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Fish Assemblage Structure, Distribution, and Trophic Ecology at Northwestern Gulf of Mexico Banks

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FISH ASSEMBLAGE STRUCTURE, DISTRIBUTION, AND TROPHIC ECOLOGY AT NORTHWESTERN GULF OF MEXICO BANKS

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Live the full life of the mind, exhilarated by new ideas, intoxicated by the romance of the unusual.

-Ernest Hemingway

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ABSTRACT

The northwest Gulf of Mexico (Gulf) shelf-edge banks both provide unique hard bottom habitat and support the northernmost coral reefs on the North American continental shelf in a region that is generally characterized by low relief, soft sediments. The habitat value of many of these banks has led to their designation as Habitat Areas of Particular Concern (HAPC) and the Flower Garden Banks National Marine Sanctuary (FGBNMS). However, little is known about the fisheries resources and dynamics of the banks outside the FGBNMS. This study had three main objectives: 1) define reef fish assemblages at northwestern Gulf shelf-edge banks and determine if assemblages were related to the varied benthic habitats present at these features, 2) define large-scale fish distributions at these same banks and determine the influence of habitat and environmental factors on distribution, and 3) examine the trophic ecology of red snapper (*Lutjanus campechanus*), a common and highly prized reef-associated fish, at these features. Assemblage definition and relation to habitat was based upon baited underwater video surveys conducted across a range of depths and habitats. Four distinct reef fish assemblages were resolved at the shelf-edge banks, the distribution of which corresponded to benthic habitat zonation. The specific habitat characteristics of mud substrate and live cover most strongly related to species distribution. Spatial distribution of fish biomass and density at the scale of individual banks was assessed using a mobile hydroacoustic approach. The highest fish biomass and density were observed directly adjacent to hard substrate, but showed high variability with regard to site, season, and habitat zone. Red snapper trophic ecology was assessed using stable isotope analyses to examine both relative trophic position and extent among bank sites. Results indicated a consistent carbon

source, but differences in basal nitrogen between mid-shelf and shelf-edge locations. Differences in isotopic, and presumable trophic, variability between banks was attributed to different red snapper size distributions, with larger individuals displaying higher isotopic variability. Results of this study indicate the less studied northwest Gulf shelf-edge banks harbor predictable, habitat-related fish species assemblages that show variable large-scale distributions.

General Introduction

The continental shelf in the northwest Gulf of Mexico (Gulf) is primarily characterized by terrigenous silt, mud, and sand sediments; however, approximately 130 topographic features are located along the continental slope and shelf-edge (Schmahl et al. 2008). Many of the large bank features along the shelf-edge are associated with salt diapirs (Rezak et al. 1985) and act as islands of hard substrate in a region dominated by soft sediments (Bright 1977). These shelf-edge banks are known to support diverse reef-fish communities (Rezak et al. 1985, Dennis and Bright 1988, Gledhill 2001, Kraus et al. 2006, Weaver et al. 2006, Schmahl et al. 2008), and harbor the northernmost coral reefs on the North American continental shelf (Asch and Turgeon 2003).

In the 1970s and 1980s, baseline studies investigated the geology, flora, and fauna of many topographic features in the NW Gulf to inform the development of protective regulations regarding oil and gas drilling operations (Boland et al. 1983, Rezak et al. 1985). As a result, the Minerals Management Service (MMS), now the Bureau of Offshore Energy Management (BOEM), designated a number of "No Activity Zones" (NAZ) around many banks both preventing oil and gas operations, structures, or anchoring within the zone and requiring special treatment of effluent for structures nearby (MMS 2006). Additionally, 13 northwest Gulf banks have been designated as "Habitat Areas of Particular Concern" (HAPC) by NOAA, through the Gulf of Mexico Fishery Management Council (GMFMC) and the National Marine Fisheries Service (NMFS), as specific habitats that are particularly important to federally-managed fish species (GMFMC 2005). HAPC designation prohibits bottom anchoring and the use of trawling gear, bottom longline, buoy gear, and traps/pots at sites with significant coral reefs only (East and West Flower Garden Banks, McGrail,

Stetson). Finally, the Flower Garden Banks National Marine Sanctuary (FGBNMS) was created in 1992 by the US Department of Commerce through NOAA and the Office of National Marine Sanctuaries (ONMS) to "protect and manage the conservation, ecological, recreational, research, education, and historic and aesthetic resources and qualities of these areas" (P.L. 102-251 1992, Schmahl et al. 2008). The FGBNMS initially encompassed the East and West Flower Garden Banks; Stetson Bank was added in 1996. The recent review of the original 1991 management plan, finalized in April 2012, recommended the expansion of the FGBNMS boundaries to include nine additional banks (Horseshoe, McGrail, Geyer, Bright, Sonnier, Alderdice, MacNeil, Rankin and 28 Fathom) in an effort to protect the sensitive resources associated with these features, as well as preserve potential habitat connectivity between the current sanctuary and the proposed sites (FGBNMS 2012).

With the adoption of spatial and ecosystem-based fisheries management (EBFM), it is becoming increasingly important to understand interspecific interactions within ecosystems, as well as how these communities are interacting with their habitat and environment (Pittman and Brown 2011). The overall goal of EBFM is to sustain healthy marine ecosystems and thus the fisheries they support (Pikitch et al. 2004). However, Schmahl et al. (2008) report a general lack of localized data to assess fish populations associated with the East and West Flower Garden Banks, the most intensively studied features of the bank system, let alone the rest of the northwest Gulf banks. Although these banks are known to support a variety of sought-after species in the snapper/grouper complex, sharks, and migratory pelagics, detailed information is limited about species associations, distributions, or trophic interactions. Distinct differences in reef fish

assemblages, abundances, and trophic structures have been observed at a large scale across hard bottom structures throughout the Gulf bank (Gledhill 2001) and at a small scale from bank to bank (Wetmore and Rooker 2011) suggesting varying ecological roles of bank habitat at multiple scales. Effective ecosystem-based management efforts must account for such differences. Thus, information about the reef fish assemblages, abundances, distributions, and intraspecific relationships associated with these critical habitats must be characterized and such parameters defined, relative to the associated habitat and environment.

This goal of this project is to define the habitat use of reef fish communities associated with natural hard bottom in the northwest Gulf, and examine what differences may exist versus artificial reefs. The first part defines the assemblage structure of reef fish and determines the role of habitat in defining assemblages. This is accomplished with baited remote underwater video (BRUV) techniques. BRUVs have proven to be effective in assessing reef fish communities in the Gulf of Mexico (Gledhill et al. 1996, Gledhill 2001, Wells 2007, Wells et al. 2008) and worldwide (Cappo et al. 2006) by providing non-extractive methods of evaluating habitat and the associated reef fish communities in environments unsuitable for traditional sampling gear. Chapter 1 examines the clustering of reef fish into distinct assemblages and the relationship between habitat zonation and fish assemblages. BRUV techniques allow for efficient, standardized sampling of reef fish communities across a wide variety of survey depths and conditions. Chapter 2 examines how habitat characteristics define prescribed habitat zones and influence reef fish assemblage structure. Direct observations of quantitative habitat complexity

characteristics provide an opportunity to examine the relative importance of complexity characteristics in defining habitat zonation and structuring the associated reef fish assemblages.

The second focus of this project expands small-scale observations about reef fish species composition and associations to large-scale spatial distributions of biomass and density over entire features. Spatial distributions are assessed using a mobile hydroacoustic approach. Hydroacoustics have been used to effectively assess spatial distributions of reef fish associated with natural and artificial structures in the northwest Gulf (Stanley and Wilson 1996, 1997, 1998, 2000a, 2000b, 2003, Wilson et al. 2003, 2006, Wells et al. 2008, Boswell et al. 2010, Harwell 2013, Simonsen 2013), and in reef systems worldwide (Starr et al. 1996, Koenig et al. 2000, Fabi 2002, Taylor et al. 2006, Mason et al. 2006, Kracker 2007, Kracker et al. 2008, Foster et al. 2009, Rooper et al. 2010, Rudershausen et al. 2010, Costa et al. 2014). Chapter 3 takes a step back and examines the spatial distribution of reef fish biomass and density across natural and artificial reef structure. By using a mobile hydroacoustic approach, a large area was surveyed quickly, essentially capturing high resolution "snapshots" of the spatial distribution of reef fish biomass and density across the targeted bank. Complementary high-resolution bathymetry data allow me to evaluate which aspects of hard bottom bathymetry may be influencing spatial distributions of reef fishes.

The last portion of this project seeks to examine the trophic dynamics of a reef-associated fish, red snapper (*Lutjanus campechanus)*, with stable isotope analyses and a concurrent diet study (Schwartzkopf 2014). Chapter 4 examines differences in trophic dynamics of red snapper among seasons, study sites, and fish sizes. Stable isotope

techniques are limited to temporal and spatial integrated information about trophic relationships, so stomach contents data were used to inform interpretations of isotope information.

Through the use of BRUVs to define small-scale assemblage structure, hydroacoustics to examine large-scale spatial distribution, and trophic analyses to assess physical implications of habitat associations, my goal is to gain a better understanding of how natural shelf-edge banks function as habitat in the northwest Gulf and examine differences that may exist between natural and artificial reefs.

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CHAPTER 1: ASSEMBLAGE STRUCTURE OF REEF FISH ASSOCIATED WITH NORTHWEST GULF OF MEXICO BANKS

INTRODUCTION

The hard bottom banks of the northwestern Gulf of Mexico (Gulf) have long been recognized for their support of diverse and productive reef fish communities (Parker and Curray 1956). The unique combination of high relief, hard bottom substrate and persistently warm, clear water delivered via the Loop current allows many of these features to support thriving reefs exhibiting elements of Caribbean reef biota (Bright et al. 1985). The predominant benthic substrates in the northwest Gulf are terrigenous sediments (sand, mud, and silt) derived primarily from the Mississippi delta outflow (Bright et al. 1985). However, an estimated 2,700 km^2 of natural hard bottom habitat is present in the northern Gulf, located mainly along the continental shelf-edge (Parker Jr. et al. 1983). This natural hard bottom habitat has been supplemented by the installation of over 7,000 offshore oil and gas platforms throughout the Gulf of Mexico since 1947, less than 2,400 of which remain at this time (LDWF Louisiana Artificial Reef Program, BSEE). These oil and gas platforms form one of the world's largest de-facto artificial reef systems, hosting a wide variety of reef and structure oriented fishes throughout the northern Gulf (Sonnier et al. 1976, Gallaway and Lewbel 1982, Stanley and Wilson 1990, 1991, 1997, 2000a, 2000b, Wilson et al. 2003, 2006).

Active platforms are not the only artificial reef structures present. A number of artificial reef planning areas have been established as locations where decommissioned platforms may be 'reefed', providing an opportunity for oil and gas companies to limit the expense associated with Bureau of Offshore Energy Management (BOEM) mandated

removal of decommissioned platforms, while preserving any habitat structure provided by the platforms. While the true value of this habitat to reef fish is debated (Bohnsack 1989, Grossman et al. 1997, Bortone 1998, Brickhill et al. 2005), it is obvious that the structures serve to at least aggregate reef-associated fish (Hastings et al. 1976, Stanley and Wilson 1996, 1997, 1998, 2000a, 2000b, Bohnsack et al. 1997, Grossman et al. 1997, Lindberg 1997, Bortone 1998).

The majority of the natural hard bottom in the northwest Gulf is found along the continental shelf edge as a result of diapiric salt intrusions uplifting bedrock that is subsequently capped by carbonate reef structure (Dennis and Bright 1988). These structures, referred to as 'banks', form a track westward from the Mississippi River delta along the shelf edge to an area south of Galveston, beyond which features are based on relict carbonate shelf versus salt diapirs (Rezak and Bright 1983). The term 'reef' is often used to describe these underwater structures as well, in the sense that they represent underwater structure, though many do possess areas of biotic reef structure as well.

In the 1970s and 1980s, baseline studies investigated the geology, flora, and fauna of many topographic features in the northwest Gulf to inform the development of protective regulations regarding oil and gas drilling operations (Boland et al. 1983, Rezak et al. 1985). Much of the effort was devoted to the coral-rich East and West Flower Garden Banks, the largest and shallowest banks in the shelf-edge system. However, there are dozens of additional banks in the northwest Gulf, some of which also support coral reefs, and all of which serve as important hard-bottom habitat for high-biomass fish communities. These deeper banks have received much less attention due to their relative inaccessibility from normal reef survey methods such as SCUBA (Dennis and Bright 1988).

However, modern survey equipment, such as remote video technology, allows for observation and quantitative measurement of both the benthic habitats and fish communities of these deeper banks.

The baseline biological and geological studies of the northwest Gulf banks led to the identification of distinct benthic habitat zones associated with these features. Seven characteristic zones were identified and subsequently grouped into four general classifications based on the degree of reef building and primary productivity: 1) major reef-building activity and primary production, 2) minor reef-building, 3) transitional zones with minor to negligible reef-building, and 4) no reef building (Rezak et al. 1985, 1990). More recently, Flower Garden Banks National Marine Sanctuary (FGBNMS) scientists have modified and reorganized the zonation classification of Rezak et al. (1985) into a similar, but more generalized habitat classification scheme based solely on five broad biological zones: 1) coral reef, 2) coral community, 3) coralline algae, 4) deep coral, and 5) soft bottom (Schmahl et al. 2008). With increasing habitat zone depth, reef-building activity, habitat complexity, and relative hard substrate cover decrease until the soft, low relief habitat that surrounds the banks, and dominates the majority of the Gulf, is reached. Habitat zones exhibit relative uniformity with respect to epifaunal assemblages among banks; however, it should be noted that not every habitat zone exists at every bank.

Several environmental factors have been proposed as correlates and potential controls on where benthic zones exist, including distance from shore, regional patterns of substratum type, bottom depth, bank relief, water temperature, salinity, river runoff, turbidity, sedimentation, currents, and seasonal variation in water temperature, salinity, river runoff, turbidity, sedimentation, and currents (Rezak et al. 1985). Each of these

parameters differs among banks due to bank location and bathymetric structure, and thus the areas occupied by a given benthic habitat zone differ among banks. Zonation is most often described quantitatively as a depth range at a given bank because influences on epibenthic assemblages, and thus the described zonation patterns, are nearly all depth related. Light availability links a variety of the previously proposed factors (turbidity, sedimentation, depth) and defines the physical limit at which any photosynthetic corals and algae can exist. Additionally, depth must be considered when discussing temperature and salinity thresholds, which in turn may be influenced by local currents and the physical structure of the bank itself. While each factor may be discussed individually, it is important to remember the interdependence of these environmental factors.

