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Fish Communities on Natural and Artificial Reefs in the Eastern Gulf of Mexico

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Fish Communities on Natural and Artificial Reefs in the Eastern Gulf of Mexico

by

Elizabeth C. Viau

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
with a concentration in Marine Resource Assessment
College of Marine Science
University of South Florida

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ABSTRACT

Artificial reefs have been deployed throughout the world's oceans to act as habitat and fishing enhancement tools. To expand current research on the role of artificial reefs in the marine community, ordination and multivariate regression methods were used here to analyze survey data of natural and artificial reefs. The reefs, located in the Northern Gulf of Mexico (NGOM) and on the West Florida Shelf (WFS), had been previously surveyed from 2004 to 2015 using remote operated vehicle and stationary video techniques. This study tested the hypothesis that similar functional roles are accounted for at both natural and artificial reef sites even if species composition varies. Secondly, it examines the role of environment and fisheries in determining the assemblages. Artificial reefs tended to host communities that were as biodiverse as natural reefs, although not necessarily composed of the same species. Results of an ordination confirmed that as the classification was broadened from the level of species, to family, to functional group, the assemblages on each reef type (natural vs. artificial and NGOM vs WFS) appeared more similar. Dominant groups were present at all levels of classification and included the families Lutjanidae and Carangidae, as well as functional groups Red Snapper and Small Reef Fish. Both natural and artificial reefs tended to be dominated by one of the following: Lutjanidae, Carangidae, or Small Reef Fish, although a continuous gradient was found across the extremes of natural versus artificial reefs. Generalized Additive Models were developed to examine the influence of reef type, location, environment and fishing intensity covariates. Results indicated that for both natural and artificial reefs, the abundance of families and

functional groups can be influenced by environmental factors. In both cases, there is strong spatial autocorrelation suggesting connectivity with neighboring reefs.

1. INTRODUCTION

An artificial reef is one or more objects deployed on the seafloor to achieve some economic, social or conservation-related goal. Materials used to create artificial reefs have varied across the globe. Items such as concrete, tires, oil and gas production platforms, and sunken vessels have all been used (Seaman and Jensen, 2000). Commonly, artificial reefs are deployed to enhance fisheries production. However, they have been utilized as a tool to create additional habitat, increase biomass and species richness, and increase biodiversity (Ramos-Espla et al., 2000). Additional uses include protecting endangered species, expanding essential fisheries habitat, and supporting recreational uses of reefs such as diving (Pickering, 1998).

Artificial reefs might serve as valuable management tools if they contribute to the health of metapopulations under environmental and anthropogenic stressors. Many of the potential benefits of artificial reefs depend on how well they replicate natural reefs in structure and function. Numerous studies have compared artificial reef habitats to neighboring natural reefs with differing results. Research performed on artificial reefs with older deployment dates indicates that abundance and biomass can be higher on artificial reefs when compared to local natural reefs (Ableson et al., 2002; Arena et al., 2007; Burt et al., 2009). There are also studies that indicate a higher diversity of species at natural reefs when comparing them to nearby artificial reefs (Carr and Hixon, 1997; Rooker et al., 1997; Perkol-Finkel et al., 2006; Patterson et al., 2014). Many studies comparing reef types have been confounded by differences in age, structure, and size (Carr and Hixon, 1997). After decades of research, the general conclusions regarding the ability of an artificial reef to mimic a natural reef habitat depend on multiple factors: (1) the age of the artificial reef; (2) the complexity and rugosity of the artificial reef; (3) how similar the artificial structure is compared to the surrounding natural reef habitat (Bohnsack, 1989; Carr and Hixon, 1997; Rooker et al., 1997; Ableson et al., 2002; Perkol-Finkel et al., 2006; Arena et al., 2007; Burt et al., 2009). A more recent study performed by Fowler and Booth (2012) examined older artificial reef habitats, deployed in the early 1940s, and compared them to neighboring natural reef habitats. This study reported that while the species composition was significantly different between the reef types, the fish abundance, species richness, and feeding-guild structures observed on both reef types were similar. This research led me to consider the impact of taxonomic resolution of data analyzed in ecological studies. Current research indicates that examining data at different levels of taxonomic resolution can offer advantages when studying large spatial habitats, comparing multiple communities, or developing large-scale monitoring programs (Chapman, 1998; Oldsgard et al., 1998; Hewlett, 2000).

The goal of this research was to evaluate the community structure of both natural and artificial reefs, drawing comparisons between reef type and location while considering environmental parameters and human impacts such as fishing. Thus, I considered three research questions:

1) How does community structure differ between natural and artificial reefs at different levels of taxonomic resolution?
2) How does the environment and location affect community structure?
3) How has fishing impacted communities inhabiting artificial reefs?

2. METHODS

This study used ordination and multivariate regression approaches to compare community structure between natural and artificial reef sites in the Northern Gulf of Mexico (NGOM) and the West Florida Shelf (WFS). To examine the differences in functional roles of natural and artificial reefs, the assemblage composition was described at the level of species, families and functional groups, which are species aggregated by niche similarity. Even if the assemblage differs between natural and artificial reefs at the species or family taxonomic levels, a similar composition in terms of functional groups can indicate that analogous ecological roles and processes may be present. In that case, artificial reefs could be expected to react similarly to stressors facing natural reefs and may contribute to the health and resiliency of broadly connected populations. Results from this study will be of interest to fisheries managers in describing limits and considerations on the use of artificial reefs for achieving conservation and fisheries-management goals.

2.1 Reef data

Data on natural and artificial reefs located from the WFS up to the Florida panhandle in the NGOM were examined, including artificial and natural reef data from the NGOM and WFS.

Data collected at 27 sites in the eastern NGOM allowed the comparison between unfished and fished artificial reefs. The reefs were deployed by the Florida Fish & Wildlife Conservation Commission (FWC) in the spring of 2003. The coordinates of the reef sites initially went unreported to the public. In July 2007, the FWC Artificial Reef Program released the locations of nine of these artificial reefs on their public database. Between 2003–2007, no evidence of fishing was observed (W. Patterson, Pers. Comm., University of Florida, 7922 NW 71st Street, Gainesville, FL 32653). The sites were surveyed using Remotely Operated Vehicles (ROVs) from 2003–2009 (W. Patterson, Pers. Comm). A point-count method was used to sample a 15-m cylinder around isolated reef habitats and artificial reef modules. During the analysis of video samples by Patterson et al. (2014) and Addis et al. (2016), fish counts were summed and then divided by the estimated area of each sampling site. This provided abundances and population densities of species and life stages.

Data from natural reefs in the NGOM were collected via video surveys at several sites off Panama City Beach, Florida, by National Marine Fisheries Service (NMFS) from 2005–2015 (C. Gardner, Pers. Comm., NOAA, 3500 Delwood Beach Road, Panama City, FL 32408). In 2002, the Panama City NMFS Lab began development of fishery-independent trap surveys of natural reef habitats. In 2005, the collection of stationary video data was added to the existing trap-survey techniques. A combination of high definition digital video cameras and stereo-imaging systems were used at each location. In 2012, a GoPro camera was added to the survey equipment. The camera arrays were unbaited from 2005–2008, but since 2009 have been freshly baited during each deployment. Twenty minutes of video tape were reviewed from each survey, beginning when the cloud of sediment displaced by the landing of the video array had dissipated (Gardner et al., 2017). For consistency, the data used from this source were limited to the visual survey data collected from 2005–2015 by NMFS.

Data from natural reefs and a few of the artificial reefs from the WFS were provided by the Southeast Area Monitoring and Assessment Program (SEAMAP) (T. Switzer, Pers. Comm., Florida Fish and Wildlife Conservation Commission, 100 8th Avenue SE, St. Petersburg, FL 33701). The same equipment and methodology used at the Panama City NFMS Lab was used to collect the data on the WFS reefs from 2008–2015 (Campbell et al., 2014). Natural and artificial reef locations are displayed in Appendix I, Figure 1. To distinguish the differences between community composition of reefs, the data from Patterson, NMFS, and SEAMAP were consolidated into one large dataset. Each species observed was assigned a family name as well as a functional-group name. Functional groups were chosen based on classification methods implemented by Ainsworth and coauthors (2015) within their Atlantis Ecosystem Model for the Gulf of Mexico (Ainsworth et al., 2015). Each observation was then categorized by reef type and location: artificial or natural, and WFS or NGOM. To account for differences in collection methods, the combined data were normalized prior to any statistical analysis.

2.2 Ordination

The first method used to visualize the dissimilarities of the data was a Principle Coordinate Analysis (PCoA). This ordination technique utilizes a user-chosen distance measure and allows for all types of data descriptors to create a representation of the data in a Cartesian coordinate system. A PCoA will produce a set of uncorrelated orthogonal axes that summarize the variability contained within the data set. Each axis provides eigenvalues of varying magnitudes that represent the amount of variation captured by the axis. Each object in the original data set has a 'score' along each axis, which provides the coordinates for the object in the ordination plot (Buttigieg and Ramette, 2014).

A PCoA was performed at the species level, the family level, and the functional-group level. The results are displayed using a Cartesian coordinate plot and a corresponding vector biplot. The vectors are used to represent the coefficients of the principle coordinates. The vectors that point in the same direction correspond to variables that have similar response profiles. Plotting the results of a PCoA provides a visual representation of the magnitude of variance within the data set and the associated biplot indicates which species, families, or functional groups are responsible for generating the variance observed.

2.3 Diversity

In addition to a PCoA, a variety of diversity indices were calculated including Shannon-Wiener Diversity (Equation 1), Species Richness, Rarefied Richness (Equation 2), and Pielou Evenness. The Shannon-Wiener index (also called the Shannon-Weaver or Shannon index) is a metric of biodiversity based on the Shannon entropy function (Shannon, 1948). The index quantifies entropy in the system. The more different species there are and the more equal their abundance in the ecosystem, the more difficult it is to correctly predict which species any particular individual will belong to. Maximum entropy occurs when each component is in equal proportion. H' is entropy, p_i is the proportion of individuals belonging to the i^{th} species, and R is the total number of species.

$$H' = -\sum_{i=1}^{R} p_i \ln p_i \qquad \text{Eq. 1}$$

Rarefied species richness calculated using the Vegan: Community Ecology Package for R by Oksanen and coauthors (2019). It uses the rarefaction diversity measurement of Heck and coauthors (1975) where *E*(S_N) is the expected number of species in a sample of (*n*) individuals selected at random from a data set containing (*N*) individuals and (*S*) species. In this method the number of species (species richness) is calculated for the data to be compared after all data sets are scaled down to the same number of individuals.

$$E(S_N) = S - \binom{N}{n}^{-1} \sum_{i=1}^{S} \frac{N-N_i}{n} \qquad \text{Eq. 2}$$

Diversity indices were calculated for the species, family and functional-group level and categorized by location (West Florida Shelf or Northern Gulf of Mexico) and reef type (artificial reef or natural reef). To determine if the differences in composition at each location or reef type were caused by the presence of rare species, species that made up less than 5% of the observational abundance data were removed, and the diversity index was re-calculated.

2.4 Regression

Generalized Additive Models (GAMs) have been applied to a variety of research areas in science. Originally developed by Hastie and Tibshirani (1990), GAMs were designed to blend the properties of generalized linear models (GLMs) with additive models. The smoothing functions in a GAM allow for non-linear relationships between covariates and target variables. In a GAM, a response variable, Y, is related to some variables, x_j. An exponential family distribution is specified for Y, such as normal, binomial, or Poisson distributions, in addition to a link function g, which relates the value of Y to the predictor variables. The link function specifies the relationship between the predictor and the mean of the distribution function. The smoothing functions, f_i, may be specified as parametric, non-parametric, or semi-parametric depending on the class of the predictor variable, x_i. The basic formula for a GAM is seen in Equation 3:

$$g\big(E(Y)\big) = \beta_o + f_1(x_1) + f_2(x_2) + \cdots + f_m(x_m) \qquad \text{Eq. 3}$$

Utilizing a GAM for this project provided insight to the statistical significance of environmental factors on community composition at the different reef types and locations. The count data were used as the response variables, Y, and the environmental data acted as the predictor variables, x_i. The data were modeled using a negative binomial distribution with a log link function, g. A negative binomial distribution was selected for its ability to accurately depict the variance within a dataset containing many zeros (Barry and Walsh, 2002). Model selection in the GAM formula attempts to determine the suitable smoothness for each term using likelihood-based methods. Using the smoothness selection criterion 'REstricted Maximum Likelihood' or REML approach, the fit of the variance parameters was measured using the average likelihood over all the possible values of β (Wood, 2006). This smoothness selection method was modified by the addition of a small shrinkage component, which adjusted the unimportant smooth terms so that under heavy penalization they were identical to zero and 'selected out' of the model (Wood, 2016). Each smooth term has an associated degree of freedom (df), however, the df are effectively reduced by the application of the smoothing penalties associated with the REML method. Due to this method selection, the results report the effective degrees of freedom, or edf. This component clarifies which smooth terms were down-weighted and helps to measure the flexibility of the model (Wood, 2006).

