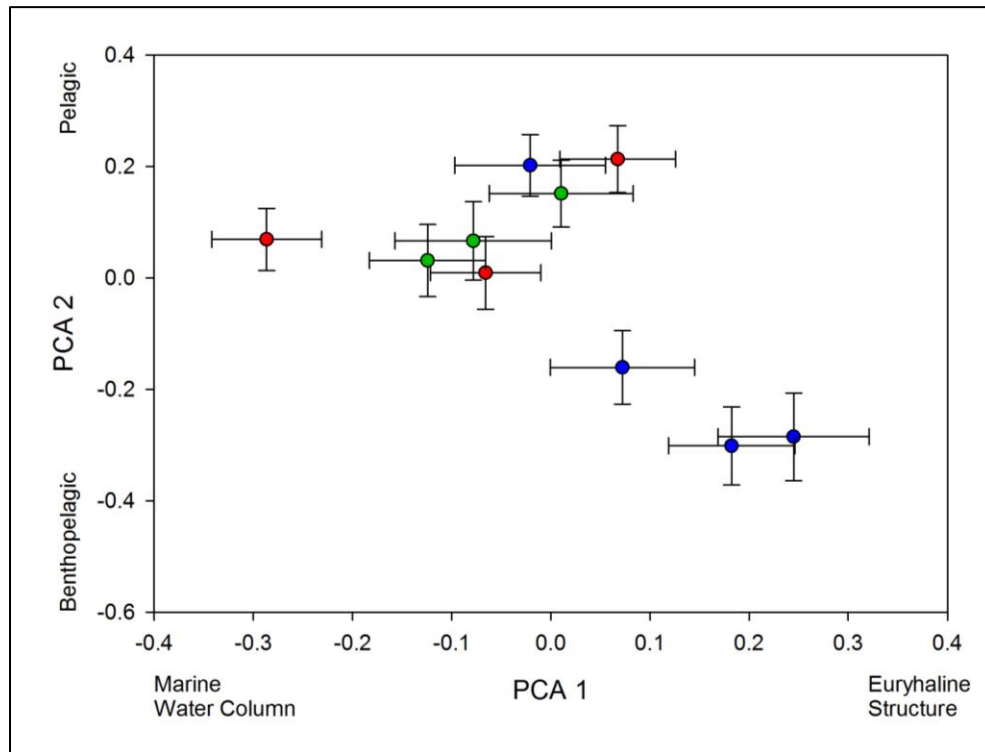


Figure 5. .PCA plot of Functional Groups

Note. The mean PCA scores for each sites is graphed with standard error. Open sites are colored red. Intermediate sites are green, and Sheltered sites are blue. Functional groups, which separate on the first two axes, are labeled on each axis.

Table 3

PCA loadings for Functional Groups

Trait	PCA1	PCA 2
Marine	-2.031	-0.922
Euryhaline	1.992	0.998
Water Column	-2.079	-0.856
Structure	2.069	0.895
Pelagic	-0.848	2.048
Benthopelagic	0.703	-1.951

Note. Information correlates with Figure 5

Discussion

My original prediction for this project was sites with intermediate exposure would contain the highest diversity in accordance with the Intermediate Disturbance Hypothesis (IDH) (Connell 1978). I assumed the high diversity of this area would lead to higher productivity rates, which in turn would sustain higher abundances as well. My results have refuted my original hypothesis, showing the intermediate sites having the lowest value in all 3 of my diversity analyses (Rarefied diversity, Shannon's diversity and species richness). The highest abundance values were found at the Open sites followed by Intermediate sites and Sheltered sites. This might be attributed to the ease of seining at open areas compared to the more narrow sheltered sites or the high abundance of the marine coastal shelf attributing immigrants to the marsh via the open sites. Beta diversity was lowest at the Intermediate sites. In other words, the same species were being caught at those sites repeatedly, which is more evidence for Intermediate sites having lower diversity. This also suggests a local retention of certain species to these sites. Beta diversity was highest at Open sites. This is justified by the indicator species associated with Open sites, which were highly mobile water column species and less linked to structure.

From my findings, I conclude the IDH does not apply to my study. Other ecological studies have reached the same conclusion. When reviewing the literature, I found several reasons why my study might have produced the opposite result than what was predicted. One study found diversity of plant species peaked at high levels of disturbance and concluded that competition was not the main mechanism driving dispersal and diversity rates (Schwilk et al. 1997). I believe this applies to my study as

well due to the highly mobile nature of the species in my study. Another study based on predictive models suggested that the IDH applies to simpler systems involving only one trophic level. The hypothesis was refuted when applied to natural multi-trophic systems (Wootton 1998), which would also be the case in my study. According to a review from Crandall et al. (2003), the IDH might not apply to mobile taxa at all. Studies performed on grasslands offer a good study area for this as grasslands are subject to large and small-scale disturbances and plants diversity is easily assessed (Tilman et al. 1997; Collins 2000). The studies on sessile organism have the most success at supporting the IDH. These include studies on plants, sessile invertebrate species, and coral reefs (Aronson and Precht 1995; Bornette and Amoros 1996; Townsend et al. 1997; Dial and Roughgarden 1998; Pollock et al. 1998; Ferreira and Stohlgren 1999; Molino and Sabatier 2001; Lenz et al. 2004; Piou et al. 2008). These sessile organisms have no other alternatives than to either cope or succumb to the effects of disturbances. Mobile organisms, however, have the capability to avoid and survive disturbances (Crandall et al. 2003). This fact makes the effect of disturbances greater for those sessile organisms. Crandall et al. (2003) noted that if there were a time of high mortality in mobile species, immigrants from other areas could restore the populations. The validity of this hypothesis is a hot topic for discussion (Wilkinson 1999; Fox 2013a; Fox 2013b; Sheil and Burslem 2013) leaving some to conclude that the definition of the IDH should be rewritten to be more precise.

Another possibility for my results is that the waves measured in this study do not constitute a disturbance as usually defined in ecological theory. The original plan for this study was sample immediately following a large storm before recolonization. The

diversity in samples taken after this larger “disturbance” event would then be compared the other non-storm samples. However, no large storms hit the Mississippi Gulf Coast over the summer months of 2015 & 2016. This could be an avenue for future research and continuation of this project. This would also allow me to test the validity of the IDH in regards to sessile vs. mobile organism.

One could argue that patterns of dispersal are too complex to be explained by simpler hypotheses. There could be other more discrete factors driving diversity changes. Vasconcelos et al. (2015) found species richness of estuaries to be controlled by predator presence, energy dynamic, history, system connectivity, and quality of habitat. Estuaries are very dynamic environments because they are the convergence point of two productive habitats: freshwater rivers and marine coastal shelf. The two extreme ends of an estuary having more diversity could be due to the different conditions found there. Certain conditions (i.e. salinity) might limit species from reaching the intermediate areas (too high salinity levels for strictly freshwater species and too low salinity levels for strictly marine species). Primary productive levels may have differed between my sites causing variation in diversity levels. In a study looking at both disturbance and productivity levels, Haddal et al (2008) found increased disturbance and decreased productivity reduced species diversity of estuaries. Productivity levels could help predict how disturbance would affect diversity (Haddal et al 2008). Increased productivity supports better competitors while increased disturbance supports poor competitors (Kondoh 2001). Although my hypothesis was not supported, it is clear from my results that open and sheltered sites are very different in terms of diversity and abundance. This was evident from the NMDS (Figure 4), where open and sheltered groups are separated on the 1st axis

and the permutational MANOVA showed there is more influencing the diversity patterns of this system than exposure. The indicator species analysis separated groups based on salinity tolerance. Significant species associated with Open sites were all marine species while the species associated with Intermediate sites were either euryhaline or freshwater species.