Reef fish assemblages at the northwest Gulf banks resemble Caribbean reef biota, though show less diversity due to the limited amount of suitable hard-bottom habitat, limited habitat diversity, and the large distance from source populations (Dennis and Bright 1988). Previous studies of the fish assemblages occurring at the shelf-edge banks have predominantly been exploratory (Parker and Curray 1956, Sonnier et al. 1976, Dennis and Bright 1988, Rezak et al. 1990, Kraus et al. 2006, Schmahl and Hickerson 2006, Weaver et al. 2006), at large scales (Gledhill 2001, Gledhill and Ingram 2002), or focused on other biology, such as invertebrates (Parker and Curray 1956, Tunnell et al. 1978, Gittings et al. 1992). Dennis and Bright (1988) reported three distinct reef fish assemblages based on cluster analysis, named for the dominant benthic habitat features with which they were observed: a *Millpora*-sponge assemblage, an algal nodule-sponge assemblage, and a drowned reef assemblage. The surveys conducted by Weaver et al. (2006) found reef fish assemblages similar to those described by Dennis and Bright (1988), as well as added

information about smaller, more cryptic species. Both studies used manned submersibles and thus were limited in their scope of observations and focused on specific features of interest. The large-scale survey conducted by Gledhill (2001), similar to the Gulf-wide Southeast Area Monitoring and Assessment Program (SEAMAP) video monitoring program (Gledhill and Ingram 2002), identified differences in fish assemblages along the entirety of the shelf-edge, from Florida to Texas, at the feature level. Three clusters of spatially and geomorphologically similar shelf-edge banks, based upon fish species composition, were reported: the Louisiana-Texas banks, Florida Middle Ground and West Florida Shelf-edge, and the Tortugas.

Quantitative surveys of reef fish communities and their association with the described habitat zonation scheme represent the next logical step in expanding upon the exploratory studies conducted at these unique and important habitats. Baited remote underwater video surveys (BRUVS) are well suited to assess the reef fish assemblage structure across a variety of habitats, as they provide a standardized, non-extractive method of comparing observations between a variety of sampling depths and conditions, minimize gear avoidance and selectivity, and provide a permanent record of observations (Cappo et al. 2006). BRUVS have been used worldwide since the late 1980's (Parrish 1989) from Hawaii (Ellis and Demartini 1995, Merritt 2005) to Australia and New Zealand (Hill and Wassenberg 2000, Cappo et al. 2004), and extensively within the Gulf as part of SEAMAP video surveys conducted by the National Marine Fisheries Service (NMFS) since 1991 (Gledhill et al. 1996). The goal of this chapter is to examine whether reef fish formed

distinct assemblages at three natural shelf-edge banks and one artificial reef and, if so, to define both the composition of these assemblages and their relation to the current FGBNMS habitat zone scheme.

METHODS

I examined the fish assemblages associated with three shelf-edge banks and one artificial reef in the northwestern Gulf. The three banks (Bright, McGrail, and Jakkula) are located on the Louisiana-Texas shelf edge, while the artificial reef is closer to shore on the Louisiana-Texas shelf in the East Cameron Artificial Reef Planning Area (Figure 1.1).

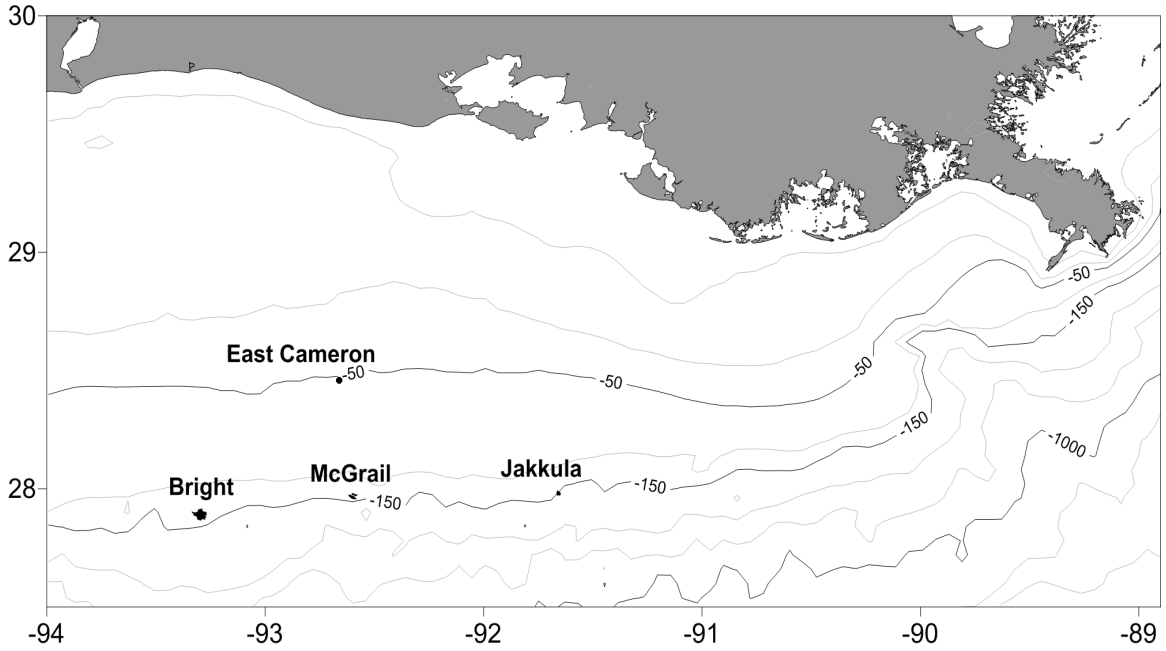

Figure 1.1: Sampling locations for video survey collection at one artificial reef (East Cameron) and three shelf-edge banks in the northwestern Gulf of Mexico.

STUDY AREA

The Louisiana-Texas shelf-edge banks are a result of diapiric salt intrusions uplifting bedrock that is subsequently capped by carbonate reef structure (Rezak and Bright 1983,

Rezak et al. 1985, 1990, Dennis and Bright 1988). The banks used in this study rise from depths of 140-160 m, crest at depths of 30-50 m below the surface, and range in size from 4 to 20 km^2. The three sites selected (Bright, McGrail, and Jakkula) were chosen to effectively sample throughout the East-West Texas-Louisiana shelf-edge bank track. The biotic reef structure has been categorized into two complementary zonation schemes, one based on the degree of reef building and primary productivity (Rezak et al. 1985, 1990), and the other on five broad biological zones, within which there are multiple specific habitat types (Schmahl et al. 2008; Table 1.1). My video surveys captured three of these broad biological habitat zones: coral community, coralline algal reef, and deep coral.

Table 1.1: Summary of revised biological zones of NWGOM banks proposed by Schmahl et al. (2008).

Zone	Depth (m)	Biology	Previous classification per Rezak et al. (1985)
Coral Reef	16-52	*Montastraea* *Madracis* *Stephanocoenia* Coral sand	*Diploria-Montastraea-Porites* *Madracis* and Leafy Algae *Stephanocoenia -Millepora*
Coral Community	16-52	*Millepora*-sponge Low density coral Leafy algae Sponge	*Millepora*-Sponge
Coralline Algal Reef	45-98	Algal nodules Coralline algal reef Leafy algae	Algal-Sponge "Partly drowned reefs"
Deep Coral	50-200+	Antipatharian Octocoral Crinoid Stony coral	Antipatharian transitional Nepheloid "Drowned reefs"
Soft Bottom	16-200+	Sand Quartz Molluscan hash	Not defined as "hard bottom" so excluded from prior evaluations

The artificial reef site I examined consisted of a mid-shelf toppled platform in the East Cameron Artificial Reef Planning Area, hereafter the East Cameron (EC) site. This artificial reef is located within an area of high acoustic backscatter and increased bathymetric relief relative to surrounding areas, discovered during a side-scan survey of the Louisiana Artificial Reef Program (LARP) planning areas (Cowan et al. 2007). The extent of natural hard-bottom in the EC planning area is the largest observed among the Louisiana artificial reef planning areas (7,855 ha total). The local bathymetry is characterized by a gradual slope from 45-55 m, with the area of interest forming a shelf in the center approximately 4 m higher than the surrounding sediments. Though my video surveys showed no epifauna, bathymetric features associated with this site are assumed to be composed of slabs of lithified bottom sediment (Cowan et al. 2007).

The relative abundances of reef fish species were estimated from video surveys conducted between December 2012 and October 2013. Surveys were carried out twice quarterly, as weather permitted. Survey sites were selected to encompass as many habitat zones on each study bank as possible during the study period, based on documented depth zones for each bank (Rezak et al. 1985, 1990, Schmahl et al. 2008). Up to two one-hour deployments, hereafter referred to as surveys, were conducted at a site during a single sampling trip, though never within the same habitat zone.

SURVEY METHOD

The BRUVS used high-definition stereo Canon VIXIA HF G10 camera arrays for all observations. The depth and scope of surveys precluded traditional SCUBA diver census techniques, while the camera arrays could be rapidly deployed to and retrieved from a wide variety of depths and sea conditions. The six-camera array consisted of a circular,

baited cage within which two stereo camera pairs, and two single cameras were mounted orthogonally to one another at a height of 0.5m, affording a near 360° view (Figure 1.2).

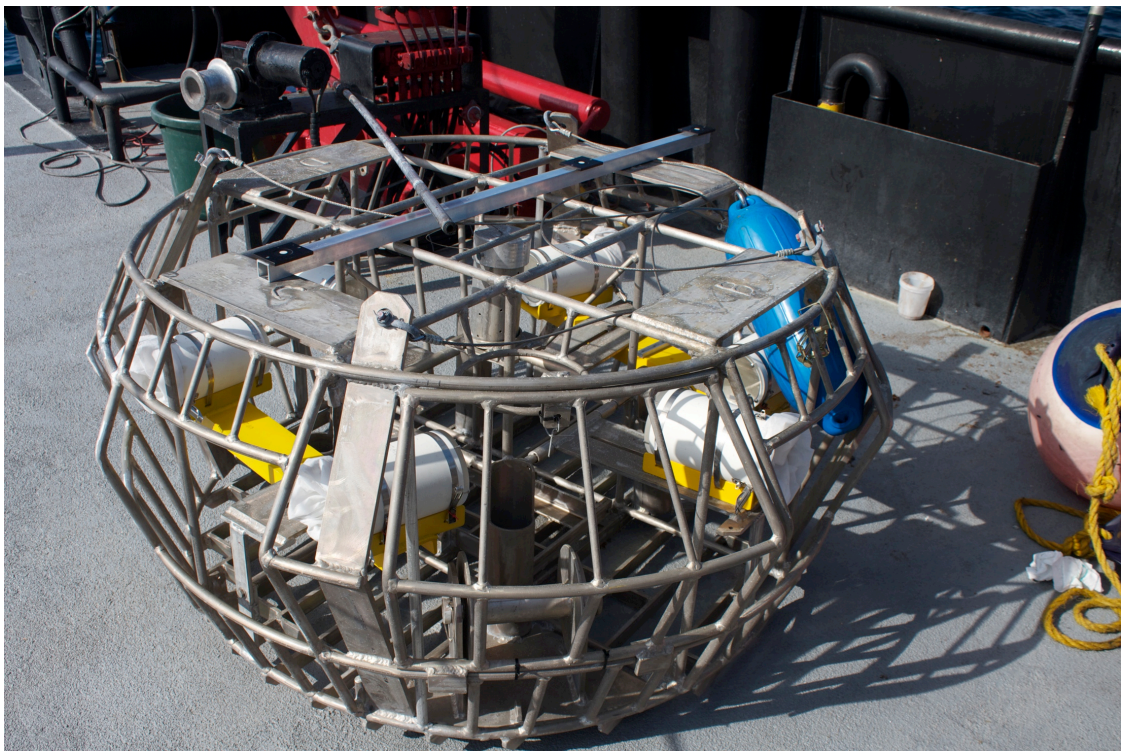

Figure 1.2: Camera array used to conduct video surveys. Composed of six cameras, two stereo pairs and two individual cameras positioned orthogonally to cover all directions around the cage.

The array was similar to that used by the SEAMAP offshore reef survey (Gledhill 2001, Somerton and Gledhill 2005). Stereo cameras were separated by 70cm from their respective stereo partner to suit both the size of individuals observed and the average range of measurement, while being angled inward at 7 degrees to maximize the overlapping area available for measurement. Prior to deployment, all stereo pairs were calibrated with a calibration cube (1m x 1m x 0.53m) and captured imagery was processed with the computer program Cal (SeaGIS Pty. Ltd.). Each video survey included a capture of a measurement bar of known length to check that appropriate calibration was obtained. Cameras were deployed for one hour of bottom time.

Videos were reviewed in EventMeasure software (SeaGIS Pty. Ltd.) to identify and enumerate all species for the duration of the recording. Identifications were made to the lowest taxonomic level possible and enumerations were calculated in the form of MaxN (Priede et al. 1994). MaxN is the maximum number of individuals of a given species seen in a single video frame, a conservative estimator of the number of fish of said species present during a survey (Priede et al. 1994). MaxN is used for stationary systems, rather than a running total typically used with transect-type surveys, because it is possible that individual fish might be counted repeatedly when leaving and then re-entering the field of view during video analysis, especially due to the centralized bait location relative to the camera layout (Kallayil et al. 2003). The use of two stereo-pairs in each camera array allowed for length measurements of many of the fish observed during the surveys, as well as habitat features. Adhering to the conservative MaxN principle, only the MaxN fish observed were measured, to avoid measuring the same fish twice. Video surveys were used to determine the relative abundance and composition of reef fish species associated with the three shelf-edge banks and one artificial reef.

DATA ANALYSIS

The relationships between observed fish assemblages, study sites, and habitat zones at shelf-edge banks were investigated with traditional assemblage analysis metrics (richness, evenness, diversity), permutational multivariate analysis of variance (PERMANOVA), cluster analysis in conjunction with non-metric multidimensional scaling (MDS), and similarity percentages (SIMPER) within Plymouth Routines In Multivariate Ecological Research version six (PRIMER 6). These procedures were chosen as a natural progression of specificity. Traditional metrics gave a quick and simple picture of global

patterns. PERMANOVA provided a global test of whether significant assemblage differences were present at the bank and/or habitat zone level. Cluster analysis and MDS ordination were used as complimentary methods to elucidate more detailed relationships between surveys. SIMPER highlighted which individual species were driving any grouping observed. Analytical methods were restricted to observations made to the species level.

The individual camera data was combined from all four camera directions for each deployment, such that the highest MaxN observed for a given species on any camera was used as the MaxN for that survey. Individual camera information was combined at the survey level in an effort to preserve independence of observations and avoid pseudo-replication (Hurlbert 1984). The species abundance data was square-root transformed, a moderate-strength pre-treatment procedure intended to down-weight the importance of highly abundant (and usually highly variable) species, so that future calculations were not overly influenced by only the most abundant species.