Lastly, due to nature of ecological data and the vicinity of neighboring reef habitats, our model had to account for existing spatial autocorrelation. The model first converted latitude and longitude to eastings and northings, and the interaction between two these terms in the model equation, *te(X,Y)*, accounted for the spatial autocorrelation at a broad scale (Gruss et al., 2018). Residuals are represent using QQ plots . If the model assumptions were met, the plots displayed a relatively straight line, indicating residuals are randomly situated around the mean. The GAM was fitted using the 'mgcv' package in RStudio version 1.0.143 environment (Wood, 2016). I developed GAMs for Lutjanidae (Snappers) and Carangidae (Jacks) at the family level, and Small Reef Fish, Red Snapper, and Jacks at the functional-group level. Since Family Carangidae and the Jack functional group are identical, only one GAM was developed for this group.

The environmental predictors incorporated into each GAM equation included depth, bottom salinity, bottom temperature, bottom dissolved oxygen (DO), turbidity, current speed, chlorophyll-a concentration, and distance from shore. Smoothing functions were used for depth, bottom salinity, bottom temperature, bottom DO, turbidity, current speed, chlorophyll-a and distance from shore, each based on a thin-plate regression spline and employing 4 knots per spline. Binary predictors represented whether reefs were artificial or not, and whether they were located on the WFS or not. Sampling month and year were also included to identify any seasonal or interannual variation. The converted GPS coordinates were also included as (X,Y) and a tensor product [te()] smoothing function was applied. A tensor product can be used to model nonlinear interactions between covariates of different scales, such as latitude and longitude. Including latitude and longitude as a spatial coordinate as opposed to separate smoothed terms allowed the GAM to analyze distances between observations

2.5 Environmental data

The GAM utilized environmental data compiled by Gruss and coauthors (2018) to explain the spatial distribution patterns of organisms in the GOM. The database included categorical variables such as sediment type and presence/absence of seagrass, continuous variables such as bottom depth and SST, and “climatologies” that depicted long-term, average monthly environmental conditions from 2000-2016. Examples of these data include bottom salinity and current speed. The database created by Gruss and coauthors (2017) is now housed by the Gulf Research Initiative and Data Cooperative (GRIIDC). The GRIIDC Data and Discovery portal provides researchers the opportunity to search for and download a variety of data collected since the year 2000 throughout the Gulf of Mexico. Using global positioning system coordinates, an assortment of environmental data was downloaded from GRIIDC to correspond with the reef site locations from the WFS and NGOM. Environmental data chosen for this research included bottom salinity, bottom temperature, distance from shore, current speed, chlorophyll-a, bottom dissolved oxygen, turbidity, and depth.

3. RESULTS

3.1 Principle Coordinate Analysis

At the species level (Fig.1A,B), the first and second principle coordinate axes together describe approximately 18% of the variation within the data. This indicates that, at the species level, natural and artificial reefs in both the NGOM and WFS are relatively distinct from one another. The relationship depicted in Figure 1A shows some overlap of the natural reef sites in both regions. Artificial reefs in the NGOM appear to be isolated from the majority of other observations, clustering tightly together in one quadrant of the plot. This can be further explained by examining the vector biplot (Fig. 1B). The vector representing Red Snapper (*Lutjanus campechus*) indicates that this species is driving the differences between NGOM artificial reefs and all other reefs examined. Overall, at the species level, reef type and location have the most influence on community structure.

As hypothesized, classifying individual species into their respective families resulted in more similarities between the different reef types and locations (Fig. 2A,B). The variance explained increased to over 40% and all data points shifted closer together. The vector representing the Snapper family, Lutjanidae, showed a high level of correlation with the artificial reef observations in the NGOM, consistent with the results of the species-level analysis. According to the vector biplot (Fig. 2B), other species of interest also drove differences between reef observations at this level. There appeared to be reefs that are strongly associated with the Jack family, Carangidae, as well as reefs associated with a variety of small-bodied families, Labridae (Wrasse), Sparidae (Porgies), Serrandiae (Seabass), and Haemulidae (Grunts). Both of these clusters primarily consisted of natural reef sites on both the WFS and the NGOM.

At the functional-group level (Fig. 3A,B), the variance explained was almost identical to the variance observed at the family level. The specific functional groups chosen were based on the importance of the species relative to their habitat and their functional role in the community. Examining the vector biplot (Fig. 3B), the Jack group was strongly correlated with many natural reef habitats on both the WFS and the NGOM. Due to their importance and presence throughout the Gulf of Mexico, Red Snapper were assigned their own functional group. This particular vector correlated strongly with the artificial reef habitats in the NGOM, consistent with the species and family level analyzed. The functional group Small Reef Fish had a long vector present on the vector biplot, strongly correlating with natural reef communities in both locations. This was consistent with the family level results as Labridae, Sparidae, Serrandiae, and Haemulidae were all major families categorized into this functional group. Two additional prominent vectors were Large Reef Fish and Other Demersal Fish, both of which correlated largely with the artificial reef sites in the NGOM. Fishes categorized into these functional groups included many snapper and grouper species.

Coordinates associated with the major clusters relative to specific families and functional groups were plotted in ArcGIS (Fig. 5–7, and Appendix I, Fig. 1). The maps created indicated that Reef Fish were found at a variety of depths from shallow coastal waterways out to the shelf edge at 200 m. There was also an apparent gradient at the family level, in plotting Carangidae and Lutjanidae, as well as at the functional-group level, in plotting Red Snapper and Jacks. Carangidae and Jacks are identical groups, therefore the coordinate points are the same for each map. Family Carangidae (Jacks) occurred on reefs in more shallow waters. Observations were concentrated from <20 m out to ~35–40 m depth. There were relatively few observations of this family beyond 50 m depth. Family Lutjanidae and Red Snapper rarely occurred in waters shallower than 20 m. They began to appear in higher concentrations at ~35 m and were observed as deep as ~150 m. These groups appeared to overlap substantially at reefs located in a depth range of ~35–50 m. Notably, all the artificial reef sites monitored are in relatively shallow waters, <50 m. The natural reef sites observed spanned a depth range of <20 m out to the shelf edge ~200 m.

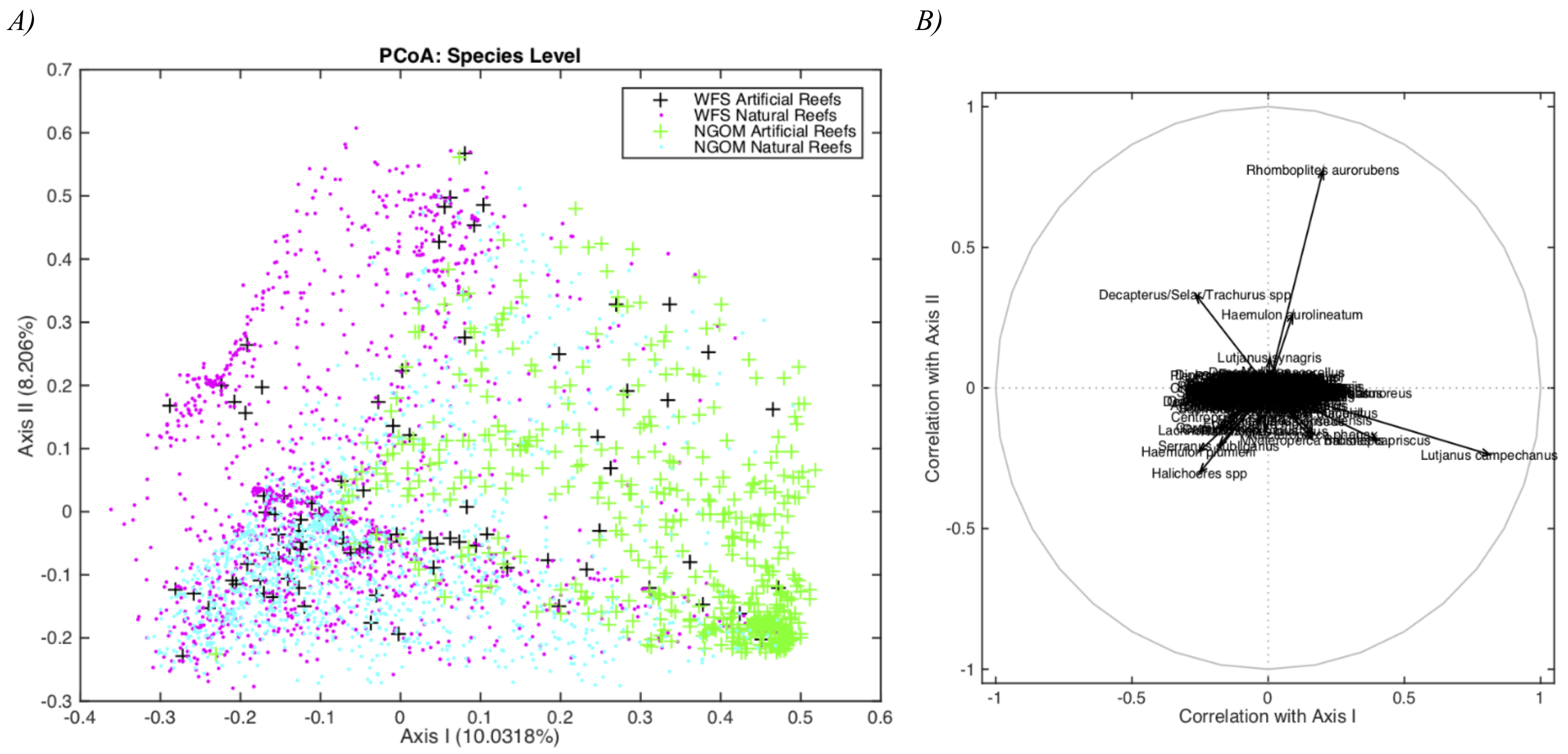

Figure 1 Principle Coordinate Analysis at the species level. A) Each point represents a single observation at a given time, B) Vector Biplot.

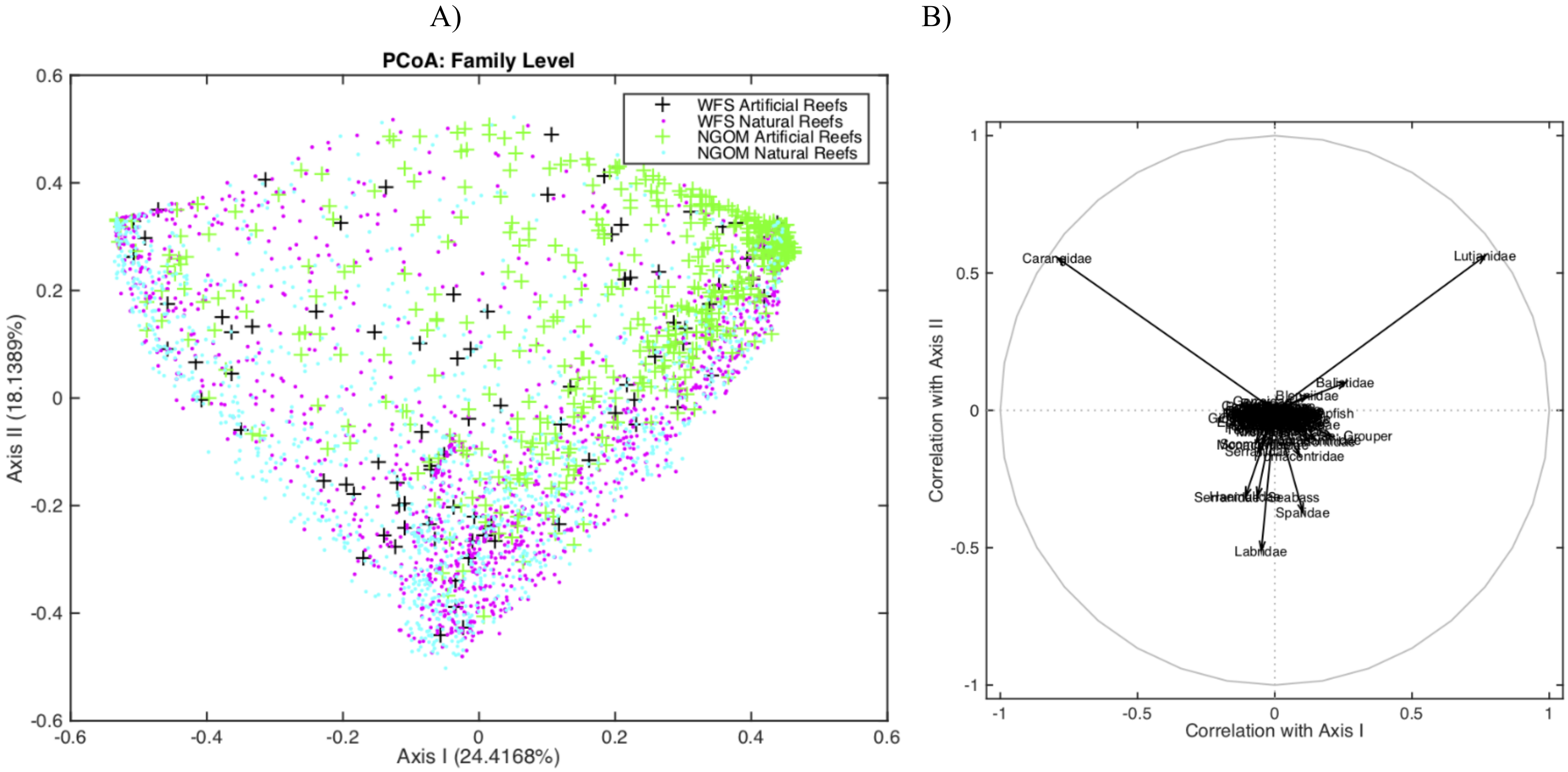

Figure 2 Principle Coordinate Analysis at the family level. A) Each point represents a single observation at a given time, B) Vector Biplot.