In the analysis of the functional richness of each exposure type, no significant effect of exposure was found. When looking at the PCA plot (Figure 4), salinity seems to separate 3 of the sheltered sites from the others on axis 1 while there is a slight separation of benthic and pelagic species on axis 2. However, there seems to be functionally equivalent species across treatments. This would make sense as similar niches are filled by different species at each exposure type. From the NMDS, taxonomic differences clearly exist among the exposure types, but these assemblages are functionally similar. My functional trait matrix might not be big enough to have clear separations in groups. Therefore, this also might be an opportunity for future research.

A linear relationship between weight loss and exposure type was evident even though, weight loss at the Intermediate sites were not significantly different from weight loss at Sheltered sites. This proved successfully in quantitatively showing the difference wave velocities over an exposure gradient. My findings are similar to the results of other studies using this same method (Muus 1968; Komatsu and Kawai 1992; Fulton and Bellwood 2005), where plaster ball weight loss was positive correlated with increased flow velocity.

The marsh profile findings refuted the prediction that openly exposure sites would have the steeper slopes. I would assume that the higher velocity flow found at the Open

sites would shape the slope and the habitat. Sheltered sites had the steepest slopes out of any of the groups, but the significant interaction effect between site and exposure suggests that other factors are affecting the coastline besides exposure type. The steep slope at sheltered sites is probably due to dredging. Dredging is a common practice in inner bays and bayous where sediments are dug from the bottom to increase the depth of those areas. This allows for boats to move more inland. This is not as common at the opening of the marsh, where my Open sites are found, allowing for a more gradual slope. The steepest slope was found at Site SB1 (sheltered site), which is located in a bayou bordering a waterfront neighborhood and is dredged to increase the depth for resident boats. The most gradual slope belongs to Site BUC1 (open site). This site is right off of a beach and is popular tourist spot but no boats come close to this site (Appendix A).

CHAPTER II – EXPOSURE EFFECT ON BODY SHAPE

Introduction

Phenotypic variation can derive from genetic differentiation or plasticity. Certain environmental stimuli can affect shape of different populations (Lowell 1987; Robinson and Wilson 1994; Fulton and Bellwood 2005; Marks et al. 2005; Hendry et al. 2006; Jacquemin et al. 2013; Foster et al. 2015; Haas et al. 2015). Environmental conditions affecting fish shape can range from the presence of predators (DeWitt and Langerhans 2002; Langerhans et al. 2004; Langerhans 2009), varied feeding habits (Kaeuffer et al. 2012; Franssen et al. 2012), and changes in habitat (Fulton et al. 2001; Imre et al. 2002; Favaloro and Mazzola 2003; Langerhans 2008; Franssen et al. 2012). Ultimately, these changes, whether they are plastic (occurring over short periods of time; may be able to revert back) or evolutionary (occurring over long periods of time; cannot revert back), increase fitness and optimize energy conservation in those habitats.

Previous body morphology studies have found that fish living in habitats with faster flow regimes exhibit more streamline bodies, smaller heads, larger fins, and deeper caudal peduncles when compared to individuals of the same species from a low flow habitat (Fulton et al. 2001; Fulton and Bellwood 2005; Hendry et al. 2006; Franssen et al. 2012; Jacquemin et al. 2013; Foster et al. 2015; and Haas et al. 2015) to aid with energy conservation when holding position in the water column. The majority of these studies were performed in freshwater systems (i.e. stream versus reservoir). However, I wanted to determine if the same shape variations were found when comparing fish from a gradient of flow regimes applies to the estuary habitat. Sites with different exposures to the gulf experience different flow rates. Openly exposed sites have a high water

movement rate as waves move across the habitat while sheltered sites have calmer waters that are still subject to tidal cycles. Although these calm waters do experience waves produced by storms and boats, they experience them on a much lower frequency than the openly exposed sites. This change of flow between sites could lead to plastic changes in body morphology of conspecifics sampled from different areas.

The purpose of this chapter is to determine if body shape changes along a wave exposure gradient at replicate sites. Geometric morphometrics was used to assess shape changes. Geometric morphometrics is a powerful new approach to measuring shape variations between groups and detecting of the causes of the variations (Mitteroecker and Gunz 2009). This method is based on the detection of homologous landmarks placed in areas of interest on a shape and compare how the landmarks vary when changing treatments (Loy et al. 2000). This method works particularly well with ichthyofauna species due to their laterally compressed bodies, which are easy to photograph. Fin insertion and placement are ideal areas for landmark placement and are known to have plastic response in the presence of certain stimuli (Pakkasmaa and Piironen 2000; Fulton et al. 2001; Imre et al. 2002; Favaloro and Mazzola 2003; Langerhans 2008).

I predict there would be a morphological change when comparing fish sampled in different exposure and my results will mimic those found by previous studies: fish from faster waters (Open sites) will exhibit more streamline bodies and increased fin area when compared to the conspecifics in slower waters (Sheltered sites).

Methods

The individuals used in this analysis were caught from the same sites (Appendix A) and using the same sampling methods described in the first chapter. No special trips

were taken to obtain these fishes; they were selected from lots located in the USM Ichthyology Museum.

Geometric Morphometrics

The four species (including bay anchovies, *Anchoa mitchilli*; inland silversides, *Menidia beryllina*; pinfish, *Lagodon rhomboides*; and spot, *Leiostomus xanthurus*) used were selected due to their high abundance at each site (Appendix B). The left lateral side of each fish was photographed using either a Canon PowerShot A1100 or Casio Exilim EX-ZR100. The order of pictures during digitization was randomized (using tpsUtil software) to prevent bias, and the body shape was quantified using tps Utility program (version 1.65) and R. Due to the different shapes of the fish, each species had a different number of landmarks (Fig 6). Therefore, there is no global model, and each species was analyzed separately. Each individual was scaled using a reference and a general Procrustes analysis (GPA) was used scale and rotation on body shape variation. The PCA results from the GPA output were plotted for each species to visualize trends across the exposure gradient (Figure 7).

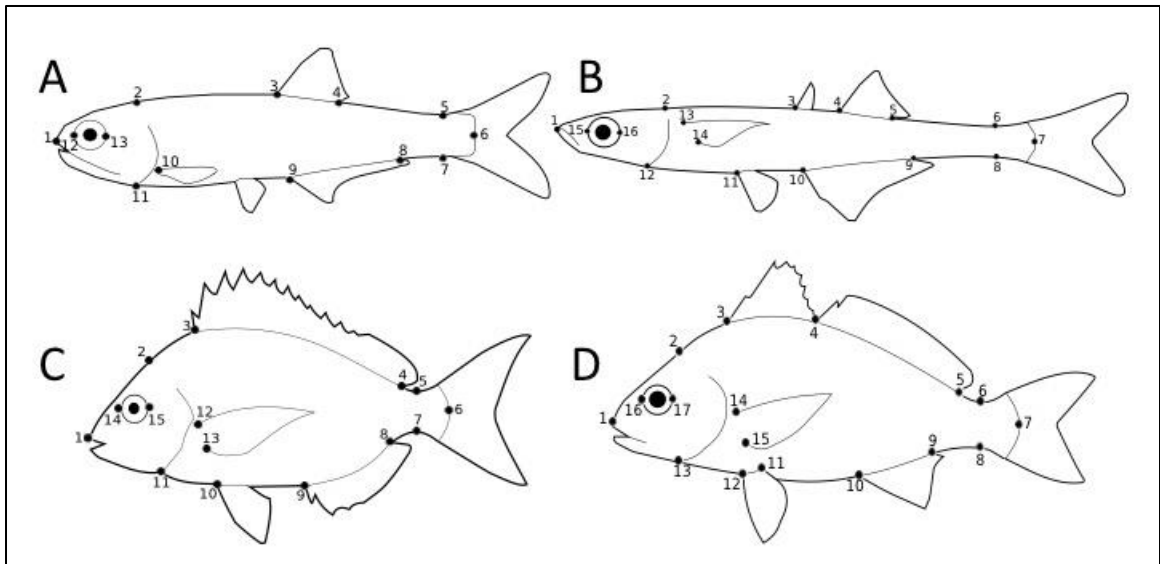


Figure 6. Landmark Locations on Each Species.