The traditional assemblage analysis metrics calculated were species richness (*S*), Shannon's diversity index (*H'*), and Pielou's evenness (*J'*). Metrics were computed for each survey. Richness (*S)* was expressed simply as the number of species present, with no adjustment, as all surveys were collected in the same manner and differing sample size was a result of where the survey was conducted, not the sampling effort. Diversity was expressed as the Shannon diversity index (*H'*):

$$H' = -\sum_i p_i \ln p_i$$

where p_i was the proportion of the total individual count within that survey arising from the *i*th species (Shannon 1948). Evenness, or equitability, was expressed as Pielou's evenness index (*J')*:

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

where H' and H'_{max} were the observed and maximum possible value of Shannon diversity for that survey, respectively (Pielou 1966). Because every habitat was not present at every site, a one-way analysis of variance (ANOVA) with a site*habitat effect was fit, from which contrasts were used to construct tests for site and habitat main effects, as well as available interaction terms (SAS 9.3).

A PERMANOVA routine was run to test for significant global effects of site and/or habitat zone on the observed fish assemblages. The null hypothesis (H_0) was that there were no differences in assemblage composition between sites or habitat zones. The PERMANOVA routine is a permutational multivariate analog to Fisher's *F*-ratio and is calculated from a dissimilarity matrix, a matrix of pairwise dissimilarities between surveys (M. J. Anderson, 2001; McArdle & Anderson, 2001). Further explanation of the procedure can be found in Appendix A.

Given that the global PERMANOVA test was significant (α=0.05), pairwise tests were computed to determine which levels of each factor were significantly different (α=0.05) from one another. The pairwise test statistic was calculated by taking each pair of levels, treating it like a contrast, and calculating a pseudo-*t* statistic as the square root of the pseudo-*F*. P-values for all pairwise tests were obtained by comparing the observed pseudo-*t* against a distribution of simulated pseudo-*t* values generated by permuting labels. In the event that too few unique permutations were available to produce a meaningful test

(<<999), constructed asymptotic permutation distributions were generated with Monte Carlo sampling and used to obtain a more meaningful test statistic (M. J. Anderson, 2005; M. Anderson & Robinson, 2003).

Clustering of surveys was achieved via hierarchical agglomerative grouping of the Bray-Curtis similarities between surveys with the square-root transformed species abundances (Bray & Curtis, 1957). Dendrogram construction employed group-average linkage and a series of similarity profile (SIMPROF) permutation tests were computed to highlight statistically significant (α=0.01) clusters of samples that were *a priori* unstructured. The SIMPROF procedure tested each node of the final dendrogram to see if the samples within that group could be significantly differentiated. The resulting cluster arrangement was then compared to identifying factors for each survey, including the bank, season, and habitat zone within which the survey was conducted, and examined for correlated patterns.

Non-metric multidimensional scaling (MDS) analysis of video surveys was based on the same resemblance matrix of Bray-Curtis similarities used in the PERMANOVA and cluster procedures. MDS is as an ordination technique used to create a configuration of the surveys in two and three dimensions that attempts to satisfy the relationships present in the similarity matrix, such that more similar surveys were located nearer to one another than to less similar surveys (Kruskal, 1964; Shepard, 1962). More detail about the procedure can be found in Appendix A. The final ordination plot was examined for grouping of surveys and overlaid with clusters from the cluster analysis as a check of adequacy and mutual agreement between MDS and cluster representations of the survey data (Van Sickle, 1997).

Similarity percentages analysis (SIMPER) was conducted to examine which species were responsible for discrimination between, and typical of, the groups generated by the cluster and MDS procedures. The average contribution for each species to similarity within, and dissimilarity between, groups was calculated. Further details of this calculation can be found in Appendix A. Additionally, the ratio of contribution to standard deviation of contribution was used to pinpoint those species that consistently contribute a large amount to the (dis)similarity. Those species with a high dissimilarity ratio are deemed 'discriminating species', while a high similarity ratio indicates a 'typical' species (Clarke and Warwick 2001).

PERMANOVA, cluster analysis, MDS, and SIMPER routines were performed on datasets combined at the genus and family levels to determine whether coarser taxonomic classification would impact assemblage composition or discrimination. Species were pooled, by survey, at the genus and family levels, square root transformed, and Bray-Curtis similarities between surveys were calculated to produce resemblance matrices based on similarities at the genus and family level. The same PERMANOVA design as used at the species level, fixed site and habitat factors, was tested. Cluster and MDS routines were run in the same manner as applied at the species-level. SIMPROF tested each node of the final cluster arrangements to define statistically significant clusters (α=0.01). SIMPER definition of typical and discriminatory taxa was performed if prior analyses indicated significant and meaningful assemblages at the coarser taxonomic levels.

RESULTS

Between December 2012 and October 2013 a total of 26 camera-array surveys were conducted. 93 fish taxa in 27 families were observed at three shelf-edge banks and one artificial reef (Appendix Table A.1). Creolefish (*Paranthis furcifer)* were the most abundant fish, accounting for over 29% of individuals observed across all surveys, followed closely by threadnose bass (*Anthis tenuis*, 25.5%) and brown chromis (*Chromis multilineata*, 20%). Red snapper (*Lutjanus campechanas)* and greater amberjack (*Seriola dumerili)* were the most prevalent species, meaning they were present in the most surveys, observed in 69% of the video surveys.

SPECIES-LEVEL ANALYSES

Mixed model analysis of traditional assemblage metrics indicated significant habitat zone and site effects for all metrics examined (Table 1.2). The interaction between site and habitat zone was not significant for any metric, though it should be noted this interaction was constructed from natural sites and habitats alone, given that artificial habitat does not occur within natural sites, nor vice versa.

Table 1.2. Constructed tests of habitat, site, and habitat*site effects for each assemblage metric. Asterisk (*) indicates a significant (α=0.05) effect.

Index	Effect	F Value	p-value
Richness	Habitat	20.27	<0.001*
	Site	8.36	0.001*
	Habitat*Site	0.62	0.61
Diversity	Habitat	3.37	0.04*
	Site	3.45	0.04*
	Habitat*Site	0.86	0.48
Evenness	Habitat	3.09	0.05*
	Site	4.32	0.02*
	Habitat*Site	1.31	0.30

Post-hoc examination of site and habitat effects for each index revealed how individual sites or habitat zones differed from one another (Figure 1.3). LSMean species richness was lowest at the artificial habitat and increased with decreasing natural habitat

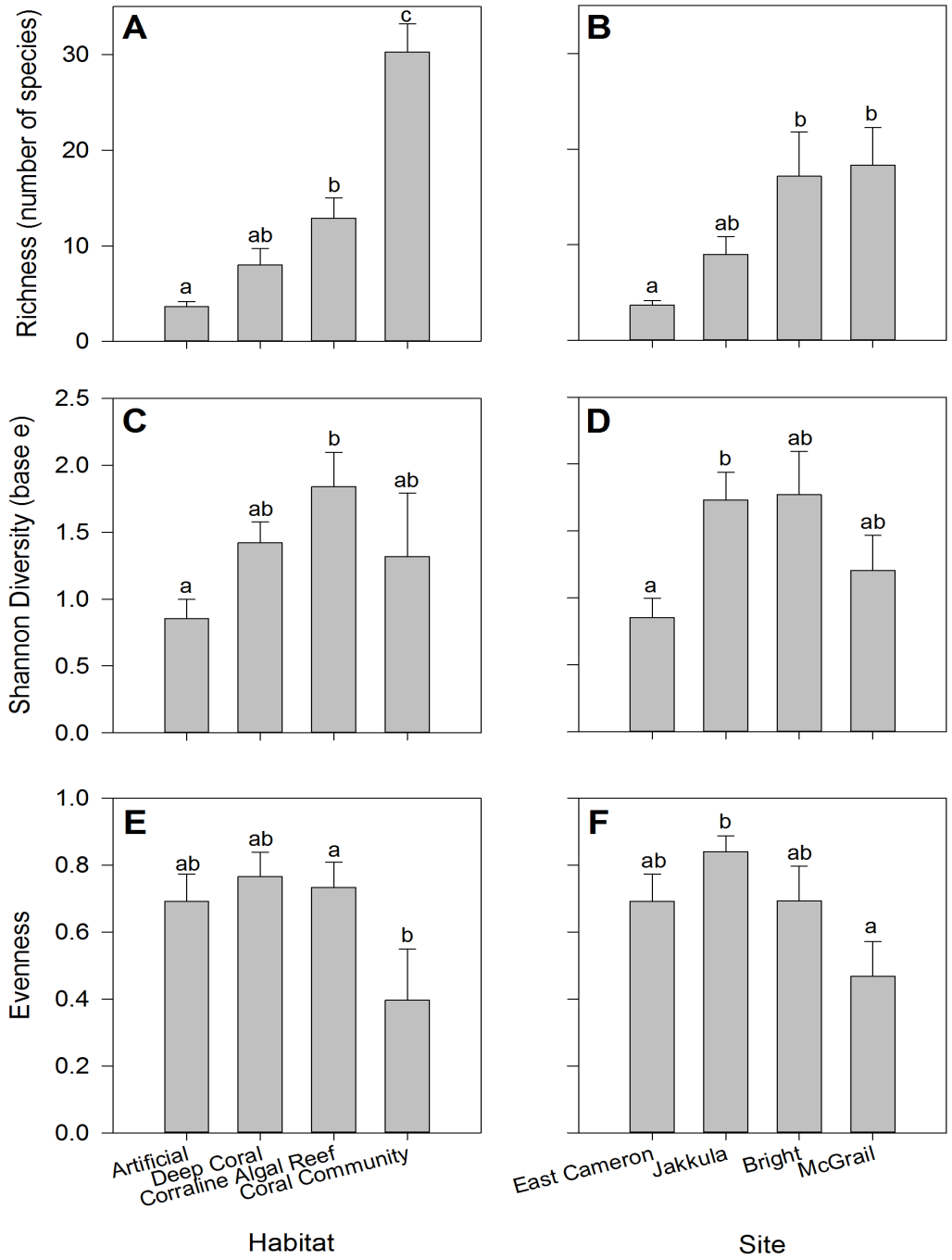

Figure 1.3. LSmean richness, Shannon diversity, and Pielou's evenness by habitat zone and site. Error bars indicate standard error. Groups sharing a letter within a plot are not significantly different (α=0.05).

zone depth (Figure 1.3A). LSMean richness was significantly higher at Bright and McGrail than at East Cameron (Figure 1.3B). LSMean diversity peaked in the coralline algal reef zone and was significantly higher than in the artificial habitat (Figure 1.3C). East Cameron showed a significantly lower LSMean diversity than Jakkula, with Bright and McGrail not differing significantly from either East Cameron or Jakkula (Figure 1.3D). The coral community habitat zone showed the lowest LSMean evenness of the four habitat zones and was significantly lower than the coralline algal reef zone (Figure 1.3E). LSMean evenness was lowest at McGrail, significantly less than at Jakkula (Figure 1.3F).

When examined from a multivariate perspective (PERMANOVA), a significant habitat ($p=0.0001$) effect was found (Table 1.3). However, the site effect ($p=0.08$) and the interaction between site and habitat ($p=0.33$) were not found to be significant. Pairwise comparisons between habitats indicated significant assemblage differences between the coral community zone relative to the two other natural habitats, based on the Monte-Carlo estimated p-values due to the low number of unique permutations available (Table 1.4). Pairwise comparisons between sites were not conducted because the main effect was not significant, and differences between sites is not especially meaningful given the differences in habitats present at various sites.

Table 1.3. Global two-factor PERMANOVA results. Asterisk (*) indicates a significant factor ($\alpha=0.05$). Perms: number of permutations against which each effect was tested.

Effect	Df	Perms	Pseudo F	P
Site	2	999	1.28	0.08
Habitat	2	999	2.49	0.001*
Site x Habitat	3	999	1.08	0.33

Table 1.4. Pairwise comparisons of assemblages between habitats. Asterisk (*) indicates a significant difference (α=0.05). CC- Coral Community, CAR- Coralline Algal Reef, DC Deep Coral, Art- Artificial. Perms: number of permutations against which each effect was tested. P (perm): p-value obtained from the available permutations. P (Monte Carlo): p-value obtained from Mote Carlo estimation.

Pair	t	Perms	P (perm)	P (Monte Carlo)
CC - CAR	1.64	60	0.09	0.019*
CC – DC	1.81	30	0.04*	0.029*
CAR – DC	1.16	346	0.22	0.238
Art – CC	1.93	3	0.001*	0.096
Art - CAR	1.52	24	0.001*	0.095
Art - DC	1.42	12	0.001*	0.104

Cluster arrangement and subsequent SIMPROF testing yielded four significantly different (α=0.01) clusters of surveys. When superimposed with identifying factors associated with each survey (habitat zone, bank, and season), the significant clusters appeared to be most closely aligned with the habitat zone factor (Figure 1.4). Out of the 93 species observed over the course of this study, 55 (59%) were specific to a given cluster.

Cluster A, the "coral cluster", consisted of only three surveys, all of which were conducted in the coral community zone. Over the course of these three surveys 58 species were observed, 25 of which (43%) were only present within the coral cluster.

Cluster B, the "low relief" cluster, consisted of 11 surveys that included all six of the artificial reef surveys, three deep coral surveys, and two coralline algal reef surveys. Cluster B showed a subsequent internal division that nearly separated artificial and bank habitat zones, though it was not significant at the 1% level of discrimination. This cluster also included the strongest pairwise Bray-Curtis similarity (65.8), observed between two artificial habitat surveys. The low relief cluster included 27 species, 10 of which (37%) were not observed in any other cluster.