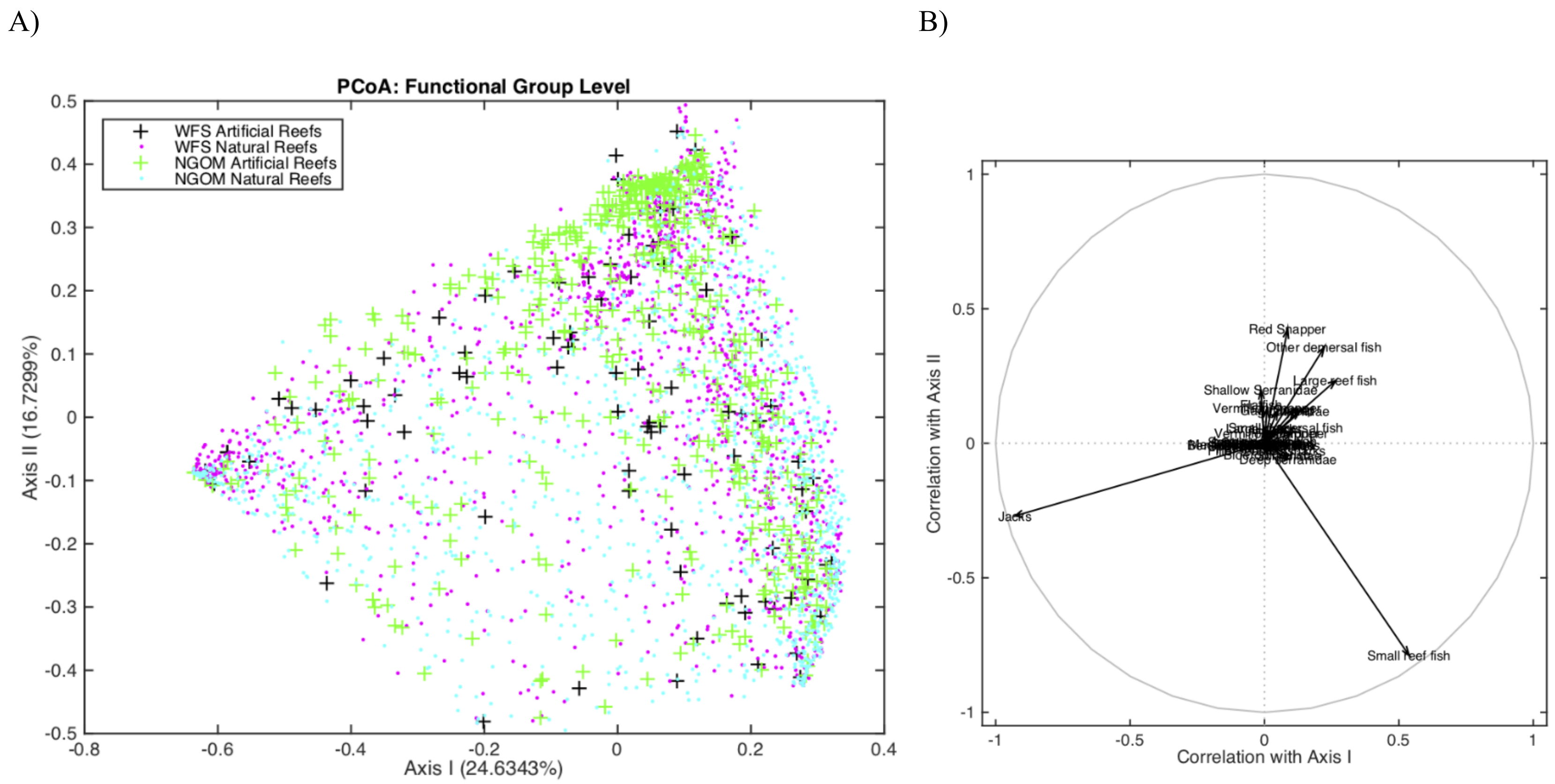

Figure 3 Principle Coordinate Analysis at the functional group level. A) Each point represents a single observation at a given time, B) Vector Biplot.

3.2 Diversity

The Shannon-Wiener Diversity Index and Rarefied Richness results are displayed in Figure 4(A,B). The Species Richness and Pielou Evenness results are displayed in Appendix I, Figures A2-A3. Regarding this study, the standard richness measure was not particularly useful as it strongly reflects sampling opportunities. Therefore, rarefied richness was the primary focus. The Shannon Diversity is mostly reflecting evenness in the case of this study. The Pielou Evenness results were very similar and included in Appendix I, Figure 2B. The box plots for all diversity measures have similar results and show that the diversity of species is similar at all levels and are not likely to be statistically significant. However, there are a few noteworthy observations made from the series of plots. There is a slight difference in the diversity at the species level compared to the functional group level. When comparing the two locations, the NGOM has a marginally higher diversity at the species level than the WFS, but this difference is lost at the functional group level. The range of diversity, regarding both evenness and richness, appears to vary more on natural reefs compared to artificial reefs. Lastly, the removal of the rare species decreases the diversity index for each group and at each level of taxonomic resolution.

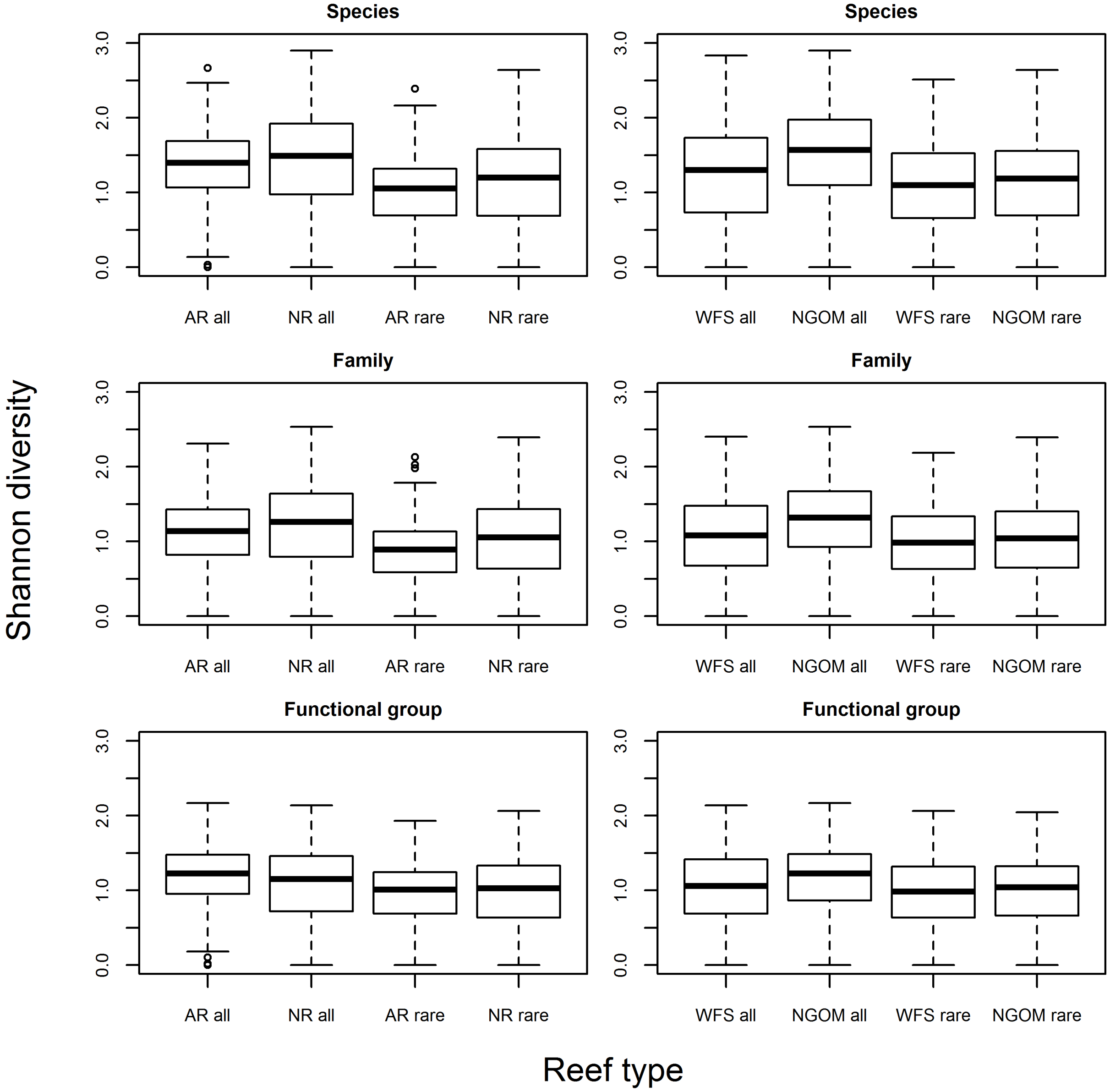

Figure 4A: Shannon-Weiner Diversity Index for Artificial compared to Natural Reefs and WFS compared to NGOM at the species, family, and functional group level.

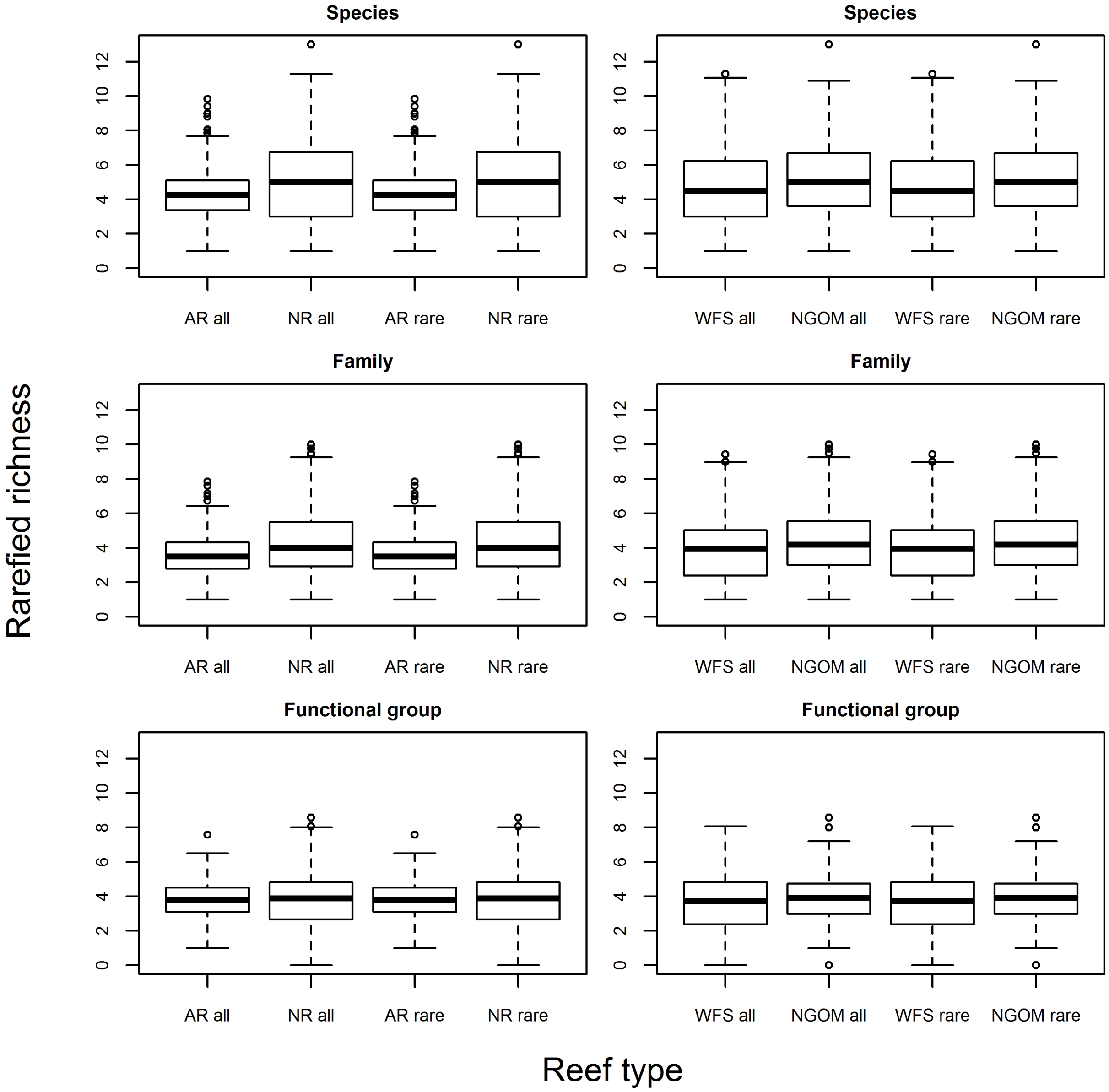

Figure 4B: Rarefied Richness for Artificial compared to Natural Reefs and WFS compared to NGOM at the species, family, and functional group level.