Note. Outlines created using Inkscape/ The species are as follows (A) *Anchoa mitchilli*, (B) *Menidia beryllina*, (C) *Lagodon rhomboides*, (D) *Leiostomus xanthurus*

Morphological Divergence Vector

To compare the body shape changes between each group, I calculated a morphological divergence vector following the methods described by Langerhans (2009). This vector describes the linear combination of dependent (shape) variables that contribute the greatest difference between treatments (exposure types) (Langerhans 2009). To test the effect of exposure on shape, I used 4 MANCOVA tests for each species with exposure type as a fixed factor and centroid size, which is the square rooted sum of all the distances between each landmark to the individual's centroid, as a covariate. To calculate the species scores, I multiplied the results of a PCA applied to the exposure type's sums of squares from the MANOVA (Langerhans 2009). This resulted in morphological divergence vector scores for each individual, which were then grouped by exposure type. The pooled vector scores yielding an average score for individuals from Open, Intermediate, and Sheltered sites for each of the four species.

Results

A total of 718 individuals were digitized in this study: 206 *Anchoa mitchilli* (80 individuals from Open sites, 20 from Intermediate sites, and 106 from Sheltered); 298 *Menidia beryllina* (157 from Open, 58 from Intermediate, and 83 from Sheltered); 129 *Lagodon rhomboides* (26 from Open, 51 from Intermediate, and 52 from Sheltered); and 85 *Leiostomus xanthurus* (35 from Open, 11 from Intermediate, and 39 from Sheltered).

Table 4

MANCOVA Results

Source	Effect size	d.f.	F	P
<i>Anchoa mitchilli</i>				
Exposure	0.28	1	4.58	<0.001*
Centroid Size	0.44	1	6.49	<0.001*
Exposure × Centroid Size	0.18	1	1.82	0.018*
<i>Menidia beryllina</i>				
Exposure	0.49	1	9.30	<0.001*
Centroid Size	0.40	1	6.36	<0.001*
Exposure × Centroid Size	0.19	1	2.30	<0.001*
<i>Lagodon rhomboides</i>				
Exposure	0.20	1	1.05	0.416
Centroid Size	0.58	1	5.35	<0.001*
Exposure × Centroid Size	0.18	1	0.84	0.692
<i>Leiostomus xanthurus</i>				
Exposure	0.59	1	2.65	<0.001*
Centroid Size	0.68	1	3.90	<0.001*
Exposure × Centroid Size	0.31	1	0.81	0.72

Note. Asterisks emphasize significant P values

Centroid size had the strongest effect in the 4 MANCOVA tests except for *M. beryllina* (F= 9.30, P <0.001), for which exposure type was the greatest effect. For *A. mitchilli* and *L. xanthurus*, centroid size has the strongest effect but was closely followed by exposure type (Table 4). Effect size was calculated for each factor to determine which effect had the most influence. For each species, individual morphological divergence

score was averaged by exposure type (Table 5). Because the species were analyzed separately and there was no global model, scores for one species do not correlate with scores from another species. Therefore, I focused on comparing intraspecific trends within groups.

Table 5

Morphological Divergence Scores

Species	MDV	± 95% conf
<i>Anchoa mitchilli</i>		
Open	-0.686	0.184
Intermediate	0.205	0.326
Sheltered	0.479	0.162
<i>Menidia beryllina</i>		
Open	0.649	0.132
Intermediate	-0.538	0.147
Sheltered	-0.852	0.118
<i>Lagodon rhomboides</i>		
Open	-0.593	0.309
Intermediate	-0.243	0.227
Sheltered	0.535	0.271
<i>Leiostomus xanthurus</i>		
Open	-0.782	0.217
Intermediate	-0.487	0.395
Sheltered	0.839	0.187

For all four species, the most difference came when comparing open and sheltered sites. The largest confidence intervals correlate with groups with low sample size. Overall there is a trend for each species where Open and Sheltered are on two ends of a gradient with intermediate landing somewhere in between. PCA scores for each species were plotted (Figure 7). The vector scores are visualized in a bar graph (Figure 8).

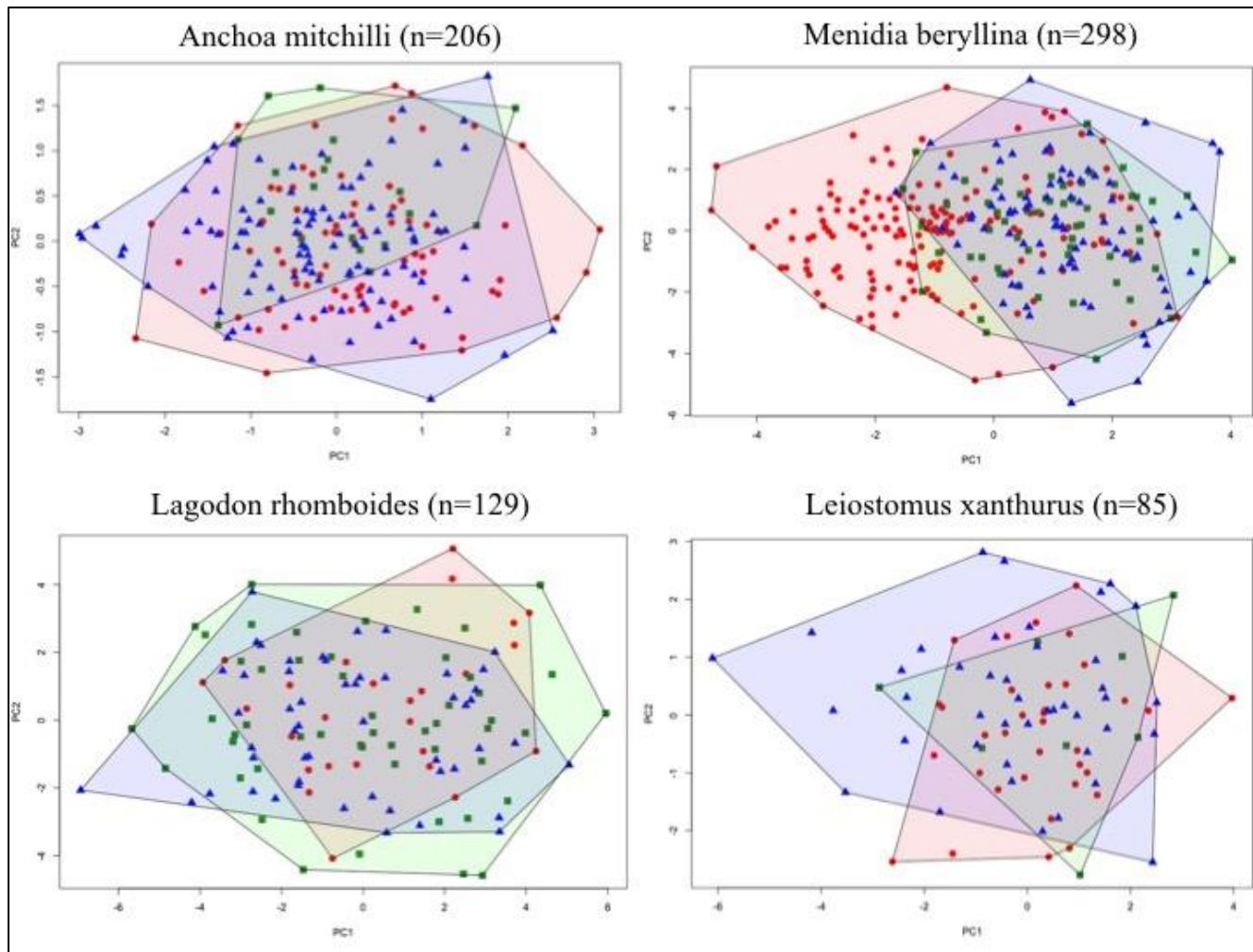


Figure 7. PCA Scores for each Species.