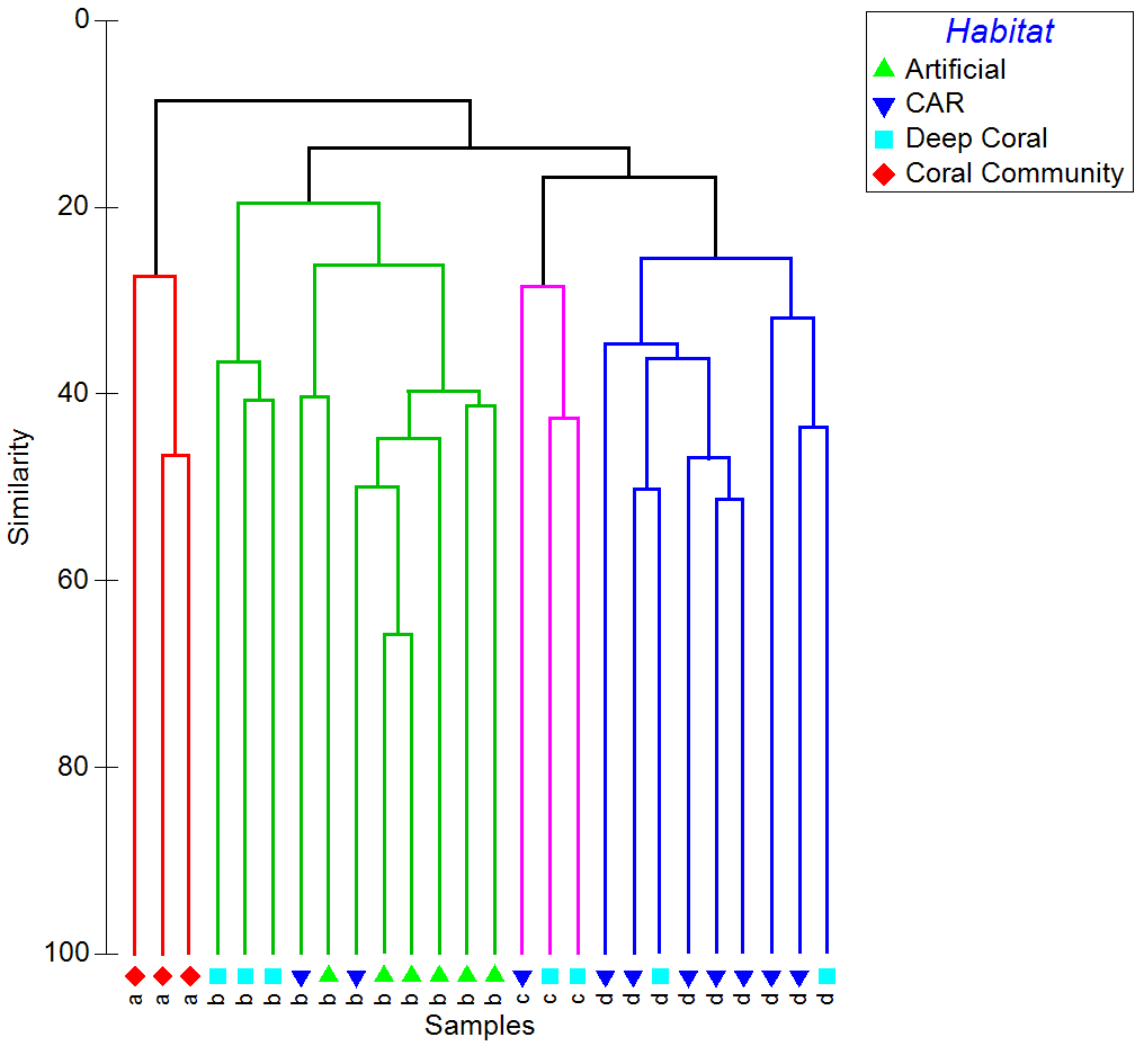

Figure 1.4. Cladogram displaying results of species-level cluster analysis of similarity between surveys. Colored lines and letters (a-d) indicate significantly different (α=0.01) clusters identified by the SIMPROF procedure. Colored symbols indicate the habitat zone within which each survey was conducted. CAR- Coralline algal reef.

Cluster C, the "transition cluster", included three surveys: two from the deep coral zone and one from the coralline algal reef zone. The transition cluster was based on only eight species, two of which were not seen anywhere else. Cluster C was more similar to cluster D than the other two.

Cluster D, the "coralline cluster", included nine surveys, all but two of which were conducted in the coralline algal reef zone, the final members being deep coral surveys. This final cluster included 54 species, 18 of which (33%) were specific to the coralline cluster.

The MDS ordination of surveys produced a complementary visualization of survey similarity to the cluster analysis. The best three-dimensional configuration of 1000 iterations achieved a stress level of 0.12, while the best two-dimensional configuration had a stress level of 0.17. Identifying factors such as habitat, study site, and season were again superimposed on the survey ordination and the grouping pattern most obviously aligned with survey habitat zone, as suggested by the cluster analysis (Figure 1.5). When a similarity isocline at a Bray-Curtis value of 25 was drawn, five groups were created. Three of the isocline groups aligned with clusters A, C, and D from the cluster analysis. The final

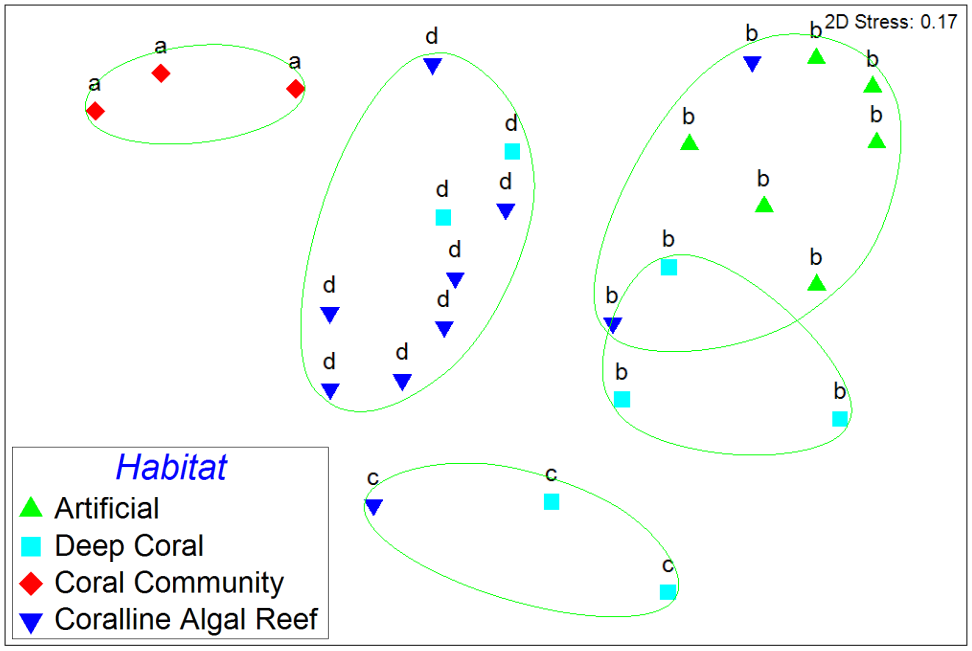

Figure 1.5. Two-dimensional MDS ordination of individual video surveys based on species-level data. Superimposed letters indicate significantly different clusters identified with SIMPROF in the cluster analysis. Colored symbols indicate the habitat zone within which a survey was conducted. Green contour lines represent a Bray-Curtis similarity of 25.

two isocline groups were composed of cluster B surveys divided along the internal division observed in the cluster analysis. These groups (as opposed to clusters) were not necessarily based on significantly different communities; rather they represented surveys that showed a Bray-Curtis similarity level of at least 25. As a check on cluster analysis, the MDS ordination agreed with the significant SIMPROF clusters, showing internal consistency of the significant clusters; no surveys that were clustered in the SIMPROF testing appeared to group with other clusters when ordinated.

SIMPER analysis broke down similarities within the four significantly different clusters, and dissimilarity between clusters, into contributions from individual species to characterize those species most typical of (Table 1.5), or most important in discriminating between (Table 1.6), the different clusters. Typifying or discriminating species showed a high ratio of similarity or dissimilarity to standard deviation, meaning they were consistently important in defining or differentiating groups.

The similarity between surveys within the coral cluster (Cluster A) was dominated by creolefish (*Paranthis furcifer)* which accounted for nearly 37% of the average Bray-Curtis similarity; however, scamp (*Mycteroperca phenax)* achieved the highest $\overline{S_i}/SD(S_i)$ of the group at 6.95 with a contribution of 3.16% to the average similarity. Other notable species typical (high $\overline{S_i}/SD(S_i)$) of the coral cluster were horse-eye jack (*Caranx latus,* S/SD=5.77, Contrib=5.14%), reef butterflyfish (*Chaetodon sedentarius*, S/SD=5.28, Contrib=4.00%), rock beauty (*Holacanthus tricolor)*, black jack (*Caranx lugubris)*, and yellowmouth grouper (*Mycteroperca interstitialis)* all with a S/SD=5.28 and contributing 2.83% to the similarity.

Table 1.5. Species contributing the most to survey similarity within significant clusters, ranked by percent contribution (Contrib%). Also included are the average abundance of the species within the group, average similarity contribution relative to its standard deviation (Sim/SD), and the cumulative percent contribution of species to the average group similarity (Cum.%, species up to 85% included).

Group	Species	Av.Abund	Sim/SD	Contrib%	Cum.%
Group a Av similarity: 33.82	*Paranthias furcifer*	21.59	1.16	36.71	36.71
	Chromis insolata	4.34	1.8	6.28	42.99
	Caranx latus	3.24	5.77	5.14	48.13
	Holocentrus adscensionis	1.96	2.08	4.94	53.07
	Sphyraena barracuda	2.77	1.66	4.44	57.51
	Chaetodon sedentarius	1.82	5.28	4	61.51
	Chromis enchrysurus	7.56	0.58	3.86	65.37
	Prognathodes aculatus	1.28	2.45	3.3	68.68
	Canthigaster rostrata	1.38	4.63	3.19	71.87
	Mycteroperca phenax	1.55	6.95	3.16	75.04
	Holacanthus tricolor	1.14	5.28	2.83	77.87
	Caranx lugubris	1	5.28	2.83	80.7
	Mycteroperca interstitialis	1.33	5.28	2.83	83.53
	Canthidermis sufflamen	2.34	0.58	2.15	85.68
Group b Av similarity: 28.97	*Lutjanus campechanus*	2.34	1.75	76.27	76.27
	Seriola dumerili	1.05	0.46	9	85.27
	Seriola rivoliana	0.4	0.33	5.44	90.72
Group c Av similarity: 33.18	*Seriola dumerili*	1.58	4.18	59.39	59.39
	Serranus phoebe	0.67	0.58	21.42	80.8
	Sphyraena barracuda	1.89	0.58	19.2	100
Group d Av similarity: 31.96	*Seriola dumerili*	1.76	2.92	13.51	13.51
	Chromis enchrysurus	2.09	1.22	13.42	26.93
	Centropyge argi	1.37	0.82	7.79	34.73
	Serranus annularis	1.08	0.81	6.65	41.37
	Chaetodon sedentarius	0.9	0.8	6.26	47.64
	Lutjanus campechanus	1.24	0.79	6.14	53.77
	Malacanthus plumieri	0.97	0.78	5.28	59.05
	Mycteroperca phenax	0.98	0.79	5.16	64.22
	Serranus phoebe	0.8	0.82	4.76	68.98
	Pronotogrammus martinicensis	2.43	0.34	4.57	73.55
	Opistognathus aurifrons	1.36	0.43	3.6	77.15
	Seriola rivoliana	0.86	0.56	3.48	80.62
	Prognathodes aculatus	0.65	0.61	2.82	83.44
	Carcharhinus plumbeus	0.49	0.43	2.05	85.49

Table 1.6. Species contributing the most to survey dissimilarity between significant clusters, ranked by percent contribution (Contrib%). Also included are the average abundance of the species within the groups being compared, and the average dissimilarity contribution relative to its standard deviation (Diss/SD). Only the top four species (based on percent contribution) are shown, see appendix A for a more complete list.

Groups	Species	Av.Abund	Av.Abund	Diss/SD	Contrib%
A vs B		Group a	Group b		
Av dissimilarity = 96.80	*Paranthias furcifer*	21.59	0.09	1.74	20.27
	Anthias tenuis	13.27	0	0.7	13.2
	Chromis multilineata	12.49	0	0.82	8.71
	Chromis enchrysurus	7.56	0	1.12	5.54
A vs C		Group a	Group c		
Av dissimilarity = 95.85	*Paranthias furcifer*	21.59	0	1.67	20.8
	Anthias tenuis	13.27	0	0.67	13.48
	Chromis multilineata	12.49	0	0.79	8.87
	Chromis enchrysurus	7.56	0.47	1.12	5.58
A vs D		Group a	Group d		
Av dissimilarity = 83.42	*Paranthias furcifer*	21.59	1.24	1.68	18.42
	Anthias tenuis	13.27	0.3	0.71	12.82
	Chromis multilineata	12.49	0	0.81	8.81
	Chromis enchrysurus	7.56	2.09	1.25	5.23
B vs C		Group b	Group c		
Av dissimilarity = 87.97	*Lutjanus campechanus*	2.34	0	1.58	20.72
	Sphyraena barracuda	0.09	1.89	1.14	13.94
	Seriola dumerili	1.05	1.58	1.54	11.86
	Caulolatilus microps	0	0.75	0.66	7.71
B vs D		Group b	Group d		
Av dissimilarity = 85.92	*Pronotogrammus martinicensis*	0	2.43	0.65	7.67
	Chromis enchrysurus	0	2.09	1.43	7.08
	Lutjanus campechanus	2.34	1.24	1.06	5.49
	Seriola dumerili	1.05	1.76	1.39	5.1
C vs D		Group c	Group d		
Av dissimilarity = 83.25	*Pronotogrammus martinicensis*	0	2.43	0.64	8.17
	Chromis enchrysurus	0.47	2.09	1.26	6.61
	Sphyraena barracuda	1.89	0.57	1.06	5.85
	Centropyge argi	0	1.37	1.3	4.9

The low relief cluster (Cluster B) that was composed of deep coral and artificial habitat surveys had over 85% of the average similarity between surveys accounted for by just two species, red snapper (*Lutjanus campechanas,* S/SD=1.75, Contrib=76.3%*)* and

greater amberjack (*Seriola dumerili*, S/SD=0.46, Contrib=9.0%). It should be noted that although these species accounted for a huge portion of the average similarity, the $\overline{S_i}/SD(S_i)$ ratios were low relative to typical species in other groups, an indication that the presence and/or number of individuals in a given survey was inconsistent.

The transitional cluster (Cluster C) that consisted of deep coral and coralline algal reef zones was completely defined by three species: greater amberjack (*Seriola dumerili*, S/SD=4.18, Contrib=59.4%), tattler (*Serranus phoebe*, S/SD=0.58, Contrib=21.4%*)*, and great barracuda (*Sphyraena barracuda*, S/SD=0.58, Contrib=19.2%). The similarities within the coralline cluster (Cluster D) were partitioned between many species, six different species were required to reach a cumulative contribution of 50%. The top three species driving intragroup similarity were greater amberjack (*Seriola dumerili*, S/SD=2.92, Contrib=13.5%), yellowtail reef fish (*Chromis enchrysurus*, S/SD=1.22, Contrib=13.4%), and cherubfish (*Centropyge argi*, S/SD=0.82, Contrib=7.8%).

Decomposition of intragroup similarities allowed for an examination of species typifying a cluster, however the same procedure using dissimilarities provided a more practical metric of discriminating species, those species most important in differentiating between clusters (Table 1.6). The highest average dissimilarity, 96.8, was observed between the coral (A) and low relief (B) clusters, while the lowest, 83.2, was between the transitional (C) and coralline clusters (D).