3.3 Generalized Additive Model

The coefficients and fits of each model are displayed in Appendix I, Tables A1-A8, and in Figures A4-A7. The smoothed terms for each model were plotted and presented in Appendix I, Figures. Appendix I, Figure A8 contains the QQ plots, which indicate the overall fit of each model. Based on the results of the QQ plots, all four models fit the data very well. Results for Lutjanidae indicate that all environmental variables except Current Speed had significant impacts on the count observations of this family. The most influential environmental factors included the coordinate location, bottom temperature, distance from shore, and depth. The prominent parametric coefficients were reef type and location. The percent deviance explained by the model for this family was ~62%. The most significant smoothed terms for Family Carangidae were the coordinate location, depth, and distance from shore. Both reef type and location were significant, and the percent deviance explained by this model was ~42%. The model summary for the functional group Small Reef Fish presented equally significant p-values for coordinate location, bottom salinity, and bottom temperature. Current speed, chlorophyll-a concentration, and depth also displayed slightly larger but significant p-values. The parametric coefficients had varying levels of significance. This functional group had significant p-values for each individual sampling year as well as reef type and location. The percent deviance explained by this model was ~56%. The Red Snapper summary displayed significant p-values for coordinate location, bottom salinity, current speed, turbidity, and chlorophyll-a concentration. The important parametric coefficients included sampling years 2005–2008 and 2011–2014. The reef type and location also had very low p-values. The percent deviance explained by this model was ~85%. To determine differences in sample years for the Red Snapper, a t-test was run on the sampling years before and after fishing commenced. This test detected a significant difference ($p<5.6e^{-5}$)

between the means of sample years before and after fishing. Figures 5–7 present maps of the study area. Figure 5 displays the locations of the family observations for both Lutjanidae and Carangidae, Figure 6 displays the locations of the functional-group observations for Red Snapper, and Figure 7 displays locations of the Small Reef Fish observations.

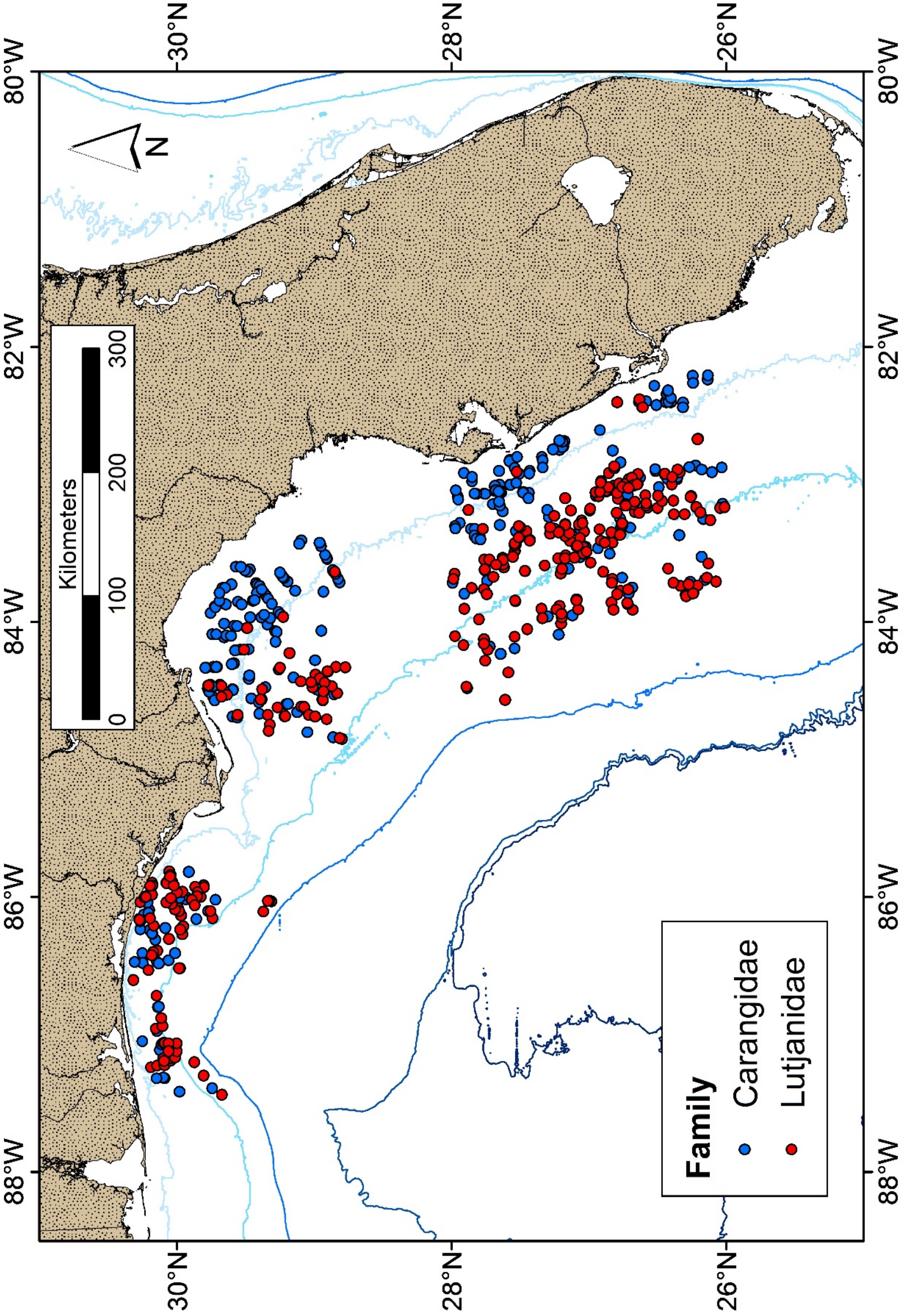

Figure 5: Distributions of the Families Carangidae and Lutjanidae

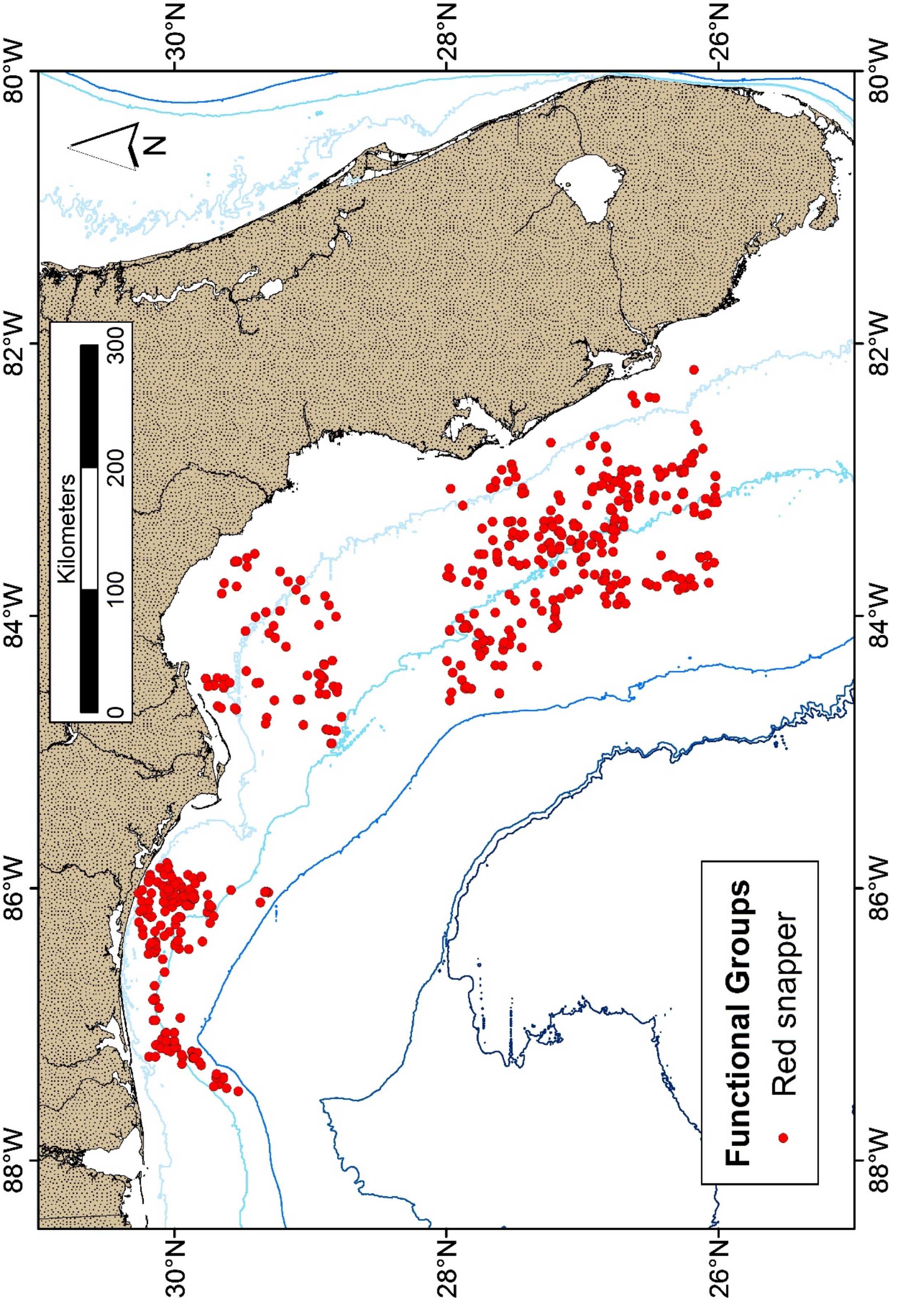

Figure 6: Distribution of the Red Snapper Functional Group

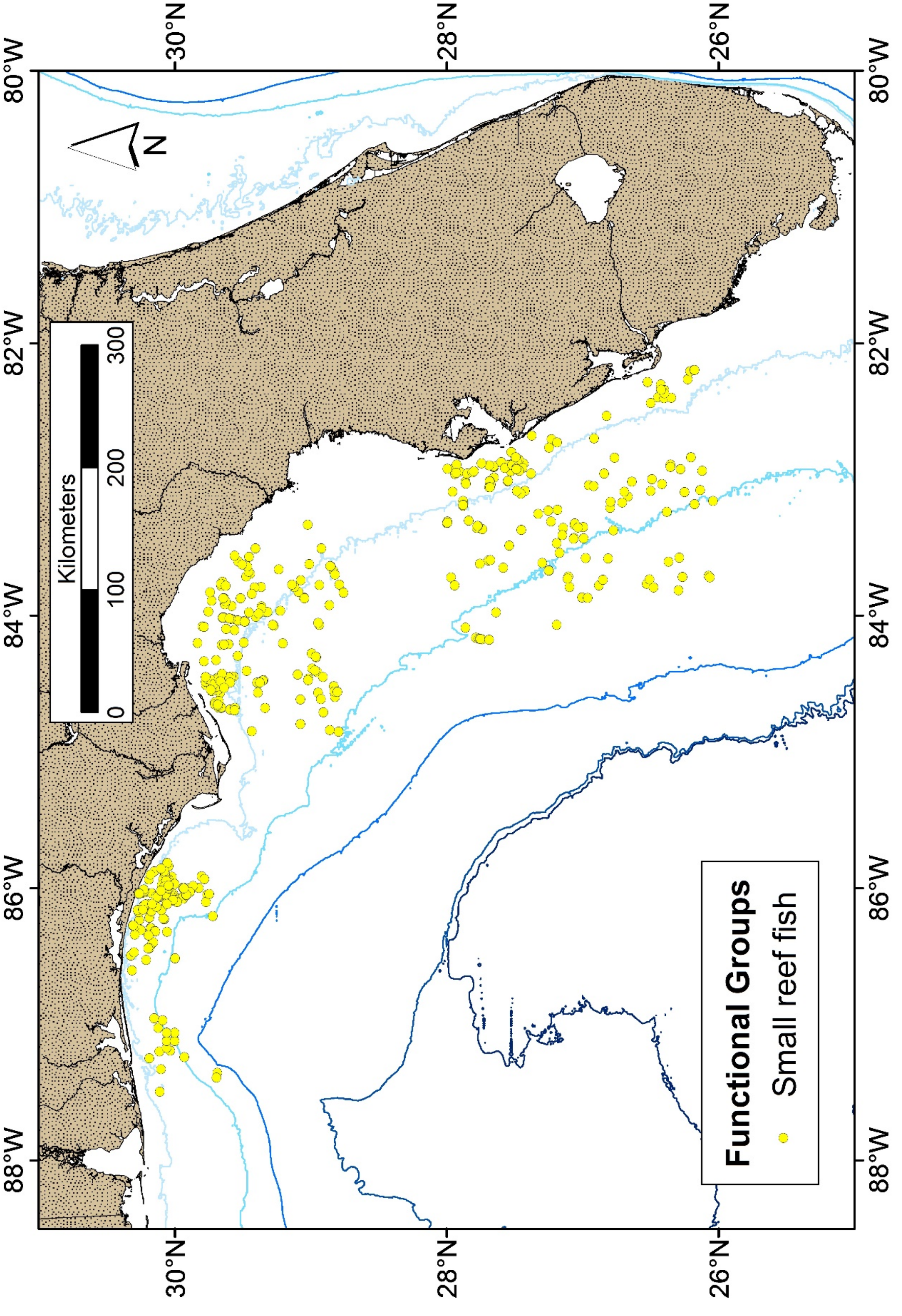

Figure 7: Distribution of the Small Reef Fish Functional Group

4. DISCUSSION

The first research question of this study was: “How does community structure differ between natural and artificial reefs?” The working hypothesis was that, when examining community composition at the species level, the reefs would be different, but when examining composition at the level of functional groups, the reefs would appear more similar indicating that similar niches and functional roles were filled. The results of the PCoA support this hypothesis as the variability explained increased from ~18% at the species level, to >40% at the family and functional-group level. The variance explained at the family and functional-group levels were almost identical. Results at the family level indicated that species composition was indicative of the presence of certain dominant families. The three major clusters on the PCoA plot were (1) Lutjanidae, (2) Carangidae, and a combination of (3) Labridae, Sparidae, Haemulidae, and Serranidae (Seabasses specifically). While there were clearly defined clusters of observations in ordination space, there was also a substantial amount of overlap, indicating a continuous gradient in reef-assemblage composition between these clusters. Both natural and artificial reefs as well as reefs in the NGOM and WFS were all present within the gradients. A possible explanation for the overlap could be the role of environmental conditions in determining the assemblage, which suggests that the functional differences between natural and artificial reefs are not entirely inherent.