Note. Individuals caught from Open sites are in red circles. Those caught from Intermediate sites are in green squares and individuals caught from Sheltered sites are in blue triangles. Polygons with the same coloring are placed around exposure types to better visualize overlap among exposures.

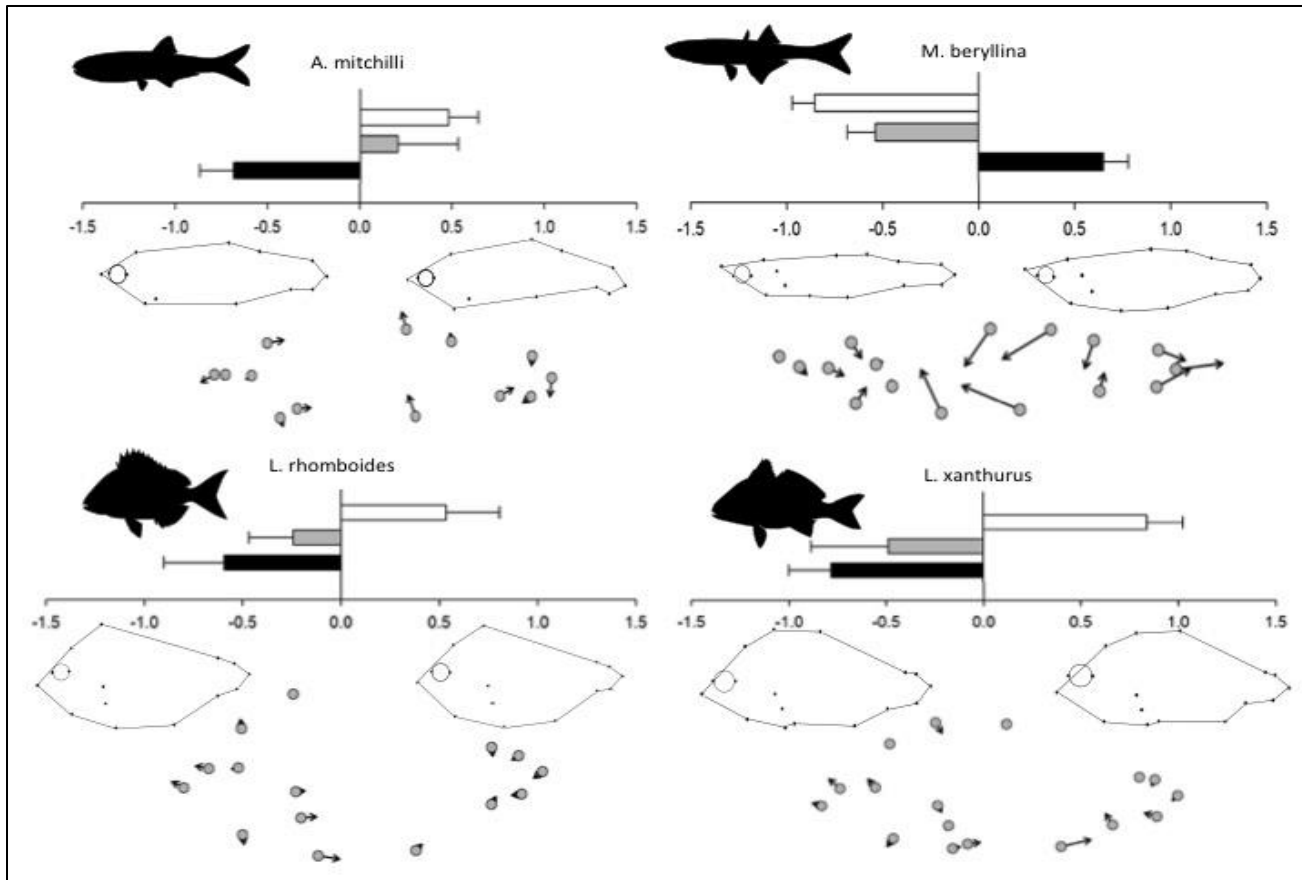


Figure 8. Morphological Divergence Bar Graph.

Note. The black bar represents average individual scores from Open sites. The gray bar represents averages from Intermediate sites, and the white bar represents average scores from Sheltered sites. The fish outlines were created using InkScape with TPS grids as a guide (magnified 5x). The vector score dot diagrams show how landmarks change when moving from Open to Sheltered sites (magnified 10x for better visualization).

Discussion

Like the previous chapter, the overall outcome did not fall in line with my predictions. Presumably, there is strong selection for phenotypes toward better swimming performance in different flow rates. Three of the four species studied had significant changes in body shape with exposure, and the morphological divergence vector for each species shows there is a shape change between fish caught in different exposures. However, the actual changes observed were opposite of what was predicted.

For both *A. mitchilli* and *M. beryllina*, the MANCOVA resulted in a significant effect of exposure, size, and interaction effect. The average *A. mitchilli* individual has a narrower head, longer anal fin, and narrower caudal peduncle when moving from open to sheltered areas. *M. beryllina* individuals have smaller heads, slender bodies, longer and narrower caudal region, and fins are located further forward on the body. This is the opposite of what we would expect when comparing to other studies (Fulton and Bellwood 2005; Hendry et al. 2006; Franssen et al. 2012; Jacquemin et al. 2013) where individuals from a habitat with faster flow had more streamline bodies and larger fin area. The PCA plots for both of these species show some structure in within groups on the first axis.

One reason for this outcome could be due to the size range of the individuals. Larger bodied individuals were generally caught in more open areas, leading to trend for larger bodies found in these areas. Maximum size was not taken into consideration when choosing individuals for digitizing. This could account for the significant interaction effect between size and exposure in both *A. mitchilli* and *M. beryllina*. Filtering out larger individuals would to minimize this effect. The mean centroid sizes for each exposure type

were not exceptionally different (*A. mitchilli*: Open – 64.6, Intermediate – 57.7, Sheltered – 59.7; *M. beryllina*: Open – 93.8, Intermediate – 86.1, Sheltered – 92.9); however there was still a size effect. Due to time restrictions, I was unable to properly filter; therefore, this would be a goal for the future of this study.

For *L. xanthurus*, the MANCOVA found a significant effect of exposure and size but no interaction. The average individual spot have slightly shorter bodies, smaller caudal regions, and shorter anal fins when moving from Open to Sheltered sites. The significant effect of exposure for *L. xanthurus* was not as strong (Effect size = 0.59) as the effect of body size was stronger (Effect size = 0.68). A smaller sample size was used with this species compared to the other species (n=85, compared to n= 206, 298, and 129), which means the variations between groups might not be as clear. The PCA plot shows less variation in open and intermediate groups (smaller polygons). For the first three species, there was a trend for larger caudal peduncles in open areas. This could be attributed the need for a stronger swimming ability in areas of faster velocity (Fulton et al. 2001; Langerhans 2008).