For all dissimilarity decompositions involving the coral cluster (A), the top four species contributing to the average Bray-Curtis dissimilarities between clusters were the same: creolefish (*Paranthis furcifer*), threadnose bass (*Anthis tenuis*), brown chromis (*Chromis multilineata*), and yellowtail reeffish (*Chromis enchrysurus*). The relative

contributions of each of these species to the average dissimilarity was very consistent across comparisons, with creolefish accounting for 18-20%, threadnose bass 12-13%, brown chromis 8%, and yellowtail reeffish 5%. However, when considering the $\overline{\delta_i}/SD(\delta_i)$ ratio as the defining metric for differentiating species between the coral cluster and all others, yellowmouth grouper (*Mycteroperca interstitialis)* and rock beauty (*Holacanthus tricolor)* consistently displayed the highest contribution-to-standard deviation ratio, ranging from 6.5-8 and 3.5-7.6 respectively. A large majority (87%) of species that made up the top 90% of cumulative dissimilarity contributions between the coral cluster and all others were found either exclusively or in higher abundances within the coral cluster surveys. This indicates that the dissimilarity between the coral cluster of surveys and all other clusters was mostly driven by species found exclusively, or at higher average abundances, at coral community habitat.

Average dissimilarity between the coralline cluster (D) and the low relief (B) and transitional (C) cluster surveys was partitioned across a wide range of species, each of which contributed a relatively small amount to the total dissimilarity. The same two species had the highest contributions to average dissimilarity between both cluster pairs, coralline-low relief and coralline-transitional: roughtongue bass (*Pronotogrammus martinicensis*) accounted for 7.6 and 8.1%, while yellowtail reeffish (*Chromis enchrysurus*) accounted for 7.0 and 6.6%. The most discriminating species (largest $\overline{\delta_i}/SD(\delta_i)$ ratio) for both cluster pairs was yellowtail reeffish (*Chromis enchrysurus*) with a ratio of 1.43 for the coralline-low relief comparison and 1.26 for the coralline-transitional comparison. Dissimilarity-to-deviation ratios tended to be low for these two comparisons, relative to the coral community comparisons previously described.

Similar to the coral cluster comparisons, nearly all species (92%) that made up the top 90% of cumulative dissimilarity contributions between the coralline cluster and the low relief and transitional clusters were found either exclusively or in higher abundances within the coralline cluster surveys. The average dissimilarity between the coralline cluster of surveys and the low relief and transitional clusters was mostly driven by species found exclusively, or at higher average abundances, within surveys composing the coralline cluster group.

Finally, the contributions to dissimilarity between the low relief (B) and transitional (C) clusters were topped by red snapper (*Lutjanus campechanus)* accounting for 20.7%, great barracuda (*Sphyraena barracuda)* at 14%, and greater amberjack (*Seriola dumerili*) at 12%. The same three species showed the highest dissimilarity-to-deviation ratios at 1.6, 1.1, and 1.5 respectively. Contrary to the other dissimilarities, the species contributing to dissimilarity between low relief and transitional clusters were not heavily biased to one cluster. Only 55% of the species that made up the top 90% of cumulative dissimilarity contributions between the low relief and transitional clusters were found exclusively or in higher abundances within the transitional cluster.

GENUS-LEVEL ANALYSES

At the genus level, the two-way PERMANOVA (Table 1.7) suggested significance for both the site effect (F_{pseudo}=1.42, p=0.05) and the habitat effect (F_{pseudo}=2.52, p=0.002), while the interaction between site and habitat was not significant (F_{pseudo}=1.23, p=0.19). Post-hoc pairwise comparisons between habitat zones indicated that the coral community habitat assemblage was significantly different than the assemblages at the other natural habitats, according to Monte-Carlo estimated p-values (Table 1.8).

Table 1.7. Genus-level global two-factor PERMANOVA results. Asterisk (*) indicates a significant factor (α=0.05). Perms: number of permutations against which each effect was tested.

Effect	Df	Perms	Pseudo F	p
Site	2	999	1.42	0.05*
Habitat	2	999	2.52	0.002*
Site x Habitat	3	999	1.23	0.19

Table 1.8. Post-hoc pairwise comparison of habitat levels from the global genus-level PERMANOVA. Asterisk (*) indicates a significant difference (α=0.05). CC: Coral Community, CAR: Coralline Algal Reef, DC: Deep Coral, Art: Artificial. Perms: number of permutations against which each effect was tested. P (perm): p-value obtained from the available permutations. P (Monte Carlo): p-value obtained from Mote Carlo estimation.

Pair	t	Perms	P (perms)	P (Monte Carlo)
CC - CAR	1.69	60	0.09	0.019*
CC – DC	1.79	30	0.03*	0.039*
CAR – DC	1.05	341	0.47	0.370
Art – CC	2.11	3	0.001*	0.090
Art - CAR	1.56	24	0.001*	0.091
Art - DC	1.35	12	0.08	0.166

Cluster analysis and subsequent SIMPROF testing indicated four significantly different (α=0.01) clusters of surveys (Figure 1.6). Superimposition of habitat zone factors suggested a strong correlation between significant cluster groups and the habitat zone within which a survey was conducted. The genus-level cluster groups showed very high internal consistency with regards to the habitat factor, including a maximum of two dissimilar surveys within a given group.

Cluster A was composed of the same three coral community surveys as associated with the species-level analysis. Cluster B contained all six artificial reef surveys and two coralline algal reef surveys. Cluster C contained seven coralline algal reef surveys and two deep coral surveys. Finally, cluster D contained the remaining five deep coral surveys and one coralline algal reef survey.

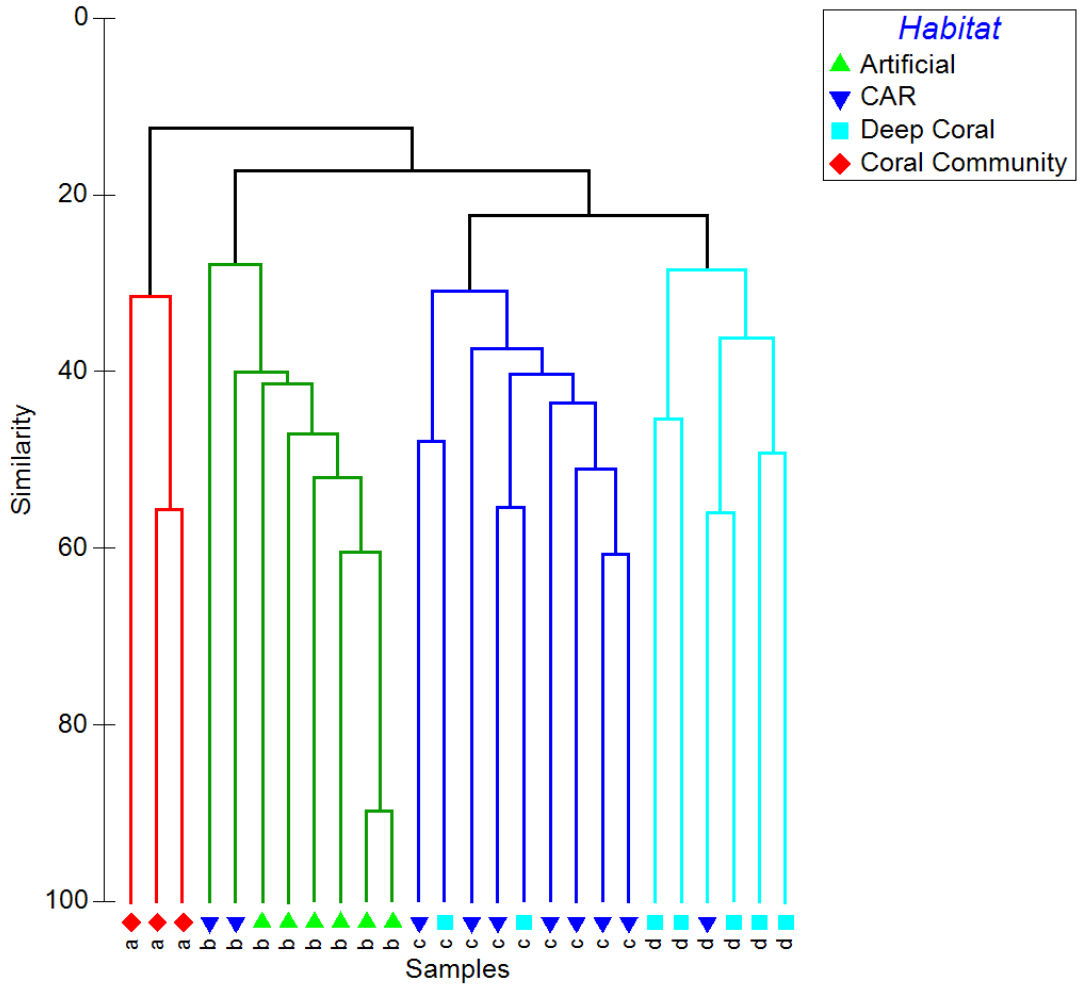

Figure 1.6. Cladogram displaying results of genus-level cluster analysis of similarity between surveys. Colored lines and letters (a-d) indicate significantly different (α=0.01) clusters identified by the SIMPROF procedure. Colored symbols indicate the habitat zone within which each survey was conducted. CAR: coralline algal reef

The complementary MDS analysis achieved a two-dimensional stress of 0.16 and a three-dimensional stress of 0.11. Identifying factors were again superimposed on the survey ordination and the grouping pattern most obviously aligned with survey habitat zone, as suggested by the cluster analysis (Figure 1.7). When a similarity isocline at a Bray-Curtis value of 25 was drawn, the four significant cluster groups were highlighted. As a check on cluster analysis, the MDS ordination agreed with the significant SIMPROF clusters,

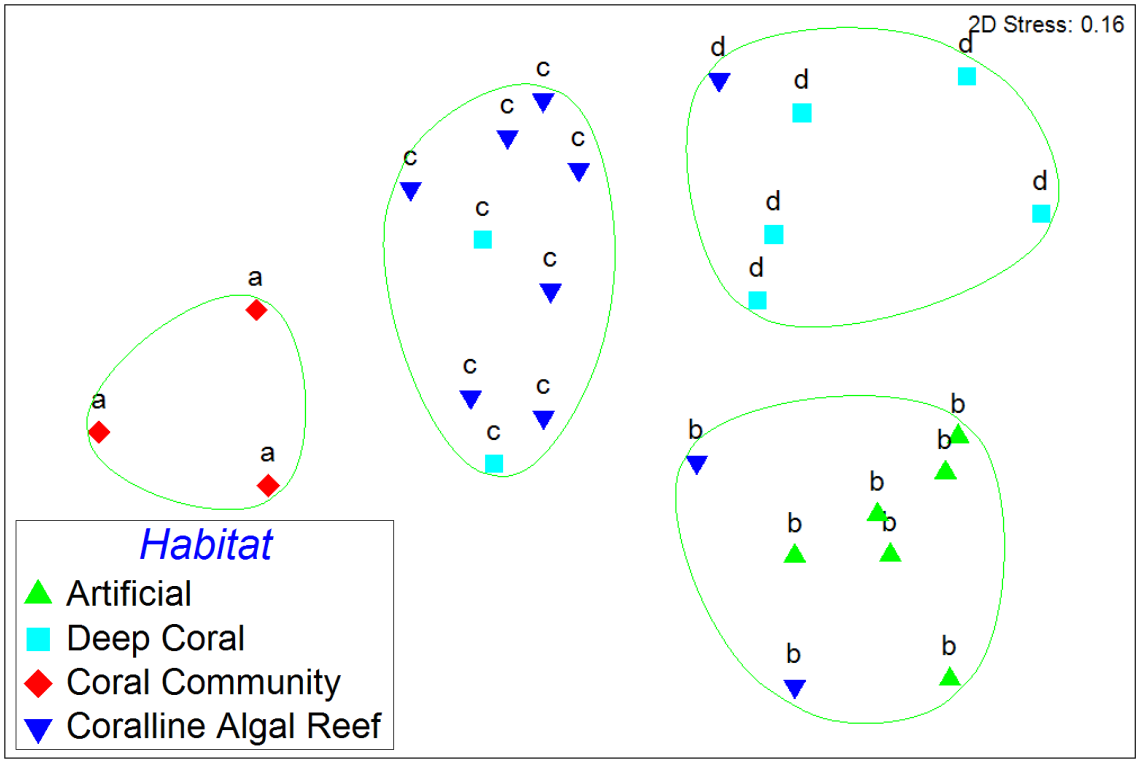

Figure 1.7. Two-dimensional MDS ordination of individual video surveys based on genus-level data. Superimposed letters indicate significantly different clusters identified with SIMPROF. Colored symbols indicate the habitat zone within which a survey was conducted. Green contour lines represent a Bray-Curtis similarity of 25.

showing internal consistency of the significant clusters; no surveys that were clustered in the SIMPROF testing appeared to group with other clusters when ordinated. Ordination also allowed for the presence of a gradient from one habitat zone to the next to be visualized, as opposed to the strict delineation of groups in cluster analysis. In this case, the ordination displayed a 'left-to-right' gradient from coral community surveys, through coralline algal reef surveys, and to either artificial or deep coral surveys.

As with the species-level analysis, similarities within clusters and dissimilarities between clusters were decomposed into individual genus contributions to determine those genera typical of each cluster, as well as those responsible for discriminating between clusters. The predominantly artificial habitat cluster (B) shower the highest average

internal similarity at 42.7, while the predominantly deep coral cluster (D) showed the lowest average similarity at 34.9 (Table 1.9). Similarity within the coral community cluster (A) was dominated by *Paranthias* which contributed 37.9% to the average similarity,

Table 1.9. Genera contributing the most to survey similarity within significant clusters, ranked by percent contribution (Contrib%). Also included are the average abundance of the species within the group, average similarity contribution relative to its standard deviation (Sim/SD), and the cumulative percent contribution of species to the average group similarity (Cum.%, species up to 85% included).

Group	Genus	Av.Abund	Sim/SD	Contrib%	Cum.%
Group A	*Paranthias*	21.59	1.11	37.9	37.9
Av. similarity:	*Chromis*	15.02	2.16	10.78	48.67
39.51	*Caranx*	3.76	5.1	7.39	56.06
	Holocentrus	1.96	2.53	4.91	60.97
	Mycteroperca	2.1	5.08	4.74	65.72
	Sphyraena	2.77	1.57	4.55	70.27
	Chaetodon	1.82	9.07	4.03	74.3
	Prognathodes	1.28	3.09	3.29	77.59
	Canthigaster	1.38	4.75	3.24	80.83
	Holacanthus	1.24	9.07	2.85	83.68
	Canthidermis	2.34	0.58	2.27	85.96
Group B	*Lutjanus*	2.8	2.38	74.84	74.84
Av. similarity:	*Seriola*	1.41	1	22.49	97.33
42.72					
Group C	*Chromis*	2.51	1.28	14.99	14.99
Av. similarity:	*Seriola*	1.95	2.61	13.61	28.6
38.23	*Serranus*	1.52	4.22	13.21	41.8
	Chaetodon	1.05	1.11	7.84	49.65
	Centropyge	1.37	0.82	7.24	56.89
	Lutjanus	1.48	0.78	5.79	62.68
	Mycteroperca	1.05	0.78	5.28	67.96
	Malacanthus	0.97	0.79	4.9	72.86
	Pronotogrammus	2.43	0.34	4.18	77.04
	Opistognathus	1.36	0.44	3.46	80.5
	Balistes	0.73	0.61	2.86	83.36
	Prognathodes	0.69	0.61	2.84	86.2
Group D	*Serranus*	1.07	3.55	37.44	37.44
Av. similarity:	*Seriola*	1.4	1.27	31.49	68.93
34.86	*Pagrus*	0.94	0.45	7.77	76.7
	Malacanthus	0.69	0.48	6.82	83.53
	Lutjanus	0.57	0.48	5.83	89.36

followed by *Chromis* (10.8%) and *Caranx* (7.4%). However, these high contributions did not translate to high contribution-to-deviation ratios ($\overline{S_i}/SD(S_i)$), indicating that these genera occurred in highly variable abundances. The most typical genera of cluster A were *Chaetodon* ($\overline{S_i}/SD(S_i)$ = 9.1) and *Holocanthus* ($\overline{S_i}/SD(S_i)$ = 9.1) which occurred at an average abundance of 1.8 and 1.2, respectively.