While the box plots displaying the diversity indices (Fig. 4A,B; Appendix I, Fig. 2A,B) did not present statistically significant results, they provided additional support for the first hypothesis and the results of the PCoA. The Shannon diversity and Rarefied Richness differences between reef type and location are larger at the species level and smaller at the functional group level, which is consistent with the hypothesis that similar functional roles are occupied on natural and artificial reefs. As shown in all diversity measures, there was a slightly larger range of species diversities observed across natural reefs compared to artificial reefs, which would be the case if artificial reefs offered less varied habitat. Natural reef substrate throughout the eastern Gulf includes both hard and soft bottom habitat consisting of numerous combinations of ancient limestone reefs, carbonate banks, foraminifera-pteropod ooze, and siliciclastic sediments of varying grain size. Natural reef habitats in this region also display a variety of relief patterns due to the array of current physical oceanographic processes as well as influences from paleoclimate events such as the Last Glacial Maximum (Hine et al., 2008). Upon removing species observations that accounted for <5% of the total species abundance, the diversity differences between the WFS and the NGOM were no longer detectable at any level of taxonomic resolution. This suggests that differences between WFS and NGOM may be driven by the presence of rare species.

In their usual role as fish aggregation sites, artificial reefs are known to aggregate valuable exploited species (Grossman et al., 1991; Bohnsack, 1997; Lindberg, 1997; Wilson et al., 2002). However, it does not necessarily follow, and in fact may be a surprise, that a complex assemblage of non-exploited species is also typically found on these structures. Here the Shannon Diversity Index and Rarefied Richness indicate that biodiversity present on natural and artificial reefs and on NGOM and WFS reefs is not statistically different. This does not mean that the species composition is the same. The PCoA highlights those differences in species composition when comparing reef types and location. It is not possible to conclude within the scope of this study to what degree exploited species are supplemented with local production at these artificial reefs, or whether they are dependent on prey from elsewhere.

Red Snapper is a dominant species on artificial reefs in the NGOM and is a valuable and important species throughout the Gulf of Mexico. Their populations have been studied in this region over the past several decades, including their use of artificial reef habitat (Patterson et al., 2009, 2014; Dance et al., 2011; Ouzts and Szedlmayer, 2011; Addis et al., 2013, 2016). The two other dominant functional groups are Jacks and Small Reef Fish, both of which appear to favor natural reef habitats. The Small Reef Fish functional group contains the prominent families observed in the PCoA family results, Labridae, Sparidae, Haemulidae, Serranidae—Seabasses. Figure 5 provides the locations of the clusters generated by Lutjanidae and Carangidae and depicts a clear gradient in the distribution of these families. Reefs closest to shore appear to be dominated primarily by Jacks. Further offshore, the dominant taxa shift to Snappers. The region where these families overlap lies between ~35–50 m depth. Research on Carangidae species in the Gulf of Mexico indicates that they dominate neritic waters and are most commonly found among shallow coastal regions (<100 m) as well as throughout inshore habitats (Froese and Pauly, 2018; Smith-Vaniz, 2018). Numerous studies on the life history of many species found throughout the gulf reveal that the population densities of Carangidae are typically highest at 15–75 m depth (Smith, 1976; Leak, 1981; Chen, 2017; Smith-Vaniz, 2018).

The distribution of Lutjanidae species has also been widely studied in the Gulf of Mexico and the depth ranges of the species included within the data set range from 55–110 m (Smith, 1976; Mitchell et al., 2004; Gallaway et al., 2009; Chen, 2017). Thus, the gradients observed (Fig. 5) are consistent with results from those previous studies. The WFS and the Pensacola regions of the NGOM include both artificial and natural reef sites, whereas the Apalachee Bay region of the NGOM includes only natural reef sites. The width of the continental shelf in each of these regions is also different. The shelf narrows from southwest Florida towards the panhandle. This distribution gradient is observed at all locations regardless of shelf width, indicating that the change of habitat size does not necessarily affect the dynamics observed from the shore to the edge of the shelf. However, local circulation could affect nutrient or larval supply and influence species composition. These factors were not taken into account by the GAMs used here and could play a role for all groups observed. These results brought attention to the next research question: "How does the environment and location affect community structure?"

The second research question was, "How do environmental conditions influence species composition?" I examined how environmental features predicted the presence of dominant fish families and functional groups: Lutjanidae, Carangidae, Small Reef Fish, and Red Snapper. The most significant term seen in all four models was the coordinate location, *te(X,Y)*, indicating a strong degree of spatial autocorrelation, meaning that reefs closer together have similar compositions. Presumably, this may indicate a high rate of exchange of adult fish or it may indicate that proximal reefs experience similar patterns of larval settlement. In either case, this indicates the interconnected nature of reef ecosystems. Connectivity has become a crucial aspect of conservation due to its importance to population perseverance and disturbance recovery (Salm et al*.*, 2006). While each model displayed significant p-values for both reef type (artificial vs. natural) and location (WFS vs. NGOM), these values were highly variable between species, indicating that reef type may be more important than location, or vice versa, when it comes to habitat selection, depending on the species.

The model representing Lutjanidae had several important environmental parameters. In addition to the coordinate location, the bottom temperature, depth, and distance from shore were all significant (see Appendix I, Table 1A-B). Reef type and location were equally significant for this family as well. There were relatively few observations of Lutjanidae at depths <20 m (Fig. 5); the majority of observations lie between 20–200 m.

Family Carangidae had just two additional significant environmental parameters, depth and distance from shore. This was consistent with the results from mapping the PCoA observations, which indicated that reefs dominated by Carangidae appeared shallower, ranging from the shallowest reefs out to ~45–50 m (Fig. 5). The Family Carangidae also had significant p-values for both reef type and location, with the stronger correlation to location. Based on the data and PCoA results, Carangidae appeared to be more dominant on the WFS compared to the NGOM, as well as on natural reef sites compared to artificial. This indicates that there may be specific qualities of natural reef habitats that are preferred by species of Carangidae.

The two functional groups examined geographically and in the GAM were Red Snapper and Small Reef Fish. All parameters analyzed except distance from shore and dissolved oxygen were deemed significant to reefs dominated by Small Reef Fish. Geographically, Figure 7 shows the wide range of reef locations dominated by this functional group (<20 m – 200 m). Closer examination of the species and families that make up this group helped to explain this trend, as this group included a large array of families that occupy a wide variety of niches within any given community. Herbivores, planktivores, and small carnivores are all classified into this functional group. The significant environmental parameters included salinity, bottom temperature, current speed, and chlorophyll-a concentration, all of which can influence the variety of dietary needs required by this large and diverse group. There was also variation in the p-values associated with reef type and location. Reef type was a highly significant parameter and location was also significant despite a relatively high p-value. This is consistent with the PCoA results indicating that reefs dominated by Small Reef Fish were primarily natural reefs throughout both locations. The variety within this functional group could offer an explanation for the higher p-value for location, as the species and families represented by this group are found throughout the Gulf of Mexico.

The significant parameters for the Red Snapper functional group included salinity, turbidity, current speed, and chlorophyll-a concentration. Consistent with the PCoA plots seen in Figures 1–3 and Figure 6, which illustrate that Red Snapper dominate artificial reefs in the NGOM, GAM results revealed that reef type and location were also highly significant. The use of artificial reefs by Red Snapper has been widely studied in recent years (Patterson et al., 2001, 2011; Addis et al., 2007; Strelcheck et al., 2007; Shipley and Cowan, 2011; Tarnecki and Patterson, 2015). Research on the diet of Red Snapper in the Northern Gulf of Mexico has shown that they feed primarily on the outskirts of the reef habitats where they reside. The deployment of artificial reefs has the potential to provide additional refuge habitat among natural reef habitats as well as farther offshore allowing them to utilize feeding grounds that would otherwise be inaccessible (Tarnecki and Patterson, 2015). The results of the PCoA and the GAM both indicated that artificial reefs are important to Red Snapper. The supplemental research regarding diet and feeding strategies offers a possible explanation of the role artificial reefs have on the life history patterns of Red Snapper in the Northern Gulf of Mexico region.

A noteworthy observation from the GAM results for Red Snapper was the specific sampling years that were characterized as significant. The artificial reefs in the NGOM were deployed by FWC in 2003 and sampling began in 2005. During the first two and half years of sampling, none of the coordinates to these reefs were released to the public. In July 2007, locations for 9 out of the 27 reef sites were posted on the FWC's artificial reef online database. The results of the GAM for this group indicated that sampling years 2005, 2006 and 2007 were highly significant, followed by a less significant sampling year 2008, and sampling year 2009 lacking a significant p-value. This demonstrates the importance of artificial reefs providing refuge habitat for important species if they are protected from fishing. In support of these findings, research performed on these artificial reefs suggested that, prior to coordinate release, there was no evidence of fishing on the reef. After the locations were revealed, fishing line and tackle fouled the artificial reef structures (Patterson et al., 2009; Addis et al., 2013, 2016). For sampling years 2010–2014, the p-values were weakly significant, with much stronger significance seen in years 2005–2007.

The GAM results led to the final question: “How do artificial reefs respond to fishing?” To corroborate the GAM results, the Red Snapper observations from the artificial reefs in the NGOM were grouped into two categories based on sample year, observations recorded before and after release of coordinates to the public. A t-test detected a significant difference between the means of these two groups. This supported the results observed in the GAM and indicated that fishing on artificial reefs had a significant impact on fish populations.

In 2010 there were two major environmental impacts in this region, The Deepwater Horizon Oil Spill (DWH) and the Lionfish invasion (Fogg et al., 2016). Numerous studies have attempted to examine the overall health impacts on commercially important species caused by the DWH oil spill. All research indicates that reproduction, growth, and general fitness were affected to some degree (Ainsworth et al., 2017; Herdter et al., 2017). During the same time period, Lionfish populations were growing exponentially and are likely to have created a shift in the community structure of reef habitats throughout the Gulf. Lionfish are generalists and have a large dietary range, including prey items of the Red Snapper. Additionally, after 2010 the frequency of surveys of these particular artificial reef modules was drastically reduced. Due to the variety of changes taking place during these sampling years, the results displayed by the GAM could have been influenced by a number of factors.

5. CONCLUSION

The results of this study suggest that both natural and artificial reef fish assemblages on the WFS and NGOM are different at the level of species, but have similar functional roles fulfilled. The analysis of a suite of environmental conditions indicates that reef type and location are not the only factors determining community composition. Regardless of reef type or location, there were sites dominated specifically by family Carangidae, family Lutjanidae, Small Reef Fish, and Red Snapper, each of which were impacted by a unique set of environmental conditions. Based on the exploration of a variety of diversity measures, the differences observed at the species level between the two locations can be driven by the presence of rare species, accounting for <5% of the community composition; whereas the difference between natural and artificial reef types appear to be driven by the dominant species present. Contrary to expectations, artificial reefs do include a full fish community, not just select target species, with similar overall biodiversity to natural structures in terms of richness and evenness. Connectivity among artificial and natural habitats is also evident. Expanding research to focus on the role of artificial reefs with respect to connectivity could provide valuable information for future management applications of artificial reefs. There are numerous objectives surrounding the use of artificial reefs. Some expectations are for artificial reefs to provide additional food, supplement production of natural reefs, and provide recruitment habitat for settling individuals that would otherwise have been lost to the population. These benefits will depend on production versus attraction effects of artificial reefs, which the present study did not attempt to address.