Lagodon rhomboides was the only species of the four that yielded a non-significant effect of exposure (P=0.416). Body size, however, was highly significant (P< 0.001). The PCA plot brings this point home with all groups overlapping. The upper size range of these specimens would have caused this result. Adults of this species are capable of quite large when compared to adults of the other species; therefore, the size range was larger with this species. Although there was no significant exposure effect, *L. rhomboides* morphological divergence vector of each exposure differed between groups. However, the confidence intervals showed a lot of individual variation. An interesting note is that A.

mitchilli and *M. beryllina* had similar results and they are both pelagic species whereas *L. rhomboides* and *L. xanthurus* are benthic species. The location in the water column might have an effect on how the flow is affecting the shape of the two groups.

In all four species, Open sites had clearly different divergence vector scores from those of the Sheltered sites. Some of the scores had very high confidence intervals (*L. xanthurus* and *A. mitchilli* from intermediate sites), due to the low sample size of these groups (n=11 & n=20, respectively). Other studies have at least 50 individuals in each treatment group (Loy et al. 2000; Fulton et al. 2001; Faraloro and Mazzola 2003; Langerhans et al. 2004). To negate any bias, each individual was chosen at random from historical lots based on size, and exposure type was not noted until after pictures were taken. Because of this, the number of fish from each exposure group was not monitored, leading to the difference sample sizes of each group.

The results of this study contradict the results found from other studies (Fulton et al. 2001; Fulton and Bellwood 2005; Hendry et al. 2006; Franssen et al. 2012; Jacquemin et al. 2013; Foster et al. 2015; and Haas et al. 2015). Many studies have demonstrated plastic variations in shape when comparing fish from stream vs. lake or reservoir habitats (Fulton et al. 2001; Imre et al. 2002; Favaloro and Mazzola 2003; Langerhans et al. 2004; Langerhans 2008; Franssen et al. 2012). However unlike typical freshwater habitat, the estuary is highly connected and lacks physical barriers. Individuals have the potential to swim between the sites. Life history studies have found these four species to be highly mobile within the estuary. The home range of *Menidia beryllina* is restricted to areas within the estuary (Hoff 1972; Gleason and Bengtson 1996). Adult *Anchoa mitchilli*, *Lagodon rhomboides*, and *Leiostomus xanthurus* all migrate into the estuary in early

spring and remain until fall when they move to their offshore wintering grounds (Hansen 1969; Vouglitosis 1987; McEachran and Fechhelm 2005). Studies reformed in the marine environment usually are in coral reef habitats where the wave velocity is much higher than that of estuaries (Fulton et al. 2008). These findings suggest that there are more factors other than wave velocity affecting body shape of fish in these habitats.

APPENDIX A – Site Descriptions

Table A1.

Descriptions for Sites

Number corresponding with Fig 1.	Site name	Exposure type	GPS coordinates	Descriptions
1	BUC1	Open	30.25°N -89.40°W	Shore seine at Buccaneer State Park
2	STL1	Intermediate	30.34°N -89.35°W	Seine at the mouth of the Jourdan River
3	OFB3	Sheltered	30.42°N -88.84°W	<i>Juncus</i> island at the junction of Old Fort Bayou and Biloxi Bay
4	SB1	Sheltered	30.38°N -88.75°W	1.5 km east of Beachview Dr, boatramp in Simmons Bayou
5	GB1	Sheltered	30.37°N -88.71°W	Western edge of <i>juncus</i> patch within Graveline Bayou
6	GB2	Open	30.36°N -88.67°W	Mouth of Graveline Bayou
7	PAS2	Sheltered	30.41°N -88.61°W	North of power line near mouth of Pascagoula; north of Hwy 90 bridge
8	PAS3	Intermediate	30.37°N -88.60°W	East bank north of large cove, south of Hwy 90 bridge
9	PAS4	Intermediate	30.35°N -88.61°W	Southeast tip of Twin Island in Pascagoula river mouth
10	PAS6	Open	30.34°N -88.56°W	East bank south of Pascagoula River mouth. Near Ingalls Shipyard

APPENDIX B Species List

Table A1. *Species List*

Species	Total Occurrence	Total Abundance	Mean Abundance	Abundance %	Rank Occurrence	Rank Abundance	ISA- exposure groups	ISA Scores	Significant P values from the ISA
<i>Adinia xenica</i>	4	24	0.07	0.01%	71	62	-	-	-
<i>Anchoa hepsetus</i>	127	6676	18.65	2.25%	8	6	O	0.58	0.001
<i>Anchoa mitchilli</i>	313	135380	378.16	45.62%	2	1	-	-	-
<i>Archosargus probatocephalus</i>	21	27	0.08	0.01%	42	57	S	0.24	0.04
<i>Ariopsis felis</i>	34	179	0.50	0.06%	32	36	-	-	-
<i>Bagre marinus</i>	4	16	0.04	0.01%	72	65	-	-	-
<i>Bairdiella chrysoura</i>	132	3577	9.99	1.21%	6	8	S	0.58	0.0002
<i>Brevoortia patronus</i>	113	67941	189.78	22.90%	11	2	-	-	-
<i>Caranx hippos</i>	58	165	0.46	0.06%	22	39	O	0.41	0.002
<i>Caranx latus</i>	7	14	0.04	0.00%	65	69	O	0.20	0.02
<i>Chilomycterus schoepfi</i>	5	7	0.02	0.00%	69	73	-	-	-
<i>Chloroscombrus chrysurus</i>	13	115	0.32	0.04%	51	43	O	0.28	0.008
<i>Citharichthys spilopterus</i>	83	323	0.90	0.11%	14	28	-	-	-
<i>Ctenogobius boleosoma</i>	110	874	2.44	0.29%	12	21	-	-	-
<i>Ctenogobius shufeldti</i>	23	153	0.43	0.05%	41	40	-	-	-
<i>Cynoscion arenarius</i>	123	1232	3.44	0.42%	10	14	-	-	-
<i>Cynoscion nebulosus</i>	139	1471	4.11	0.50%	5	10	S	0.52	0.005
<i>Cyprinodon variegatus</i>	11	20	0.06	0.01%	58	63	S	0.26	0.002
<i>Dasyatis sabina</i>	24	38	0.11	0.01%	40	52	-	-	-
<i>Dormitator maculatus</i>	12	19	0.05	0.01%	52	64	S	0.21	0.05
<i>Dorosoma petenense</i>	32	1352	3.78	0.46%	35	13	-	-	-
<i>Elops saurus</i>	34	87	0.24	0.03%	33	46	O	0.37	0.0004
<i>Etropus crossotus</i>	3	4	0.01	0.00%	76	77	-	-	-
<i>Eucinostomus harengulus</i>	64	889	2.48	0.30%	18	20	-	-	-
<i>Evorthodus lyricus</i>	6	15	0.04	0.01%	66	66	-	-	-
<i>Fundulus grandis</i>	60	379	1.06	0.13%	21	27	-	-	-
<i>Fundulus jenkinsi</i>	10	52	0.15	0.02%	59	48	S	0.25	0.003
<i>Fundulus pulvereus</i>	3	6	0.02	0.00%	77	75	-	-	-
<i>Fundulus similis</i>	42	1042	2.91	0.35%	28	18	O	0.61	0.0002
<i>Gambusia affinis</i>	4	14	0.04	0.00%	73	70	-	-	-
<i>Gobiesox strumosus</i>	14	45	0.13	0.02%	50	50	O	0.32	0.0004
<i>Gobionellus oceanicus</i>	17	29	0.08	0.01%	48	56	-	-	-
<i>Gobiosoma bosc</i>	69	271	0.76	0.09%	17	30	S	0.47	0.0002
<i>Harengula jaguana</i>	250	2016	5.63	0.68%	3	9	O	0.58	0.0002
<i>Labidesthes sicculus</i>	5	7	0.02	0.00%	70	74	-	-	-
<i>Lagodon rhomboides</i>	6	5372	15.01	1.81%	67	7	S	0.63	0.01
<i>Leiostomus xanthurus</i>	12	8125	22.70	2.74%	53	5	-	-	-
<i>Lepisosteus oculatus</i>	37	6	0.02	0.00%	29	76	-	-	-
<i>Lepisosteus osseus</i>	9	15	0.04	0.01%	61	67	-	-	-
<i>Lepomis macrochirus</i>	12	48	0.13	0.02%	54	49	S	0.26	0.004
<i>Lepomis microlophus</i>	37	272	0.76	0.09%	30	29	S	0.46	0.0002
<i>Lepomis miniatus</i>	9	25	0.07	0.01%	62	59	S	0.24	0.003
<i>Lucania parva</i>	45	784	2.19	0.26%	26	23	S	0.51	0.0002
<i>Lutjanus griseus</i>	29	55	0.15	0.02%	38	47	-	-	-
<i>Membras martinica</i>	127	14797	41.33	4.99%	9	4	O	0.59	0.0002
<i>Menidia beryllina</i>	320	30963	86.49	10.43%	1	3	I	0.67	0.007