Cluster B, composed primarily of artificial habitat surveys, was dominated and typified by two genera: *Lutjanus* and *Seriola*. *Lutjanus* contributed 74.8% to the average similarity and showed a contribution-to-deviation ratio ($\overline{S_i}/SD(S_i)$) of 2.4. *Seriola* contributed 22.5% to the average similarity and showed a contribution-to-deviation ratio of 1.

The predominantly coralline cluster (cluster C) showed an average similarity of 38.2, over 40% of which was accounted for by three genera: *Chromis* (15%), *Seriola* (13.6%), and *Serranus* (13.2%). The same three genera typified the cluster, this time led by *Serranus* ($\overline{S_i}/SD(S_i)$ = 4.2), followed by *Seriola* ($\overline{S_i}/SD(S_i)$ = 2.6) and *Chromis* (1.3).

Finally, the similarity within the predominantly deep coral cluster (cluster D) was contributed to the most by *Serranus* (37.4%) and *Seriola* (31.5%), both of which were the most typical genera of the cluster with contribution-to-deviation ratios of 3.5 and 1.3 respectively.

The average dissimilarity between genus-level clusters ranged from a low of 77.5 (C v D) to a high of 94.7 (A v B, Table 1.10). All three dissimilarity decompositions between cluster A, the coral community cluster, and the other clusters (B, C, D) shared the same four highest-contributing genera: *Paranthias (*22.9-24.2%), *Anthias* (15.1-15.3%), *Chromis*

(12.7-14.5%), and *Caranx* (3.8-4.5%). The most discriminating genus between the three pairs that included the coral community cluster (A) was *Holocanthus*, with $\overline{\delta_i}/SD(\delta_i)$ ratios ranging from 3.4 to 7.3 (Appendix A).

Table 1.10. Genera contributing the most to survey dissimilarity between significant clusters, ranked by percent contribution (Contrib%). Also included are the average abundance of the species within the groups being compared, and the average dissimilarity contribution relative to its standard deviation (Diss/SD). Only the top four species (based on percent contribution) are shown, see appendix A for a more complete list.

Groups	Genus	Av.Abund	Av.Abund	Diss/SD	Contrib%
A v B		Group a	Group b		
Av. dissimilarity:	*Paranthias*	21.59	0.13	1.86	24.07
94.75	*Anthias*	13.27	0	0.69	15.11
	Chromis	15.02	0	1.1	14.53
	Caranx	3.76	0	1.72	4.52
A v C		Group a	Group c		
Av. dissimilarity:	*Paranthias*	21.59	1.24	1.77	22.9
77.79	*Anthias*	13.27	0.3	0.71	15.33
	Chromis	15.02	2.51	0.91	12.7
	Caranx	3.76	0.61	1.43	3.82
A v D		Group a	Group d		
Av. dissimilarity:	*Paranthias*	21.59	0	1.86	24.2
92.84	*Anthias*	13.27	0	0.69	15.11
	Chromis	15.02	0.24	1.06	14.31
	Caranx	3.76	0	1.71	4.51
B v C		Group b	Group c		
Av. dissimilarity:	*Chromis*	0	2.51	1.64	9.36
84.45	*Pronotogrammus*	0	2.43	0.65	8.72
	Lutjanus	2.8	1.48	1.28	7.68
	Serranus	0	1.52	3.45	5.75
B v D		Group b	Group d		
Av. dissimilarity:	*Lutjanus*	2.8	0.57	1.45	20.9
80.33	*Seriola*	1.41	1.4	1.13	10.63
	Serranus	0	1.07	3.48	9.89
	Sphyraena	0.13	0.94	0.68	8.66
C v D		Group c	Group d		
Av. dissimilarity:	*Chromis*	2.51	0.24	1.53	9.03
77.53	*Pronotogrammus*	2.43	0	0.65	8.99
	Centropyge	1.37	0	1.29	5.41
	Opistognathus	1.36	0	0.75	5.16

As with the species-level analysis, the majority of the genera (85%) that made up the top 90% of cumulative dissimilarity contributions between cluster A and all others were found either exclusively or in higher abundances within coral community surveys. That is, the average dissimilarity between the surveys making up cluster A and all other clusters was mostly driven by genera found exclusively, or at higher average abundances, at coral community habitat.

Dissimilarities between the predominantly coralline algal reef cluster (C), and the artificial (B) and deep coral (D) clusters were contributed to the most by the same two genera: *Chromis* (9.4% v B and 9% v D) and *Pronotogrammus* (8.7% v B and 9% v D). *Chromis* was also the most discriminating genus between clusters C and D ($\overline{\delta_i}/SD(\delta_i)$=1.5), followed by *Chaetodon* ($\overline{\delta_i}/SD(\delta_i)$=1.3). Between clusters C and B however, *Serranus* was the standout discriminating genus with a contribution-to-deviation ratio of 3.5. The average dissimilarity between the surveys making up cluster C versus the B and D clusters was mostly driven by genera found exclusively, or at higher average abundances, within surveys in the predominantly coralline algal reef cluster. Most (93%) of the genera that made up the top 90% of cumulative dissimilarity contributions between cluster C versus clusters B and D were found either exclusively or in higher abundances within coralline (cluster C) surveys.

Finally, *Lutjanus* contributed the most to average dissimilarity between the artificial (B) and deep coral (D) clusters with 20.9%, followed by *Seriola* (10.6%) and *Serranus* (9.9%). *Serranus* stood out as the most discriminating species between the artificial (B) and deep coral (D) clusters with a contribution-to-deviation ratio ($\overline{\delta_i}/SD(\delta_i)$) of 3.45. The

majority (67%) of the genera that made up the top 90% of cumulative dissimilarity contributions between cluster B and cluster D were found either exclusively or in higher abundances within the deep coral cluster (D) of surveys.

FAMILY-LEVEL ANALYSES

At the family level, the only significant effect in the two-way PERMANOVA (Table 1.11) was the habitat effect (F_{pseudo}=2.5, p=0.001). The site effect and the site*habitat interaction were not significant. Post-hoc pairwise comparisons between habitat zones indicated a significantly different assemblage at the coral community habitat relative to all other habitat types, according to Monte-Carlo estimated p-values (Table 1.12).

Table 1.11. Family-level global two-factor PERMANOVA results. Asterisk (*) indicates a significant factor (α=0.05).

Effect	Df	Perms	Pseudo F	p
Site	2	999	1.68	0.07
Habitat	2	999	2.50	0.001*
Site x Habitat	3	999	1.20	0.14

Table 1.12. Post-hoc pairwise comparison of habitat levels from the global family-level PERMANOVA. Asterisk (*) indicates a significant difference (α=0.05). CC: Coral Community, CAR: Coralline Algal Reef, DC: Deep Coral, Art: Artificial. P (perm): p-value obtained from the available permutations. P (Monte Carlo): p-value obtained from Mote Carlo estimation.

Pair	t	Perms	P (perms)	P (Monte Carlo)
CC - CAR	1.94	60	0.09	0.007*
CC – DC	2.01	30	0.09	0.042*
CAR – DC	1.19	345	0.18	0.226
Art – CC	2.89	3	0.001*	0.044*
Art - CAR	1.67	24	0.001*	0.073
Art - DC	1.51	12	0.001*	0.133

SIMPROF testing of the survey cluster analysis indicated two significantly different (α=0.01) clusters of surveys (Figure 1.8). Superimposition of site and habitat zone factors indicated that the clusters nearly perfectly represented the natural versus artificial

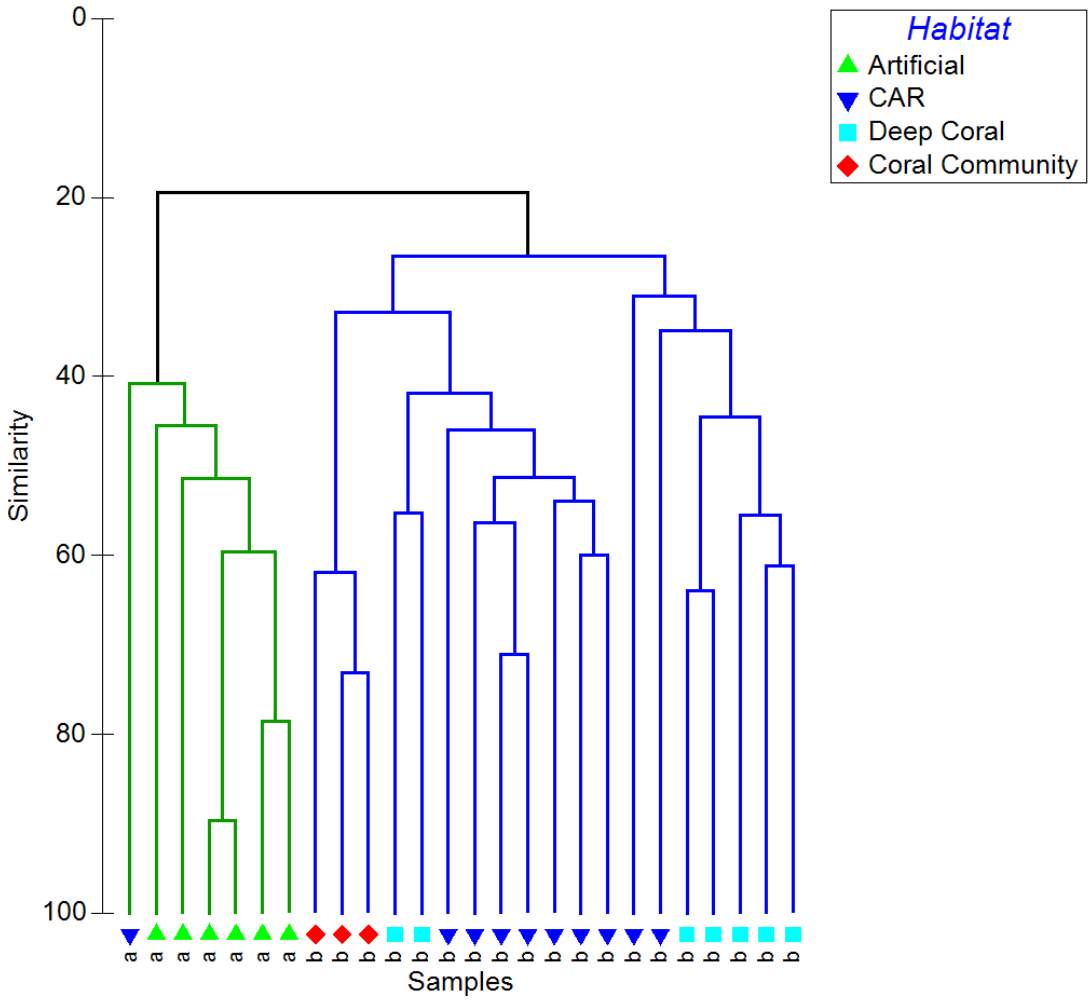

Figure 1.8. Cladogram displaying results of family-level cluster analysis of similarity between surveys. Colored lines and letters (a,b) indicate significantly different (α=0.01) clusters identified by the SIMPROF procedure. Colored symbols indicate the habitat zone within which each survey was conducted. CAR: coralline algal reef

dichotomy. Cluster A, the "artificial" cluster, was composed of all six East Cameron artificial reef surveys and a single coralline algal reef survey from Bright. Cluster B, the "natural" cluster, included the remaining nineteen surveys, all from natural habitat zones. Within the cluster, three non-significant groups of surveys aligned nearly perfectly with the three natural habitat zones.

The complementary MDS ordination achieved a two-dimensional stress of 0.15 and a three-dimensional stress of 0.11. Identifying factors were again superimposed on the

survey ordination and the grouping pattern supported the natural-artificial division observed in the cluster analysis (Figure 1.9). When a similarity isocline at a Bray-Curtis value of 25 was drawn, the two significant cluster groups were highlighted. As a check on cluster analysis, the MDS ordination agreed with the significant SIMPROF clusters, showing internal consistency of the significant clusters; no surveys that were clustered in the SIMPROF testing appeared to group with other clusters when ordinated. The ordination procedure allowed for the visualization of a gradient between habitats rather than the strict distinctions implied by cluster analysis. For the family-level MDS, the natural habitat cluster displayed a gradient of habitat zones associated with the individual surveys as ordinated, from coral community to deep coral, with coralline algal reef taking an

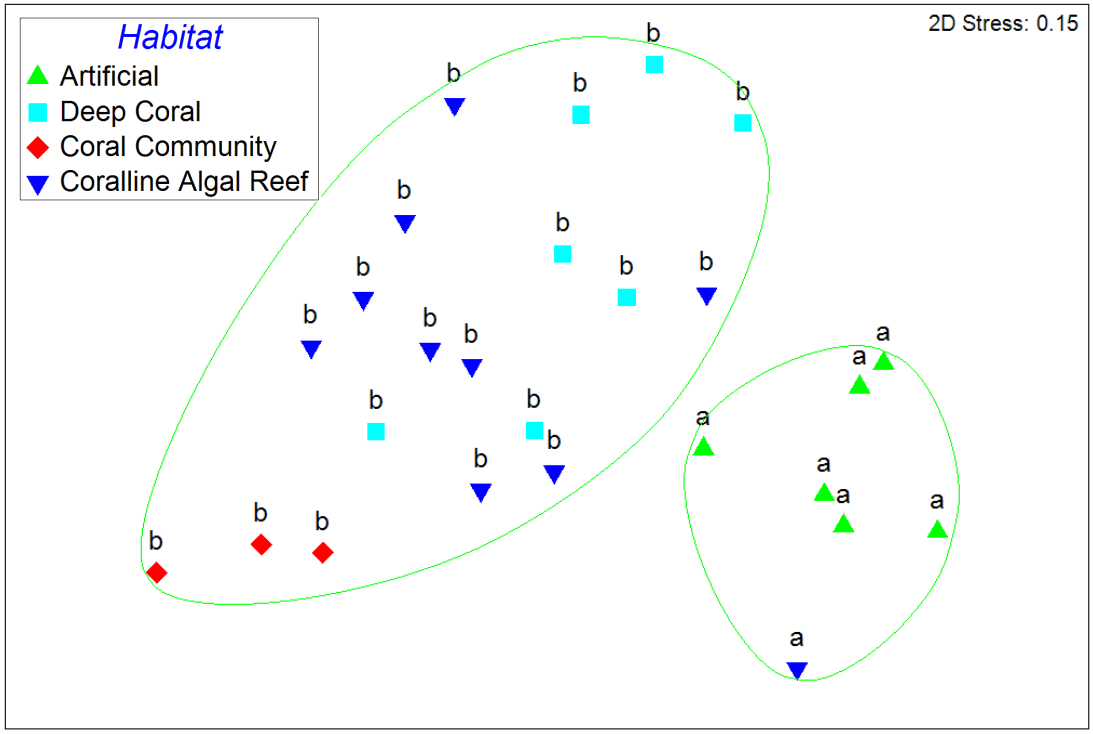

Figure 1.9. Two-dimensional MDS ordination of individual video surveys based on family-level data. Superimposed letters indicate significantly different clusters identified with SIMPROF. Colored symbols indicate the habitat zone within which a survey was conducted. Green contour lines represent a Bray-Curtis similarity of 25.

intermediate position. This arrangement of zones matches the depth distribution of the habitat zones on natural banks, with coral community habitats at the shallowest depths, followed by coralline algal reef, and deep coral habitats at progressively deeper depths.