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APPENDIX I

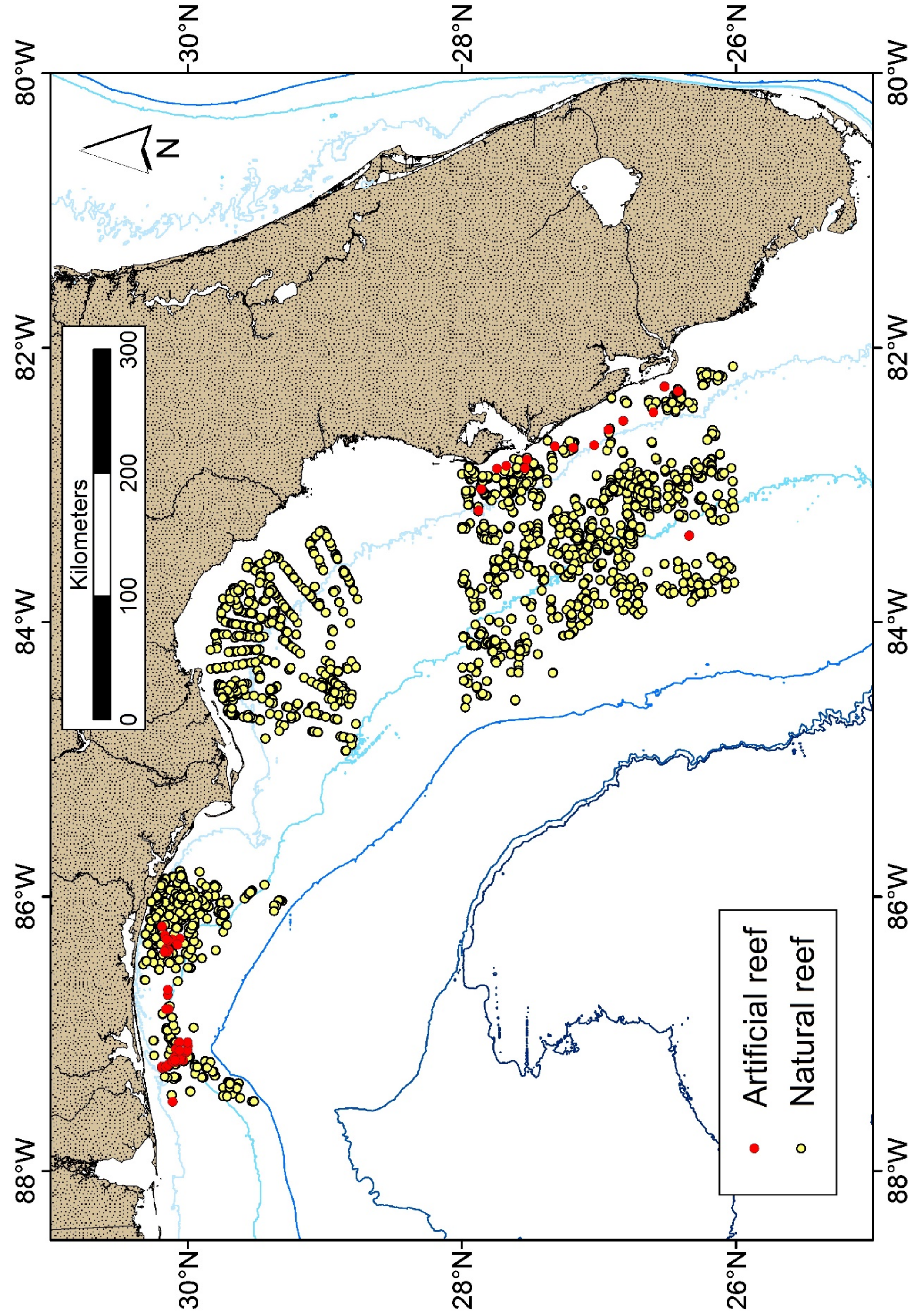


Figure A1: Map displaying Artificial and Natural Reef locations from all datasets

Figure A2: Species Richness for Artificial compared to Natural Reefs and WFS compared to NGOM at the species, family, and functional group level.

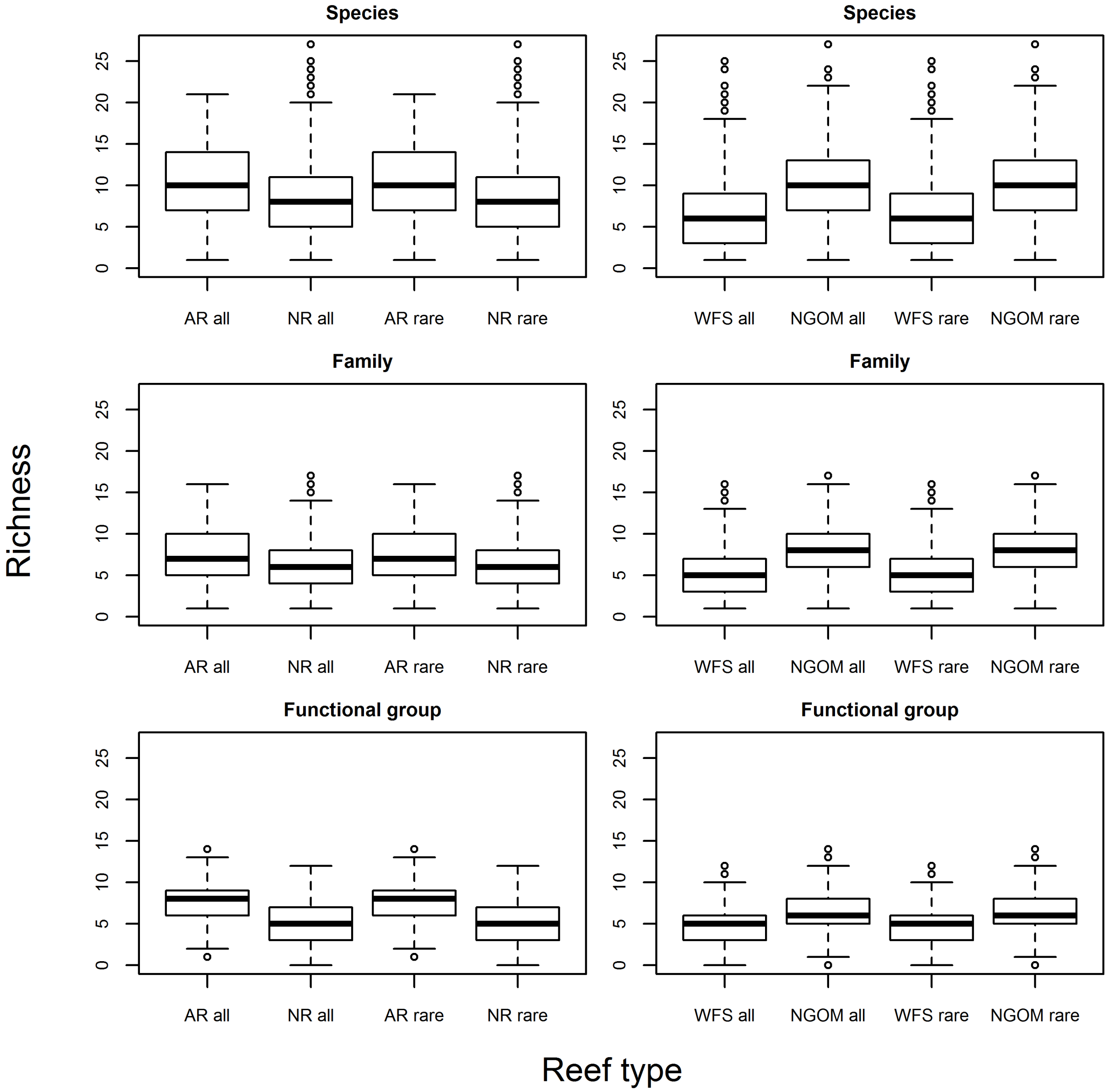


Figure A3: Pielou Evenness for Artificial compared to Natural Reefs and WFS compared to NGOM at the species, family, and functional group level.

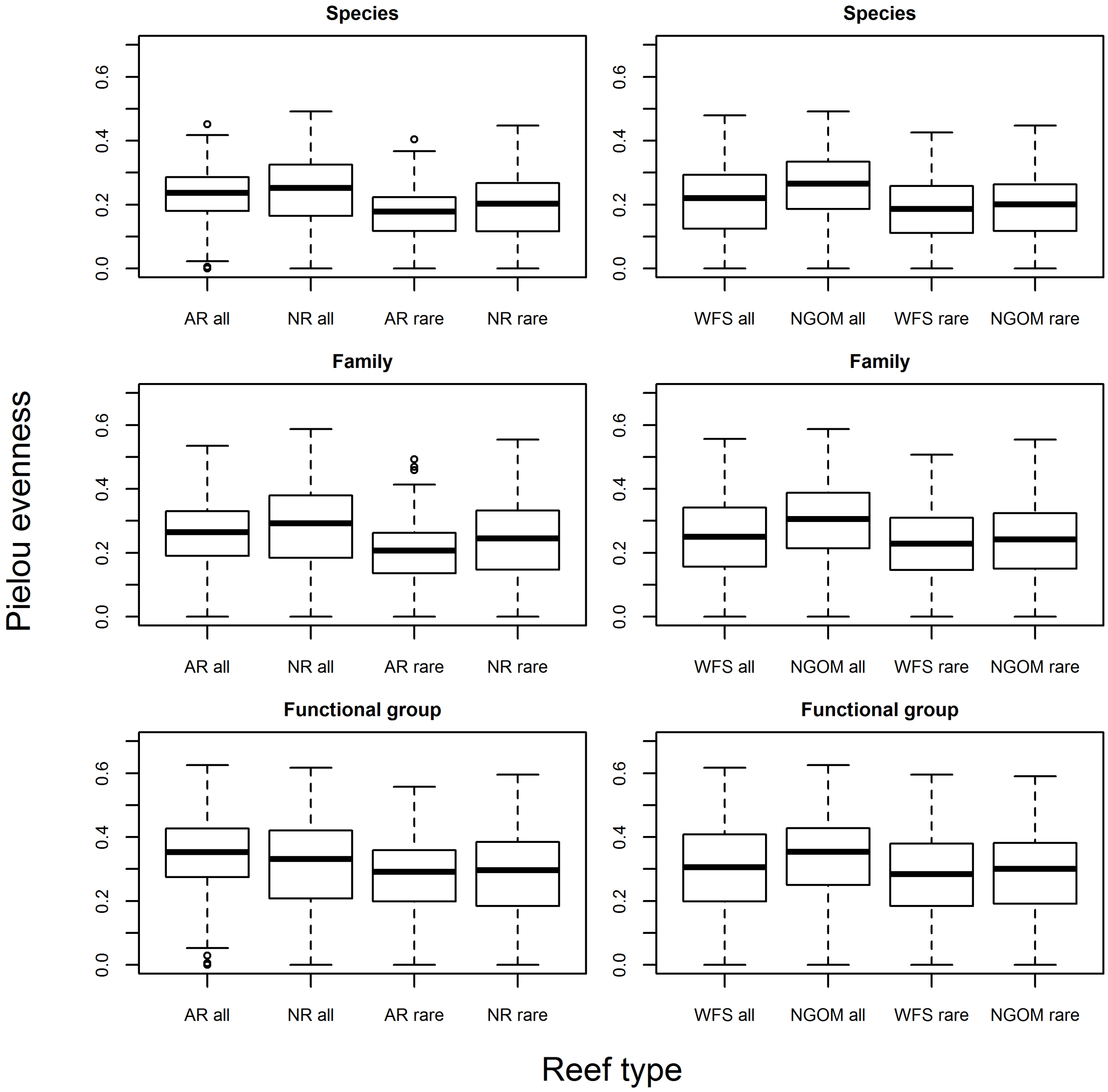


Table A1: GAM Results – Family Lutjanidae non-parametric coefficients

Smooth terms	**p-value**		**edf**	**Chi.sq**
te(X,Y)	< 2E-16	*	16.88	356.93
s(Depth)	1.99E-08	*	2.79	34.35
s(Bottom.Salinity)	1.75E-4	*	0.89	8.39
s(Bottom.Temp)	< 2E-16	*	2.73	94.50
s(Bottom.DO)	4.65E-2	*	0.66	1.85
s(Turbidity)	1.57E-05	*	2.20	17.15
s(Current.Speed)	8.67E-1		0.00	0.00
s(ChlA.Conc)	1.13E-3	*	0.92	5.71
s(Distance.from.shore)	6.12E-15	*	2.77	58.79

(*) and (.) indicated significant p-values

Table A2: GAM Results – Family Lutjanidae parametric coefficients

Parametric Coefficients		**p-value**	
Month3	-0.45	1.23E-01	
Month4	-0.12	5.64E-01	
Month5	-0.34	9.30E-02	.
Month6	-0.05	8.15E-01	
Month7	-0.32	9.81E-02	.
Month8	-0.22	2.64E-01	
Month9	-0.38	6.30E-02	.
Month10	-0.14	5.05E-01	
Month11	-0.09	6.88E-01	
Month12	-0.12	5.98E-01	
Year2005	0.62	1.95E-02	*
Year2006	0.68	1.46E-02	*
Year2007	0.57	3.14E-02	*
Year2008	0.49	8.27E-02	.
Year2009	0.20	4.66E-01	
Year2010	0.08	7.95E-01	
Year2011	-0.12	6.83E-01	
Year2012	0.21	4.75E-01	
Year2013	0.20	5.01E-01	
Year2014	0.66	1.93E-02	*
Year2015	0.28	3.28E-01	
Year2016	0.42	1.89E-01	
isWFS1	-1.64	<2E-16	*
isAR1	1.21	<2E-16	*