Table A1. continued

<i>Menticirrhus americanus</i>	56	1004	2.80	0.34%	23	19	O	0.71	0.0002
<i>Menticirrhus littoralis</i>	12	207	0.58	0.07%	55	33	O	0.33	0.0002
<i>Menticirrhus saxatilis</i>	12	191	0.53	0.06%	56	35	O	0.33	0.0002
<i>Microgobius gulosus</i>	32	129	0.36	0.04%	36	42	S	0.41	0.0002
<i>Micropogonias undulatus</i>	55	538	1.50	0.18%	24	26	-	-	-
<i>Micropterus punctulatus</i>	26	678	1.89	0.23%	39	24	S	0.37	0.0004
<i>Micropterus salmoides</i>	19	1222	3.41	0.41%	45	15	S	0.31	0.01
<i>Mugil cephalus</i>	129	1354	3.78	0.46%	7	12	O	0.50	0.02
<i>Mugil curema</i>	44	238	0.66	0.08%	27	31	O	0.43	0.0002
<i>Notropis petersoni</i>	4	9	0.03	0.00%	74	72	S	0.17	0.04
<i>Oligoplites saurus</i>	150	1043	2.91	0.35%	4	17	O	0.64	0.0002
<i>Opisthonema oglinum</i>	8	35	0.10	0.01%	64	53	O	0.21	0.03
<i>Paralichthys lethostigma</i>	20	30	0.08	0.01%	44	55	-	-	-
<i>Poecilia latipinna</i>	18	1115	3.11	0.38%	46	16	S	0.31	0.002
<i>Pogonias cromis</i>	21	41	0.11	0.01%	43	51	-	-	-
<i>Pomatomus saltatrix</i>	10	25	0.07	0.01%	60	60	-	-	-
<i>Pomoxis nigromaculatus</i>	6	26	0.07	0.01%	68	58	-	-	-
<i>Prionotus tribulus</i>	18	25	0.07	0.01%	47	61	-	-	-
<i>Sciaenops ocellatus</i>	46	175	0.49	0.06%	25	37	-	-	-
<i>Scomberomorus maculatus</i>	16	31	0.09	0.01%	49	54	O	0.23	0.04
<i>Selene vomer</i>	9	12	0.03	0.00%	63	71	O	0.20	0.04
<i>Sphoeroides parvus</i>	77	575	1.61	0.19%	16	25	-	-	-
<i>Strongylura marina</i>	80	206	0.58	0.07%	15	34	O	0.48	0.0002
<i>Symphurus plagiusa</i>	61	228	0.64	0.08%	20	32	S	0.37	0.02
<i>Syngnathus floridae</i>	4	15	0.04	0.01%	75	68	-	-	-
<i>Syngnathus louisianae</i>	62	174	0.49	0.06%	19	38	S	0.38	0.02
<i>Syngnathus scovelli</i>	105	794	2.22	0.27%	13	22	S	0.64	0.0002
<i>Synodus foetens</i>	37	100	0.28	0.03%	31	44	O	0.42	0.0002
<i>Trachinotus carolinus</i>	33	1365	3.81	0.46%	34	11	O	0.56	0.0002
<i>Trachinotus falcatus</i>	12	153	0.43	0.05%	57	41	O	0.34	0.0002
<i>Trinectes maculatus</i>	30	91	0.25	0.03%	37	45	S	0.40	0.0002

Note: Included in this table is species name, total occurrence, total abundance, mean abundance, percent abundance, rank occurrence,

and rank abundance for each species caught in this study. Also included are the results from the Indicator Species Analysis (ISA).

Abbreviations O, I, and S stand for Open sites, Intermediate sites, and Sheltered sites respectively.

APPENDIX C – Institutional Animal Care and Use Committee



THE UNIVERSITY OF
SOUTHERN MISSISSIPPI

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE

118 College Drive #5116 | Hattiesburg, MS 39406-0001
Phone: 601.266.6791 | Fax: 601.266.4377 | iacuc@usm.edu | www.usm.edu/iacuc

NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:	15051406
PROJECT TITLE:	Wave Action Effects on Fish Assemblages of Saltmarsh Habitat Across an Exposure Gradient in the Northern Gulf of Mexico
PROPOSED PROJECT DATES:	06/2015 -09/2017
PROJECT TYPE:	New
PRINCIPAL INVESTIGATOR(S):	Jake Schaefer
DEPARTMENT:	Biological Sciences
FUNDING AGENCY/SPONSOR:	N/A
IACUC COMMITTEE ACTION:	Full Committee Approval
PROTOCOL EXPIRATION DATE:	September 30, 2017

Frank Moore, PhD
IACUC Chair

June 1, 2015
Date

LITERATURE CITATIONS

- Aronson, Richard B., and William F. Precht. 1995. Landscape patterns of reef coral diversity: A test of the intermediate disturbance hypothesis. *J. Exp. Mar. Biol. Ecol.* 192: 1-14.
- Beck, Micheal W., Kenneth L. Heck, Jr., Kenneth W. Able, Daniel L. Childers, David B. Eggleston, Bronwyn M. Gillanders, Benjamin Halpern, Cynthia G. Hays, Kaho Hoshino, Thomas J. Minello, Robert J. Orth, Peter F. Sheridan, and Michael P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51: 633-641.
- Begon, Michael, Robert W. Howarth, and Colin R. Townsead. 2014. Essentials of ecology (4th ed.). Oxford: Blackwell Publishing.
- Boesch, Donald .F, and R. Eugene Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7: 460-468.
- Boesch Donald F., Michael N. Josselyn, Ashish J. Mehta, James T. Morris, William K. Nuttle, Charles A. Simenstad, and Donald P. J. Swift. 1994. Scientific assessment of coastal wetland loss, restoration, management in Louisiana. *Journal of Coastal Research* 20: 1-103.
- Bornette, Gudrun and Claude Amoros. 1996. Disturbance regimes and vegetation dynamics: role of floods in riverine wetland. *J. Veg. Sci.* 7: 615-622.
- Bulleri, Fabio and Maura G. Chapman. The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology* 47: 26-35.