SIMPER analysis broke down similarities within, and dissimilarity between, the two clusters into contributions from individual families. This characterized the families most typical of, or most important in discriminating between, the two clusters. The artificial habitat cluster (A) showed a much higher average intragroup similarity (51.6) than the natural habitat cluster (34.5, Table 1.13). Over 96% of the average similarity within the

Table 1.13. Families contributing the most to survey similarity within significant clusters, ranked by percent contribution (Contrib%). Also included are the average abundance of the family within the group, average similarity contribution relative to its standard deviation (Sim/SD), and the cumulative percent contribution of families to the average group similarity (Cum.%, species up to 85% included).

Group	Family	Av.Abund	Sim/SD	Contrib%	Cum.%
Group a	Lutjanidae	3.06	4.48	77.19	77.19
Av. similarity: 51.62	Carangidae	1.41	0.87	18.9	96.09
Group b	Serranidae	7.8	1.4	28.68	28.68
Av. similarity: 34.49	Carangidae	2.35	1.52	21.71	50.39
	Malacanthidae	0.87	0.56	8.66	59.05
	Pomacentridae	3.65	0.66	8.06	67.11
	Lutjanidae	1.28	0.69	7.39	74.5
	Chaetodontidae	1.07	0.69	6.16	80.65
	Pomacanthidae	1.06	0.59	4.63	85.28

artificial cluster (A) was accounted for by two families: Lutjanidae (77.2%) and Carangidae (18.9%). The Lutjanids most strongly typified the artificial cluster with a $\overline{S_i}/SD(S_i)$ ratio of 4.48. The average similarity within the natural cluster (B) was attributed to more families relative to the artificial cluster, however two families accounted for over 50% of the

average similarity: Serranidae (28.7%) and Carangidae (21.7%). Both families were also most typical of the cluster, with $\overline{S_i}/SD(S_i)$ ratios of 1.5 for Carangidae and 1.4 for Serranidae.

The average Bray-Curtis dissimilarity between the artificial habitat (A) and natural habitat (B) clusters was 80.5 (Table 1.14). Serranidae contributed the most to this dissimilarity with 21.9%, followed by Lutjanidae (13.4%) and Pomacentridae (9.3%). The most discriminating families between the two clusters were Carangidae and Serranidae with $\overline{\delta_i}/SD(\delta_i)$ ratios of 1.2. The average dissimilarity between the natural and artificial clusters was nearly completely attributed to families more abundant at, or exclusive to, natural habitats and sites. Of the species contributing to the top 90% of the average dissimilarity between clusters, all but one family (Lutjanidae) was more abundant, or exclusively found, at surveys in the natural cluster (Table 1.14).

Table 1.14. Families contributing the most to survey dissimilarity between significant clusters, ranked by percent contribution (Contrib%). Also included are the average abundance of the families within the groups being compared, and the average dissimilarity contribution relative to its standard deviation (Diss/SD). Families accounting for 90% of the cumulative dissimilarity between groups are shown.

Groups	Family	Av.Abund	Av.Abund	Diss/SD	Contrib%
A v B		Group a	Group b		
Av.	Serranidae	0.14	7.8	1.21	21.97
dissimilarity:	Lutjanidae	3.06	1.28	1.11	13.43
80.56	Pomacentridae	0	3.65	0.85	9.3
	Carangidae	1.41	2.35	1.22	9.22
	Malacanthidae	0	0.87	0.81	6.36
	Sphyraenidae	0.14	1.01	0.57	4.76
	Chaetodontidae	0	1.07	1.11	4.42
	Pomacanthidae	0	1.06	0.95	4.15
	Sparidae	0	0.64	0.57	3.76
	Carcharhinidae	0.29	0.38	0.73	3.17
	Balistidae	0.14	1	0.94	3.11
	Opistognathidae	0	0.65	0.47	2.78
	Labridae	0	0.83	0.69	2.54
	Holocentridae	0	0.53	0.5	1.91

DISCUSSION

The shelf-edge banks of the northwestern Gulf are known to provide important natural reef and hard bottom habitat in an area otherwise dominated by low relief, soft sediments (Rezak et al. 1985). A number of studies have investigated reef fish assemblages associated with the northwest Gulf banks and have found evidence for distinct assemblage patterns related to habitat zonation (Boland et al. 1983, Rezak et al. 1985, Dennis and Bright 1988, Weaver et al. 2006), depth (Boland et al. 1983), and study site (Wetmore and Rooker 2011). While extremely informative and crucial to the current state of knowledge, many previous studies have generally been exploratory in nature, limiting the extent of analysis possible (Weaver et al. 2006). This study attempted to quantitatively define the reef fish assemblages associated with three shelf-edge banks that have historically received less attention than the extensively surveyed Flower Garden banks, to examine whether assemblage patterns may be related to benthic habitat zonation, and to compare the assemblages at the natural banks to an artificial reef.

Three traditional assemblage indices, richness, Shannon diversity, and Pielou's evenness, showed significant differences between habitat zones and study sites. Richness and diversity were higher at natural sites and habitat zones relative to the artificial reef, consistent with previous work comparing natural shelf-edge banks to nearby artificial structure (Sonnier et al. 1976, Rooker et al. 1997, Wilson et al. 2003). The disparity between the two structure types could be due to the greater variety and total area of natural reef habitat (Rooker et al. 1997). Natural banks in the present study covered between approximately 4 and 20 km^2 (Jakkula and Bright, respectively) while the artificial reef, EC-231 "A", has a footprint of <0.01 km^2. Additionally, the artificial reef surveyed in

this study likely experiences substantially different physical conditions relative to the shelf-edge banks. While the shelf-edge banks rise from depths over 100m, the artificial reef site is located mid-shelf at a depth of 55m, making the site more susceptible to influences of the Mississippi River plume, high turbidity, and greater seasonal temperature variations, all factors that may influence biological communities in the area (Rezak et al. 1990).

A fundamental difference between the artificial reefs and natural bank structures examined in this study involves how vertical relief is expressed. While the natural banks examined in this study exhibit up to 75m of vertical relief (Gardner and Beaudoin 2005), this relief is spread out over multiple square kilometers. This means that only localized relief, on the order of meters, is captured by video surveys. Conversely, artificial reefs formed from production platforms produce vertical relief that is extremely localized with no gradient. This study was restricted to benthic surveys and only sampled the fish assemblage associated with the artificial reef at the seafloor, although it is known that assemblages vary with depth at artificial structures in the region (Shinn 1974, Sonnier et al. 1976, Gallaway and Lewbel 1982, Rooker et al. 1997, Stanley and Wilson 2000a, Wilson et al. 2003).

Considering only natural habitat zones and sites, the assemblage indices observed in the present study show very similar values and relationships to previous work. Dennis and Bright (1988) report similar habitat-related diversity relationships with the highest diversity observed in the algal habitat zone, as well as H' values consistent with those recorded at natural habitats in the present study (1.3-1.8) that did not differ significantly between banks. The same study reported an inverse relationship between diversity and evenness, where high diversity areas tended to show low evenness. In the present study, a

similar relationship was generally observed between richness and evenness. For example, the coral community habitat zone showed the highest richness of all habitat zones but the lowest evenness, with diversity taking a moderate value. Although the highest number of species was observed at the coral community habitat, the total number of individuals present was dominated by a few species, such as creolefish (*Paranthias furcifer)*, driving down the evenness. Diversity showed a moderate value between the two extremes because the calculation of the Shannon diversity index incorporates concepts of both richness and evenness. Boland et al. (1983) showed a similar pattern at the Flower Garden banks where diversity decreased with depth, while evenness increased. Such discrepancies highlight the importance of using multiple metrics when examining fundamental assemblage characteristics, as well as the limitations of condensing data-rich assemblage information into univariate assemblage indices.

At the species level, a significant habitat zone effect on reef fish assemblages was observed, though the interaction between the site and habitat was not significant. The nonsignificant interaction indicates that the assemblages within a given habitat zone were consistent among sites. Consistency of reef fish assemblages within a given habitat among multiple shelf-edge banks has been observed by a number of previous studies at a variety of sites and habitats (Bright et al. 1985, Dennis and Bright 1988, Wetmore and Rooker 2011). The consistency of assemblages between sites indicates that habitat-assemblage relationships are not chance associations. Habitat zones provide different food resources (Dennis and Bright 1988, Schwartzkopf 2014), types of shelter (Dennis and Bright 1988), and physical conditions suitable to certain species (Schmahl et al. 2008), leading to the consistent and distinct fish assemblages observed.

Four distinct reef fish assemblages were resolved at the species-level by cluster analysis at Bright, Jakkula, and McGrail banks, and the artificial reef EC-231 "A". These assemblages aligned closely with the natural biological habitat zones defined by Schmahl et al. (2008) and artificial reef habitat. Simlarly, while studying the reef fish communites at the Flower Garden banks, Dennis and Bright (1988) observed three distinct reef fish assemblages that appeared to be related to habitat zonation, naming them after the associated zones: the coral reef, algal-sponge, and drowned reef assemblages. While the habitat zone names have changed, the assemblages resolved in the present study follow a similar pattern, though the banks surveyed contained less coral habitat and an artificial reef was included for comparison. Although these assemblages are discussed independently, species are not necessarily exclusive to a particular assemblage. Rather, just as the habitat zones themselves (McGrail et al. 1982), the assemblages exist along a gradient.

The species composition of the four species-level assemblages observed agree well with commonly observed species during previous surveys and assemblage descriptions at northwest Gulf banks (Boland et al. 1983, Rezak et al. 1985, Dennis and Bright 1988, Pattengill-Semmens et al. 2000, Wilson et al. 2003, 2006, Kraus et al. 2006, Weaver et al. 2006). In the shallow coral community habitat, creolefish (*Paranthias furcifer*) were the numerically dominant species, consistent with nearly every reef fish survey conducted at the shelf-edge banks due to the extensive feeding schools they form at the shallow crests of a number of the banks (Dennis and Bright 1988). This coral community assemblage is composed of species very similar to those of Dennis and Bright's (1988) coral reef assemblage. When comparing between assemblages resolved in the present study, those

species responsible for discriminating between the coral community assemblage and any other assemblage tended to only occur, or were more abundant, in the coral community habitat zone. This is likely due to the significantly higher richness observed at the coral community habitat relative to the other habitat zones, and produced the highest relative rate of 'assemblage endemism' (43%).

The next deepest assemblage was composed of species primarily observed at coralline-algal habitats and was numerically dominated by roughtongue bass (*Pronotogrammus martinicensis)*. In their surveys of reef fishes at three shelf-edge banks, Weaver et al. (2006) also noticed this transition from *P. furcifer* dominated assemblages to *P. martinicensis* with increasing depth, an example of species replacement while maintaining a planktivore-dominated assemblage.

The multi-zone composition and high species overlap with other assemblages indicates that the transitional assemblage likely incudes species from the transitional area where coralline algal reefs shift towards deep coral habitat. Highly mobile species such as barracuda (*Sphyraenidae barracuda*) and greater amberjack (*Seriola dumerili*) dominated the assemblage, species that are not constrained to a single habitat zone, or even a single bank (Rezak et al. 1985). The presence of such transient species could indicate a preferred feeding ground on cryptic species not observed during the surveys, a known limitation of video methodologies (Willis 2001, Tessier et al. 2005, Watson et al. 2005). Alternatively, the use of a baited camera array could preferentially attract highly mobile species, or the zone may be a relatively species-poor area that roaming predators must cross to access shallower or deeper prey resources.

The final assemblage included species found at both natural deep coral and artificial reef habitat. The similarity in assemblages, dominated by species such as red snapper (*Lutjanus campechanus*) and greater amberjack (*Seriola dumerili*), is likely due to similar physical and substrate conditions between the two types of habitat. Although found at dramatically different depths, both habitats exhibit relatively low hard substrate coverage and are exposed to turbid conditions, caused by the Mississippi River plume at the East Cameron site and exposure to the bottom nepheloid layer at the natural sites. In fact, the nepheloid layer has been proposed as one of the most important environmental factors in determining assemblage composition at natural sites (Dennis and Bright 1988).

Although the natural and artificial reef habitats show similar assemblages, the different types of structure may not be equal from a life history perspective. For example, recent studies have shown that for a typical species of this assemblage, red snapper, individuals at natural habitats are in better condition, have a higher quality diet, and have a greater reproductive potential (Saari 2011, Kulaw 2012, Simonsen 2013, Glenn 2014, Schwartzkopf 2014). So while much of the attention and protective action at the shelf-edge banks has been focused on areas containing corals, the dominance of important fishery species, such as red snapper, in the deeper and peripheral habitat zones necessitates their consideration for future management and protective measures such as the proposed expansion to the FGBNMS (USDOC et al. 2012). Furthermore, deeper-crest features, such as Jakkula bank, may not possess the high-sensitivity habitat zones that have warranted protection to this point, but do provide habitat zones occupied by many commercially and recreationally important species and could serve as valuable 'stepping-stones' of reef habitat, especially for high mobility species.