(*) and (.) indicated significant p-values

Table A3: GAM Results – Family Carangidae non-parametric coefficients

Smooth Terms	**p-value**		**edf**	**Chi.sq**
te(X,Y)	< 2E-16	*	18.61	616.10
s(Depth)	< 2E-16	*	2.90	76.63
s(Bottom.Salinity)	3.66E-01		0.01	0.01
s(Bottom.Temp)	4.64E-01		0.01	0.00
s(Bottom.DO)	3.93E-01		0.06	0.04
s(Turbidity)	9.25E-01		0.00	0.00
s(Current.Speed)	2.96E-01		0.29	0.31
s(ChlA.Conc)	7.97E-01		0.00	0.00
s(Distance.from.shore)	8.00E-09	*	1.29	33.71

(*) and (.) indicated significant p-values

Table A4: GAM Results – Family Carangidae parametric coefficients

Parametric Coefficients		**p-value**	
Month3	0.37	5.49E-01	
Month4	0.98	2.02E-02	*
Month5	-0.38	3.48E-01	
Month6	0.71	6.67E-02	.
Month7	0.09	8.15E-01	
Month8	-0.23	5.53E-01	
Month9	0.56	1.56E-01	
Month10	0.32	4.32E-01	
Month11	-0.59	1.65E-01	
Month12	-0.15	7.42E-01	
Year2005	0.44	4.47E-01	
Year2006	2.09	3.84E-04	*
Year2007	2.12	1.53E-04	*
Year2008	2.16	2.75E-04	*
Year2009	1.98	7.94E-04	*
Year2010	2.20	2.65E-04	*
Year2011	5.65	< 2E-16	*
Year2012	2.58	1.53E-05	*
Year2013	2.86	2.36E-06	*
Year2014	1.76	3.12E-03	*
Year2015	2.50	2.84E-05	*
Year2016	1.15	9.04E-02	.
isWFS1	-1.17	1.13E-11	*
isAR1	0.72	3.05E-04	*

(*) and (.) indicated significant p-values

Table A5: GAM Results – Functional Group Small Reef Fish non-parametric coefficients

Smooth terms	p-value		edf	Chi.sq
te(X,Y)	< 2E-16	*	18.98	653.40
s(Depth)	2.70E-10	*	2.49	40.30
s(Bottom.Salinity)	< 2E-16	*	2.99	357.86
s(Bottom.Temp)	< 2E-16	*	2.96	226.47
s(Bottom.DO)	5.85E-01		0.00	0.00
s(Turbidity)	3.95E-03	*	0.90	7.13
s(Current.Speed)	6.11E-16	*	2.83	69.16
s(ChlA.Conc)	3.41E-14	*	2.91	57.47
s(Distance.from.shore)	6.18E-01		0.00	0.00

(*) and (.) indicated significant p-values

Table A6: GAM Results – Functional Group Small Reef Fish parametric coefficients

Parametric Coefficients		p-value	
Month3	-0.66	2.50E-01	
Month4	-0.53	2.41E-01	
Month5	-1.30	1.12E-03	*
Month6	-0.43	2.81E-01	
Month7	-1.17	3.20E-03	*
Month8	-1.23	1.88E-03	*
Month9	0.01	9.79E-01	
Month10	-0.77	5.37E-02	.
Month11	-0.45	3.05E-01	
Month12	-0.18	6.87E-01	
Year2005	1.20	7.89E-03	*
Year2006	2.14	1.76E-06	*
Year2007	2.21	1.81E-07	*
Year2008	2.57	8.44E-09	*
Year2009	2.35	1.10E-07	*
Year2010	2.41	7.26E-08	*
Year2011	4.48	< 2E-16	*
Year2012	2.64	3.91E-09	*
Year2013	2.41	8.41E-08	*
Year2014	1.79	5.89E-05	*
Year2015	2.19	9.48E-07	*
Year2016	2.37	4.57E-07	*
isWFS1	-0.41	1.26E-04	*
isAR1	1.91	< 2E-16	*

(*) and (.) indicated significant p-values

Table A7: GAM Results – Functional Group Red Snapper non-parametric coefficients

Smooth terms	**p-value**		**edf**	**Chi.sq**
te(X,Y)	< 2E-16	*	10.20	105.02
s(Depth)	3.50E-01		0.00	0.00
s(Bottom.Salinity)	< 2E-16	*	2.90	67.41
s(Bottom.Temp)	2.42E-01		0.01	0.01
s(Bottom.DO)	2.80E-01		0.00	0.00
s(Turbidity)	1.47E-04	*	2.46	13.27
s(Current.Speed)	9.40E-05	*	2.15	14.53
s(ChlA.Conc)	6.22E-02	.	0.75	2.26
s(Distance.from.shore)	5.64E-01		0.00	0.00

(*) and (.) indicated significant p-values

Table A8: GAM Results – Functional Group Red Snapper parametric coefficients

Parametric Coefficients		**p-value**	
Month3	-0.70	1.10E-02	*
Month4	-0.10	6.42E-01	
Month5	0.04	8.46E-01	
Month6	-0.22	2.85E-01	
Month7	-0.08	6.81E-01	
Month8	-0.38	6.25E-02	.
Month9	-0.13	5.42E-01	
Month10	0.22	3.05E-01	
Month11	0.04	8.44E-01	
Month12	-0.15	5.19E-01	
Year2005	0.98	1.27E-05	*
Year2006	1.02	4.24E-05	*
Year2007	1.07	1.81E-06	*
Year2008	0.43	8.84E-02	.
Year2009	0.22	3.67E-01	
Year2010	-0.23	3.88E-01	
Year2011	-0.45	9.58E-02	.
Year2012	-0.83	2.51E-03	*
Year2013	-0.52	5.66E-02	.
Year2014	-0.51	5.11E-02	.
Year2015	-0.30	2.53E-01	
Year2016	-0.10	7.58E-01	
isWFS1	-1.28	< 2E-16	*
isAR1	1.97	< 2E-16	*

(*) and (.) indicated significant p-values

Figure A4: Plots of Significant Smooth Terms for Family Lutjanidae GAM

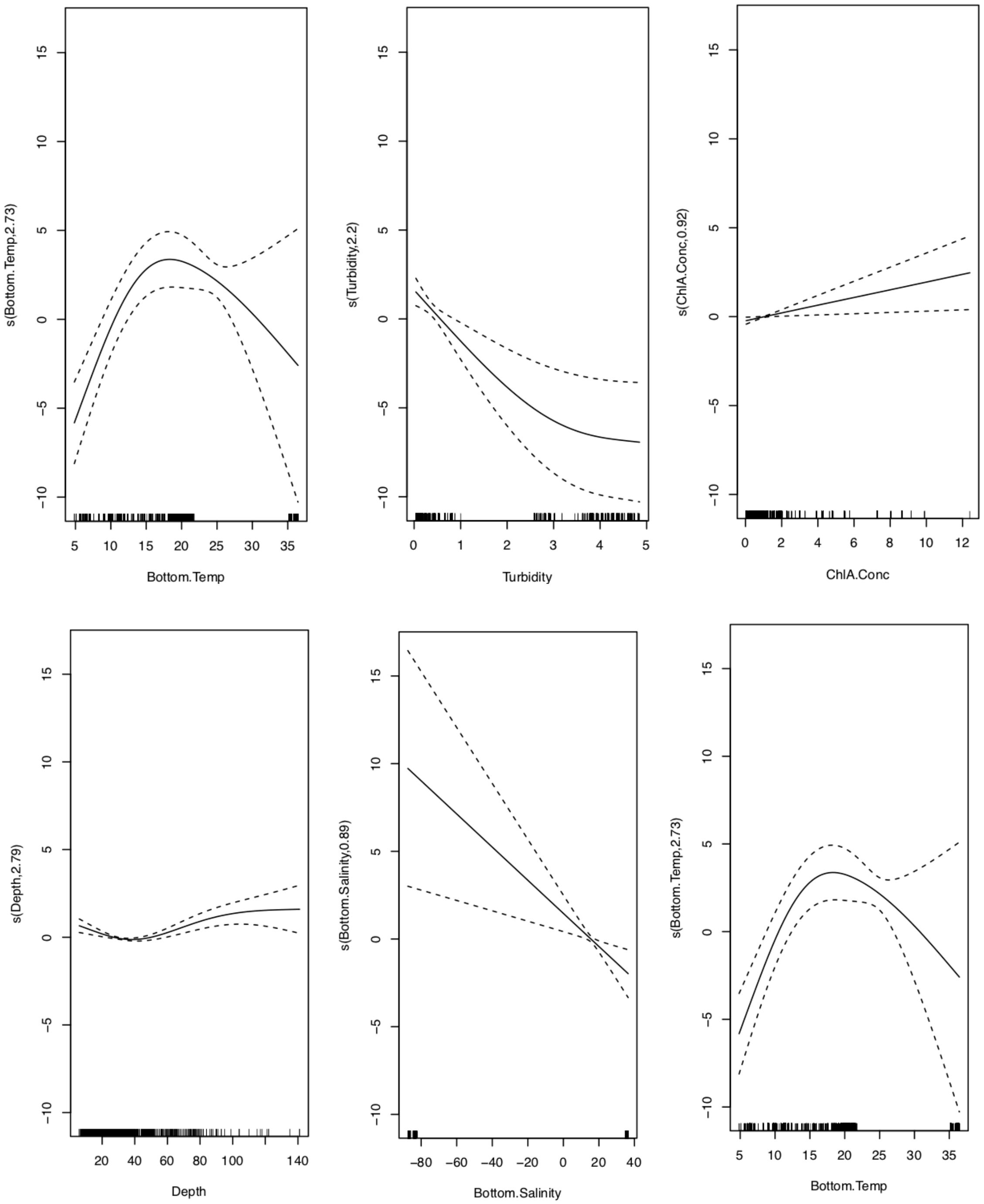


Figure A4 (cont.): Plots of Significant Smooth Terms for Family Lutjanidae GAM

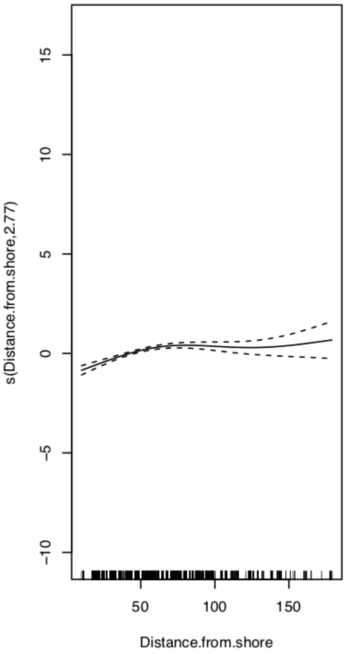


Figure A5: Plots of Significant Smooth terms for Family Carangidae GAM

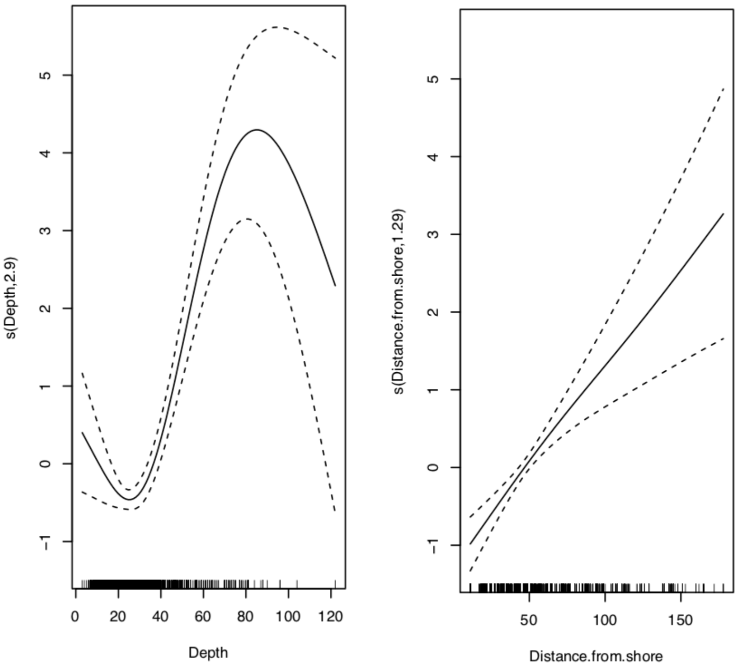


Figure A6: Plots of Significant Smooth terms for Functional Group Small Reef Fish GAM