- Chapman, M.G. and A.J. Underwood. 2011. Evaluation of ecological engineering of “armoured” shorelines to improve their value as habitat. *Journal of Experimental Marine Biology and Ecology* 400: 302-313.
- Chase, Jonathan M., Nathan J. B. Kraft, Kevin G. Smith, Mark Vellend, and Brian D. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere* 2(2): 1-11.
- Chesney, Edward J., Donald M. Baltz, and R. Glenn Thomas. 2000. Louisiana estuarine and coastal fisheries and habitats: perspectives from a fish’s eye view. *Ecological Applications* 10(2): 350-366.
- Clark, B.M., B.A. Bennett, and S.J. Lamberth. 1994. A comparison of the ichthyofauna of two estuaries and their adjacent surf zones, with an assessment of the effects of beach seining on the nursery function of estuaries for fish. *South African Journal of Marine Science* 14(1): 121-131.
- Clark, B.M. 1997. Variation in surf-zone fish community structure across a wave-exposure gradient. *Estuarine, Coastal and Shelf Science* 44: 659-674.
- Collins, Scott L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *The American Naturalist* 155(3): 311-325.
- Connell, Joseph H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199(4335): 1302-1310.
- Costanza, Robert, Ralph d’Arge, Rudolf de Groot, Stephen Farber, Monica Grasso, Bruce Hannon, Karin Limburg, Shahid Naeem, Robert V. O’Neill, Jose Paruelo, Robert G. Raskin, Paul Sutton, and Marjan van den Belt. 1997. The value of the world’s ecosystem services and natural capital. *Nature* 387: 253-260.

- Crandall, R.M., C.R. Hayes, and E.N. Ackland. 2003. Application of the intermediate disturbance hypothesis to flooding. *Community Ecology* 4(2): 225-232.
- Dial, Roman and Jonathan Roughgarden. 1998. Theory of marine communities: the intermediate disturbance hypothesis. *Ecology* 79(4): 1412-1424.
- Deegan, Linda A., David Samuel Johnson, R. Scott Warren, Bruce J. Peterson, John W. Fleeger, Sergio Fagherazzi, and Wilfred M. Wollheim. 2012. Coastal eutrophication as a driver of salt marsh loss. *Nature* 490: 388-394.
- DeWitt, Thomas J. and R. Brian Langerhans. 2002. Multiple prey traits, multiple predators: keys to understanding complex community dynamics. *Journal of Sea Research* 49: 143-155.
- Edgar, Graham J., Neville S. Barrett, David J. Graddon, and Peter R. Last. 2000. The conservation significance of estuaries: a classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. *Biological Conservation* 92: 383-397.
- Favaloro, Eugenia, and Antonio Mazzola. 2003. Shape change during the growth of sharpnout seabream reared under different conditions in a fish farm of the southern Tyrrhenian Sea. *Aquacultural Engineering* 29: 57-63.
- Ferreira, Leandro Valle and Thomas J. Stohlgren. 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia* 120(4): 582-587.
- Fonseca, Carlos Roberto & Gislene Ganade. 2001. Species functional redundancy, random extinctions and the stability of ecosystem. *Journal of Ecology* 89: 118-125.

- Foster, Kimberly, Luke Bower, and Kyle Piller. 2015. Getting in shape: habitat-based morphological divergence for two sympatric fishes. *Biological Journal of the Linnean Society* 114: 152-162.
- Fox, Jeremy W. 2013a. The intermediate disturbance hypothesis should be abandoned. *TREE* 28: 86-92.
- Fox, Jeremy W. 2013b. The intermediate disturbance hypothesis is broadly defined, substantive issues are key: a reply to Sheil and Burslem. *TREE* 28: 572-573.
- Franssen, Nathan R., Jared Harris, Scott R. Clark, Jacob F. Schaefer, & Laura K. Stewart. 2012. Shared and unique morphological responses of stream fishes to anthropogenic habitat alteration. *Proc R Soc B* 280: 1-8.
- Friedlander, A.M., E.K. Brown, P.L. Jokiel, W.R. Smith, and K.S. Rodgers. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22: 291-305.
- Froese, R. and D. Pauly. Editors. 2017. FishBase. World Wide Web electronic publication. www.fishbase.org, version (02/2017). Accessed 3 March 2017.
- Fulton, Christopher J., David R. Bellwood, and P.C. Wainwright. 2001. The relationship between swimming ability and habitat use in wrasses (Labridae). *Marine Biology* 139: 25-33.
- Fulton, C.J., and Bellwood, D.R. 2005. Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnol. Oceanogr.* 50(1): 255-264.
- Gleason, Timothy R., and David A. Bengtson. 1996. Size-selective mortality of inland silversides: Evidence from otolith microstructure. *Trans Am Fish Soc* 125: 860–873.

- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169-1194
- Haas, Travis C., David C. Heins, and Michael J. Blum. 2015. Predictors of body shape among populations of a stream fish (*Cyprinella venusta*, Cypriniformes: Cyprinidae). *Biological Journal of the Linnean Society* 115(4): 842-858.
- Haddal, Nick M., Marcel Holyoak, Tawny M. Mata, Kendi F. Davies, Brett A. Melbourne, and Kim Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters* 11: 348-356.
- Hansen, David J. 1969. Food, growth, migration, reproduction, and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulatus*, near Pensacola, Florida, 1963-65. *Fishery Bulletin* 68(1): 135-146.
- Hendry, A.P., M.L. Kelly, M.T. Kinnison, and D.N. Reznick. 2006. Parallel evolution of the sexes? Effects of predation and habitat features on the size and shape of wild guppies. *Journal of Evolutionary Biology* 19: 741-754.
- Hoff, James G. 1972. Movements of adult tidewater silverside, *Menidia beryllina* (Cope), tagged in New England waters. *The American Midland Naturalist* 88(2): 499-502.
- Imre, I., R.L. McLaughlin, and D.L.G. Noakes. 2002. Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. *Journal of Fish Biology* 61: 1171-1181.
- Jacquemin, Stephen J., Erika Martin, and Mark Pyron. 2013. Morphology of bluntnose minnow *Pimephales notatus* (Cyprinidae) covaries with habitat in a central Indiana watershed. *Am. Midl. Nat.* 169: 137-146.

- Kaeuffer, Renaud, Catherine L. Peichel, Daniel I. Bolnick, and Andrew P. Hendry. 2012. Parallel and nonparallel aspects of ecological, phenotypic, and genetic divergence across replicated population pairs of lake and stream stickleback. *Evolution* 66(2): 402-418.
- Kennish, Michael J. 2001. Coastal salt marsh systems in the U.S.: a review of anthropogenic impacts. *Journal of Coastal Research* 17(3): 731-748.
- Komatsu, Teruhisa and Hideo Kawai. 1992. Measurements of time-averaged intensity of water motion with plaster balls. *Journal of Oceanography* 48: 353-365.
- Kondoh, Michio. 2001. Unifying the relationships of species richness to productivity and disturbance. *Proc. R. Soc. Lond.* 268: 269-271.
- Langerhans, R. Brian, Craig A. Layman, A. Mona Shokrollahi, and Thomas J. DeWitt. 2004. Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution* 58(10): 2305-2318.
- Langerhans, R. Brian. 2008. Predictability of phenotypic differentiation across flow regimes in fishes. *Integrative and Comparative Biology* 48:750-768.
- Langerhans, R. Brian. 2009. Trade-off between steady and unsteady swimming underlies predator-driven divergence in *Gambusia affinis*. *J. EVOL. BIOL.* 22: 1057-1075.
- Lenz, Mark, Markus Molis, and Martin Wahl. 2004. Experimental test of the intermediate disturbance hypothesis: frequency effects of emersion on fouling communities. *J. Exp. Mar. Biol. Ecol.* 305: 247-266.
- Lowe, Michael R., and Mark S. Peterson. 2014. Effects of coastal urbanization on salt-marsh faunal assemblages in the Northern Gulf of Mexico. *Marine and Coastal Fisheries* 6: 89-107.

- Lowell, Richard B. 1987. Safety factors of tropical versus temperate limpet shells: multiple selection pressures on a single structure. *Evolution* 41: 638-650.
- Loy, A., C. Boglione, F. Gagliardi, L. Ferrucci, and S. Cataudella. 2000. Geometric morphometrics and internal anatomy in sea bass shape analysis (*Dicentrarchus labrax* L., Moronidae). *Aquaculture* 186: 33-44.
- Marks, Christopher, Tomara N. West, Brian Bagatto, and Francisco B.G. Moore. 2005. Developmental environmental alters conditional aggression in zebrafish. *Copeia* 2005: 901-908.
- McCann, Kevin Shear. 2000. The diversity-stability debate. *NATURE* 405: 228-233.
- McEachran, John D., and Janice D. Fechhelm. 2005. Fishes of the Gulf of Mexico: Volume 2. Austin: University of Texas Press.
- Minello Thomas J., Kenneth W. Able, Michael P. Weinstein, Cynthia G. Hays. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Mar Ecol Prog Ser* 246: 39-59.
- Mitteroecker, Philipp, and Philipp Gunz. 2009. Advances in geometric morphometrics. *Evol Biol* 36: 235-247.
- Molino, Jean-Francois and Daniel Sabatier. 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294: 1702-1704.
- Moody Ryan M., Just Cebrian, Sara M. Kerner, Kenneth L. Heck Jr., Sean P. Powers, and Carl Ferraro. 2013. Effects of shoreline erosion on salt-marsh floral zonation. *Mar Ecol Prog Ser* 488: 145-155.

- Munsch, Stuart H., Jeffery R. Cordell, and Jason D. Toft. 2017. Effects of shoreline armouring and overwater structures on coastal and estuarine fish: opportunities for habitat improvement. *Journal of Applied Ecology* 1-12.
- Muus, Brent J. 1968. A field method for measuring “exposure” by means of plaster balls. *2nd European Symposium on Marine Biology* 34: 61-68.
- Nicholls, Robert J. 2004. Coastal flooding and wetland loss in the 21st century: changes under the SRES climate and socio-economic scenarios. *Global Environmental Change* 14: 69-86.
- NHC (National Hurricane Center). 2016. Tropical Cyclone Monthly Summary Archive. www.nhc.noaa.gov/archive/text/TWSAT. Accessed 23 May 2017.
- NRC (National Research Council) 2007. Mitigating shore erosion along sheltered coasts. National Research Council, National Academies Press, Washington, DC
- Orson, Richard, William Panageotou, and Stephen P. Leatherman. 1985. Response of tidal salt marshes of the U.S. Atlantic and Gulf coasts to rising sea levels. *J Coast Res* 1(1): 29-37.
- Osman, Richard W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs* 47(1): 37-63.
- Pakkasmaa, Susanna, and Jorma Piironen. 2000. Water velocity shapes juvenile salmonids. *Evolutionary Ecology* 14: 721-730.
- Patricio, Joana, Fuensanta Salas, Miguel Angelo Pardal, Sven Erik Jorgensen, and Joao Carlos Marques. 2006. Ecological indicators performance during a re-colonisation field experiment and its compliance with ecosystem theories. *Ecological Indicators* 6: 43-57.

- Piou, Cyril, Uta Berger, Hanno Hildenbrandt, and Ilka C. Feller. Testing the intermediate disturbance hypothesis in species-poor systems: a simulation experiment for mangrove forests. *J. Veg. Sci.* 19(3): 417-424.
- Phillips, Jonathan D. 1986. Coastal submergence and marsh fringe erosion. *J Coast Res* 2(4): 427–436.
- Pollock, Michael M., Robert J. Naiman, and Thomas A. Hanley. 1998. Plant species richness in riparian wetlands – a test of biodiversity theory. *Ecology* 79(1): 94-105.
- Robinson, Beren W. and David Sloan Wilson. 1994. Character release and displacement in fishes: a neglected literature. *The American Naturalist* 144: 596-627.
- Small, Christopher and Joel E. Cohen. 2004. Continental physiography, climate, and the global distribution of human population. *Current Anthropology* 45(2): 259-277.
- Schaefer, Jacob, Nkrumah Frazier and Jonathan Barr. 2016. Northern Gulf of Mexico near-coastal fish assemblage dynamics following the Deepwater Horizon oil spill. *Transactions of the American Fisheries Society*. 145(1): 108-119.
- Schwilk, D.W., J.E. Keeley, and W.J. Bond. 1997. The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. *Plant Ecology* 132: 77-84.
- Shannon, C.E. 1948. A mathematical theory of communication. *Bell System Technical Journal* 27: 379-423.
- Sheil, Douglas, and David F.R.P. Burslem. 2013. Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox. *TREE* 28: 571-572.

- Smith, Everett. 1990. Regimes contributory to progressive loss of Alabama coastal shoreline and wetlands. *Gulf Coast Assoc Geol Soc Trans* 40: 793–796.
- Sousa, Wayne P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60(6): 1225-1239.
- Sousa, Wayne P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15: 353-391.
- Tilman, David, Johannes Knops, David Wedin, Peter Reich, Mark Ritchie, and Evan Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-1302.
- Tilman, David. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80(5): 1455-1474.
- Townsend, Colin R., Mike R. Scarsbrook, and Sylvain Doledec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnol. Oceanogr.* 42: 938-949.
- Turner, R. Eugene. 1990. Landscape development and coastal wetland losses in the northern Gulf of Mexico. *American Zoologist* 30(1): 89-105.
- Valdiva, Nelson, Astrid Heidemann, Martin Thiel, Markus Molis, and Martin Wahl. 2005. Effects of disturbance on the diversity of hard-bottom macrobenthic communities on the coast of Chile. *Mar Ecol Prog Ser* 299: 45-54.
- Vasconcelos, Rita P., Sofia Henriques, Susana Franca, Stephanie Pasquaud, Ines Cardoso, Marina Laborde, and Henrique N. Cabral. 2015. Global patterns and predictors of fish species richness in estuaries. *Journal of Animal Ecology* 84(5): 1331-1341.

- Villegger, Sebastien, Norman W. H. Mason, and David Mouillot. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89(8): 2290-2301.
- Vouglitois James J., Kenneth W. Able, Robert J. Kurtz, and Kenneth A. Tighe. 1987. Life history and population dynamics of the bay anchovy in New Jersey. *Trans Am Fish Soc* 116: 141–153
- Wilkinson, David M. 1999. The disturbing history of intermediate disturbance. *Oikos* 84(1): 145-147.
- Willmer, Pat, Graham Stone, and Ian Johnston. 2000. Environmental Physiology of Animals. Oxford: Blackwell Science.
- Wootton J. Timothy. 1998. Effects of disturbance on species diversity: a multitrophic perspective. *The American Naturalist* 152: 803-825