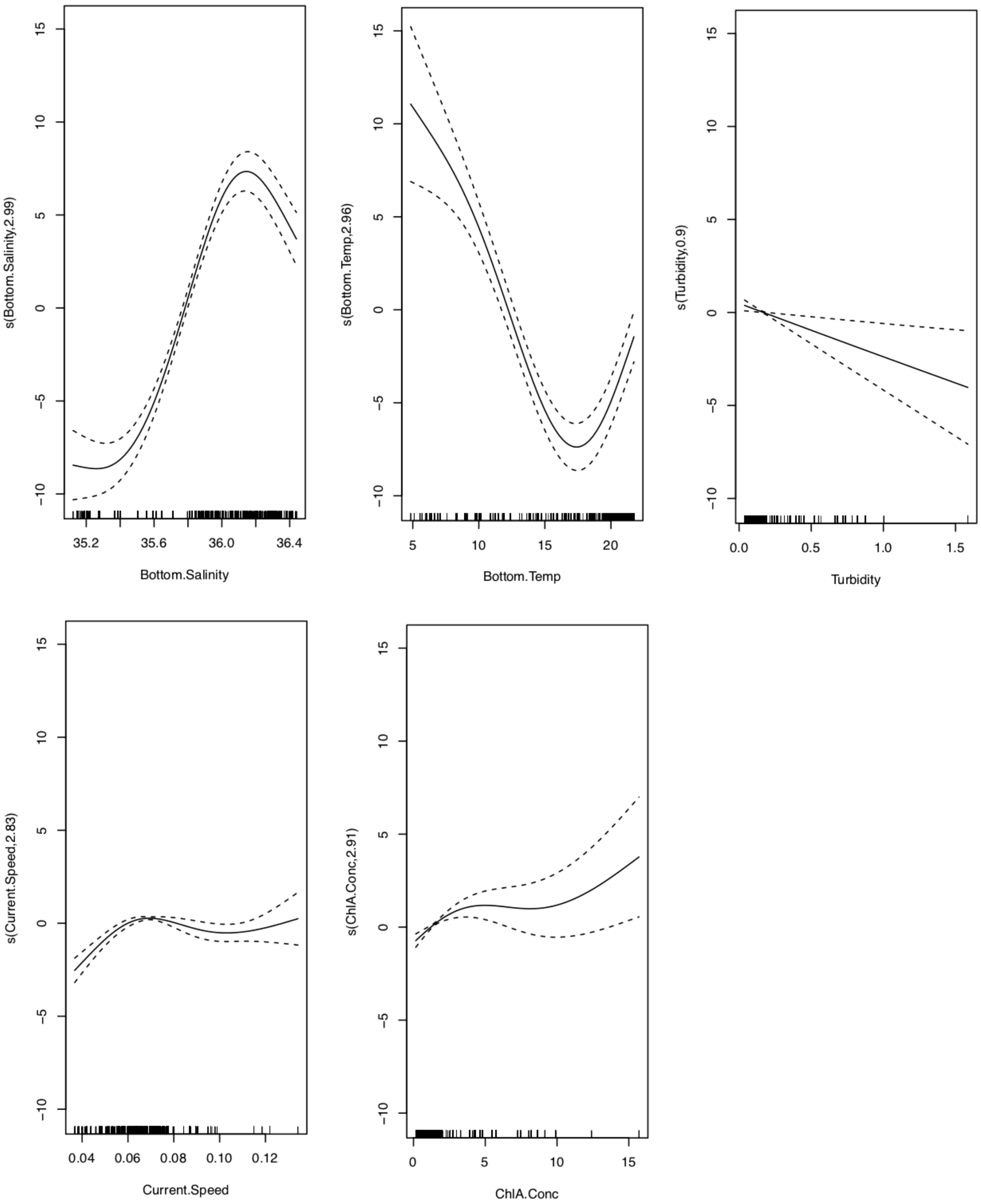


Figure A7: Plots of Significant Smooth terms for Functional Group Red Snapper GAM

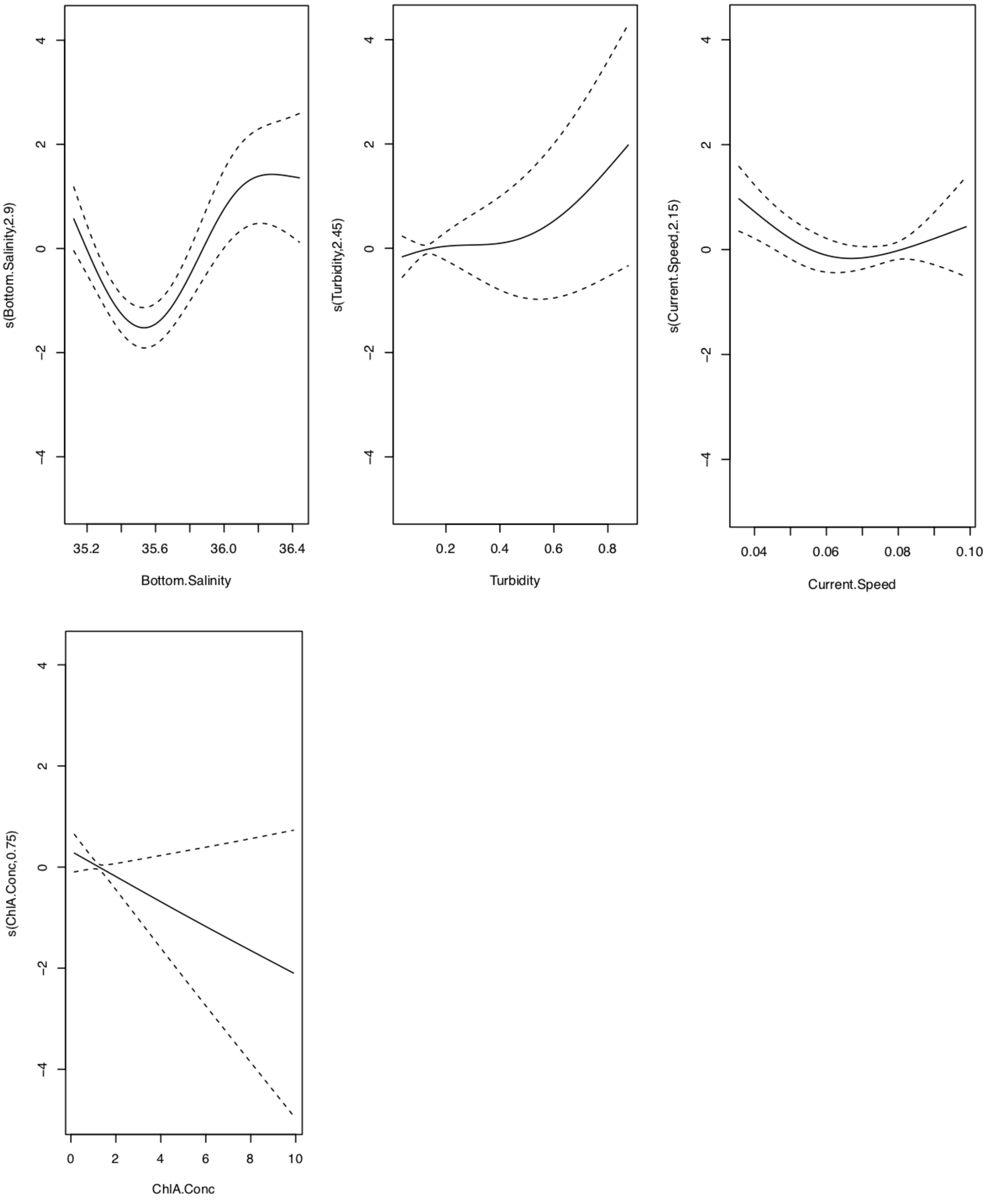
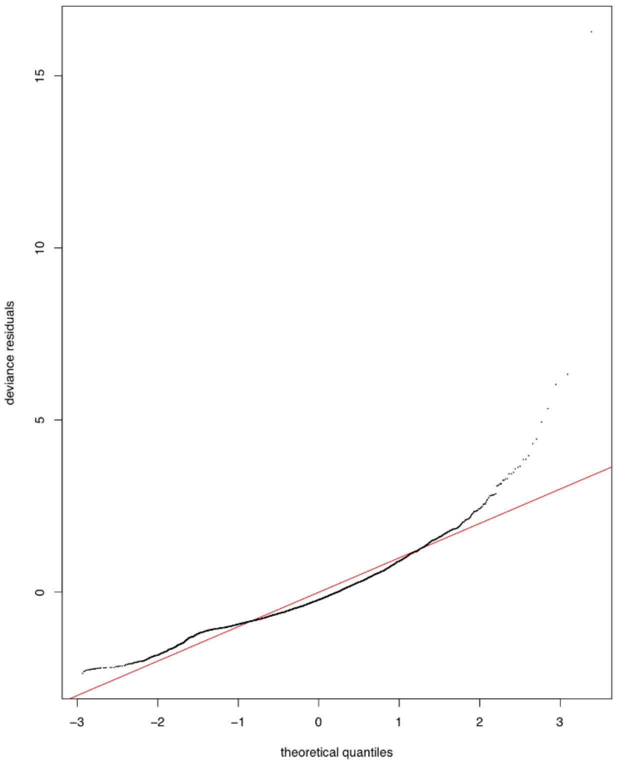
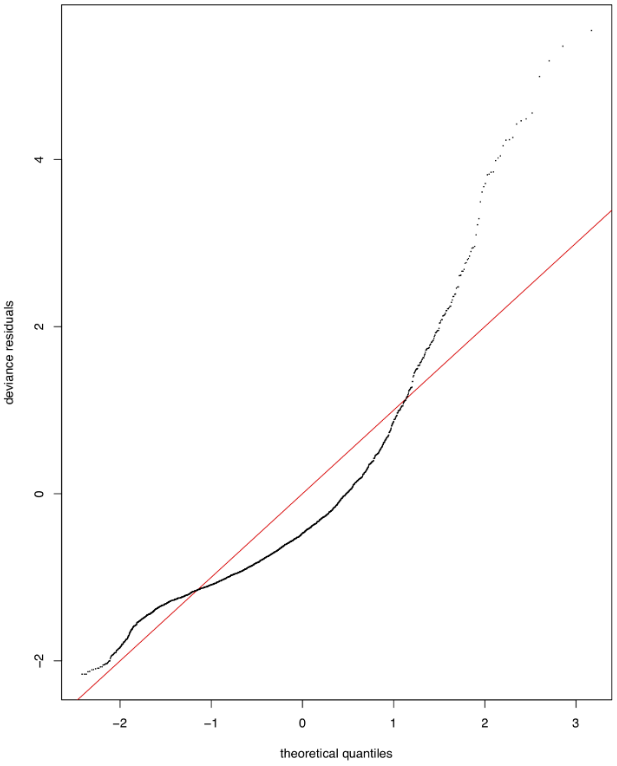


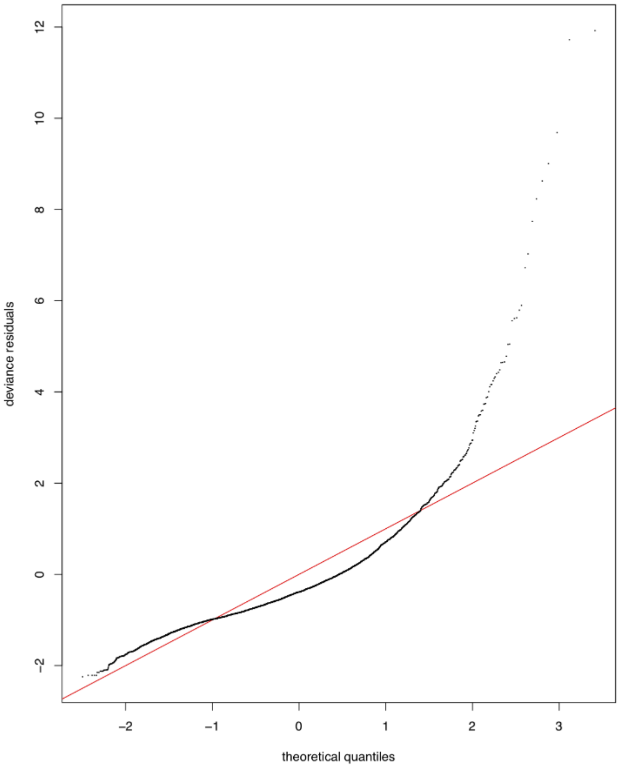
Figure A8: QQ Plots



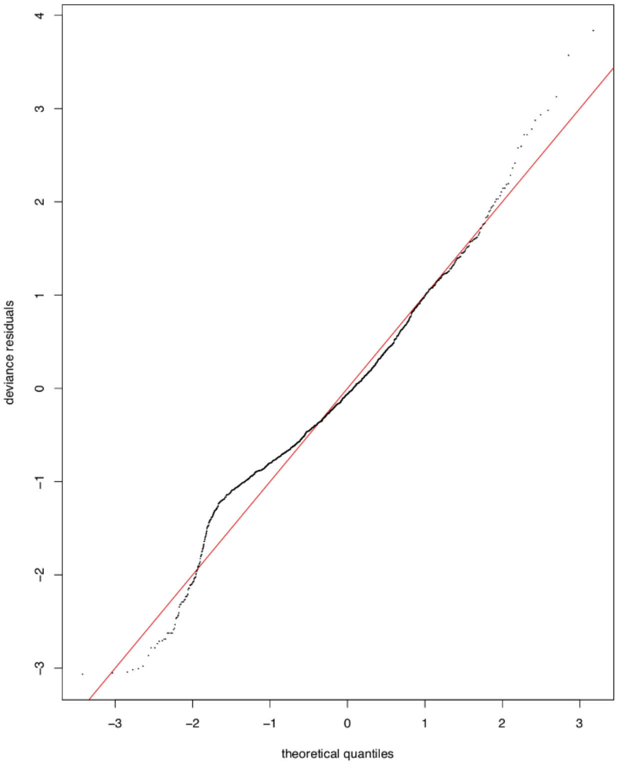
Family Lutjanidae QQ Plot



Family Carangidae QQ Plot



Functional Group Small Reef Fish QQ Plot



Functional Group Red Snapper QQ Plot