The extensive reef fish surveys conducted by Weaver et al. (2002) at the Pinnacles Reef Tract in the northeastern Gulf provide an interesting point of comparison for species composition and assemblage distributions. The features in this reef tract are predominantly drowned reefs, as opposed to salt diapir structures in the northwest Gulf, and exhibit relatively less relief and deeper crests (Weaver et al. 2001). Similar to the findings in this study, the reef fish assemblages found at the Pinnacles reefs differed in both species richness and composition in relation to biotopes, or reef zones. Reef crests showed the highest species richness, similar to the richness observed at the shallow coral community habitat zone in this study. Despite similarities in species distribution patterns between the regions, the Pinnacles reefs showed a reduced number of species relative to northwestern Gulf reefs, attributed by the authors to low winter temperatures and low light levels limiting epifaunal growth and the subsequent habitat available for reef fishes (Weaver et al. 2001). The species observed at the Pinnacles Reef Tract were most similar to those observed at deep coral habitat zone in the present study, a logical relationship given the similarity in environmental conditions (light, temperature, turbidity) and reef structure origin (drowned reefs).

Habitat-assemblage associations were even more apparent at higher taxonomic levels, with the four genus-level assemblages matching nearly perfectly with the four habitat zones surveyed (coral community, coralline algal reef, deep coral, and artificial) and the two family-level assemblages defined by natural or artificial habitat. This is the first study to examine assemblage patterns at the genus and family-level at the shelf-edge banks. The underlying similarities between individual surveys, however, displayed the same gradient of assemblages between habitat zones as observed at the species-level. This

can be attributed to the coarser taxonomic resolution resulting in more shared genera or families between assemblages, leading to a higher overlap between assemblages, as well as the inherent gradation of the habitat zones themselves (McGrail et al. 1982).

Assemblage description at coarser taxonomic resolution has been proposed as one method of addressing the logistical difficulties and high cost of detailed, high volume data processing by taxonomic experts (Ellis 1985). This idea of taxonomic sufficiency (TS) suggests "identifying organisms to a level of taxonomic resolution sufficient to satisfy the objective of a study" (Bertrand et al. 2006). Should such a method of assemblage description be desired for long-term monitoring of the shelf edge banks in the Gulf, the information presented in this study would provide a baseline against which future information may be compared.

Future studies of the reef fish assemblages at northwestern Gulf shelf edge banks would benefit from more dense and regular data collection than available in the present study. Higher density surveys across the variety of depths (and thus habitats) covered by individual banks would improve the spatial resolution of both assemblage and benthic habitat distributions and provide information about the generality of the assemblages resolved in the present study. More regular, long-term sampling would provide the opportunity for seasonal effects to be examined, a potential source of assemblage variability (Boland et al. 1983, Pattengill et al. 1997, Rooker et al. 1997). Future comparisons of natural and artificial reef assemblages would benefit from surveys covering multiple depths at artificial reefs to account for known differences in species composition with depth (Shinn 1974, Sonnier et al. 1976, Gallaway and Lewbel 1982, Rooker et al. 1997, Stanley and Wilson 2000a, Wilson et al. 2003).

My results agree with previous reef fish surveys at northwest Gulf banks that show distinct assemblages generally structured relative to the benthic habitat zonation outlined by Rezak et al. (1985) and Schmahl et al. (2008) (Boland et al. 1983, Dennis and Bright 1988, Weaver et al. 2006). These assemblages appear to be consistent across multiple shelf-edge banks, likely due to the similarity in habitat available at each bank. The reef fish assemblage at the base of the artificial reef examined in this study, EC-231 "A", most closely resembles that of deep reef habitat, though generally shows lower species richness and diversity than any natural habitat zone. Assemblages based on coarser taxonomic classification differed from those at the species-level, especially assemblages at the family level that aligned closely with the distinction between artificial and natural reefs versus benthic habitat zones. The data suggest that reef fish assemblages are strongly related to benthic habitat zonation, and that substantial differences may be present between natural and artificial reef fish assemblages.

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CHAPTER 2: EFFECTS OF HABITAT COMPLEXITY ON REEF FISH ASSEMBLAGES AT NORTHWEST GULF OF MEXICO BANKS

INTRODUCTION

The northwest Gulf of Mexico (Gulf) shelf-edge banks support a wide variety of reef-dependent and reef-associated fish species, many of which are important to commercial and recreational fisheries in the Gulf region. Effective fisheries management is necessary both to protect these resources and to ensure long-term sustainability. A paradigm shift in recent years has seen management procedures transition from single-species based approaches to ecosystem-based fisheries management (EBFM), essentially reversing the order of traditional management priorities to focus on the ecosystem rather than the target species (Pikitch et al. 2004, Frid et al. 2005). Link (2002) suggests that EBFM is not specifically managing an ecosystem itself, but rather fisheries management within an ecosystem context. This includes consideration of whole ecosystems into fisheries management plans, rather than just a single species of interest.

Brodziak and Link (2002) propose a three-step approach to EBFM: goals, metrics, and management. Goals are an important part of maintaining direction in management, but they need to be defined in terms of measurable ecosystem aspects. The overall goal of EBFM is to sustain healthy marine ecosystems and thus the fisheries they support (Pikitch et al. 2004). Metrics, or reference points, are used as the intermediary between generalized goals and specific management actions. They are the actual observable or measurable aspects of an ecosystem that indicate the status of ecosystem attributes. Goals are defined through metrics and management decisions seek to achieve those goals. Identifying

important habitat characteristics that related to species distribution, as well as the temporal and spatial scales of such relationships, are fundamental metrics upon which effective EBFM relies (Hinz et al. 2003).

Relationships between benthic habitat characteristics and fish assemblages, diversity, and abundance have been well documented, though the specific mechanisms behind these relationships are highly dependent on the system in question (Almany 2004a, Gratwicke and Speight 2005a, 2005b). Habitat 'complexity' is cited very frequently as an important determinant of abundance and diversity (e.g. Risk 1972, Luckhurst and Luckhurst 1978, Gorman and Karr 1978, Roberts and Ormond 1987, Gorham and Alevizon 1989, McClanahan 1994, Caley and St John 1996, Beukers and Jones 1997, Ferreira et al. 2001, Charbonnel 2002, Almany 2004a, 2004b, Gratwicke and Speight 2005a, 2005b). However, 'complexity' has been assessed through a wide variety of methods, often dependent on the type of habitat being examined. Gratwicke and Speight (2005b) provide a well-defined list of six recognized components of complexity gleaned from the literature: topographic complexity or rugosity, substrate diversity, variety of refuge hole sizes, vertical relief, percentage live cover, and percentage hard substrate.

The benthic habitats associated with the northwest Gulf banks were classified by Rezak et al. (1985) into seven characteristic zones, nested within four general classifications based on the degree of reef building and primary productivity: 1) major reef-building activity and primary production, 2) minor reef-building, 3) transitional zones with minor to negligible reef-building, and 4) no reef building. More recently, Flower Garden Banks National Marine Sanctuary (FGBNMS) scientists have modified and reorganized the zonation classification of Rezak et al. (1985) into a similar, but more generalized, habitat

classification scheme based solely on five broad biological zones: 1) coral reef, 2) coral community, 3) coralline algae, 4) deep coral, and 5) soft bottom (Schmahl et al. 2008). While these broad zones have been used to generally delineate between fish assemblages at the banks, little quantitative information exists about either the specific habitat characteristics or the complexity factors that are associated with different zones, or which of these characteristics are driving the differences between fish assemblages.

Understanding what specific habitat characteristics are most strongly associated with the delineation of reef fish assemblages is important to understanding how this hard-bottom habit is utilized by reef fish assemblages at a localized scale. This is especially important in the northwest Gulf where these natural, hard bottom, high relief banks support large numbers of reef-associated fish, many of which are commercially and recreationally important, including species of snapper [red (*Lutjanus campechanus*), vermillion (*Rhomboplites aurorubens*)], grouper [yellowedge (*Hyporthodus flavolimbatus*), Warsaw (*Epinephelus nigritus*), gag (*Mycteroperca microlepis*), scamp (*Mycteroperca phenax*), yellowfin (*Mycteroperca venenosa*)], pelagics [wahoo (*Acanthocybium solandri*), king mackerel (*Scomberomorus cavalla*), greater amberjack (*Seriola dumerili*)], sharks [silky (*Carcharhinus falciformis*), sandbar (*Carcharhinus plumbeus*), great hammerhead (*Sphyrna mokarran*), Atlantic sharpnose (*Rhizoprionodon terraenovae*)], and other reef fish [gray triggerfish (*Balistes capriscus*)]. However, the fine-scale information about how individual banks are utilized that is needed to assess the fisheries resources present is lacking (Schmahl et al. 2008).

The large-scale shelf-edge bank survey conducted by Gledhill (2001) found that depth, bank size, and the distance of a site from the Caribbean Sea were the most important

factors influencing fish assemblage structure at a regional scale (100-1000 km). Wetmore and Rooker (2011) reported that coral diversity influenced fish assemblage structure, showing significant assemblage differences between high coral diversity (East and West Flower Garden) and low coral diversity (Sonnier and Stetson) banks. At small scales (1m), surface rugosity and degree of fouling on a production platform at the perimeter of East Flower Garden Bank have been correlated with the abundance and richness of reef fishes (Rooker et al. 1997). Abundance and richness of invertebrate assemblages, including many species used to define habitat zonation at the shelf-edge banks, on smaller topographic features in the northeast Gulf were shown to increase with the amount of exposed hard bottom, vertical relief, substrate rugosity, and the number of habitat types available within a given feature (Gittings et al. 1992).

The goals of this chapter are to correlate the current FGBNMS habitat zone scheme with specific habitat characteristics and environmental variables, and to determine the influence of those characteristics or variables on reef fish assemblages. Baited remote underwater video surveys (BRUVS) are well suited to assess the reef fish communities across a variety of habitats, as they provide a standardized, non-extractive method of comparing observations among a variety of sampling depths and conditions, minimize gear avoidance and selectivity, and provide a permanent record of observations (Cappo et al. 2006). Additionally, BRUVS provide a stable, consistent platform for both observing and characterizing the habitat within which surveys are conducted and have been used extensively for defining the habitat characteristics associates with fish surveys (Gledhill 2001, Gledhill and Ingram 2002, Somerton and Gledhill 2005, Wells 2007, Wells et al. 2008a, 2008b, Brooks et al. 2011, Misa et al. 2013).

METHODS

I examined the fish assemblages and habitat characteristics associated with three shelf-edge banks and one artificial reef in the northwestern Gulf. The three banks (Bright, McGrail, and Jakkula) are located on the Louisiana-Texas shelf edge, while the artificial reef is closer to shore on the continental shelf in the East Cameron Artificial Reef Planning Area (Figure 2.1).

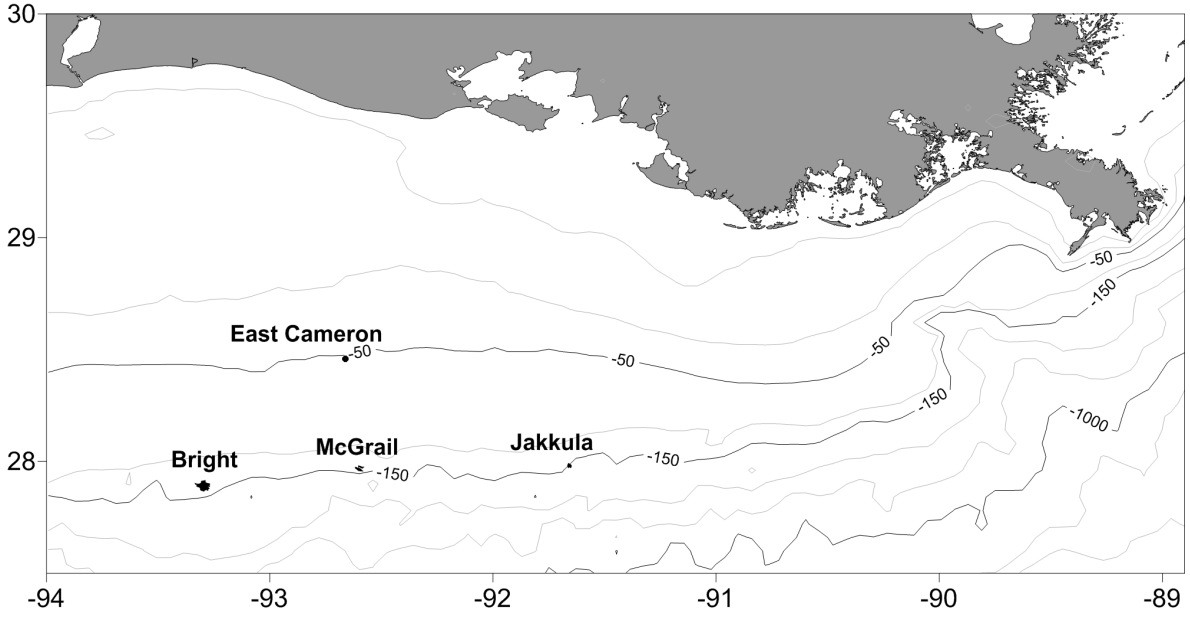

Figure 2.1: Sampling locations for video survey collection at one artificial reef (East Cameron) and three shelf-edge banks (Bright, McGrail, and Jakkula) in the northwestern Gulf of Mexico.

STUDY AREA

The Louisiana-Texas shelf-edge banks are a result of diapiric salt intrusions uplifting bedrock that is subsequently capped by carbonate reef structure (Rezak and Bright 1983, Rezak et al. 1985, 1990, Dennis and Bright 1988). The banks used in this study rise from depths of 140-160 m, crest at depths of 30-50 m below the surface, and range in size from 4 to 20 km^2. The three sites selected (Bright, McGrail, and Jakkula) were chosen to effectively

sample throughout the East-West Texas-Louisiana shelf-edge bank track. The term 'reef' is often used to describe these underwater structures as well, in the sense that they represent underwater structure, though many do possess areas of biological reef building as well. This biotic reef structure has been categorized into two complementary zonation schemes, one based on the degree of reef building and primary productivity (Rezak et al. 1985, 1990), and the other on five broad biological zones, within which there are multiple specific habitat types (Schmahl et al. 2008; Table 2.1). My video surveys captured three of these broad biological habitat zones: coral community, coralline algal reef, and deep coral.

Table 2.1: Summary of revised biological zones of NWGOM banks proposed by Schmahl et al. (2008).

Zone	Depth (m)	Biology	Previous classification per Rezak et al. (1985)
Coral Reef	16-52	*Montastraea* *Madracis* *Stephanocoenia* Coral sand	*Diploria-Montastraea-Porites* *Madracis* and Leafy Algae *Stephanocoenia -Millepora*
Coral Community	16-52	*Millepora*-sponge Low density coral Leafy algae Sponge	*Millepora*-Sponge
Coralline Algal Reef	45-98	Algal nodules Coralline algal reef Leafy algae	Algal-Sponge "Partly drowned reefs"
Deep Coral	50-200+	Antipatharian Octocoral Crinoid	Antipatharian transitional Nepheloid "Drowned reefs"
Soft Bottom	16-200+	Stony coral Sand Quartz Molluscan hash	Not defined as "hard bottom" so excluded from prior evaluations

The artificial reef site I examined consisted of a mid-shelf toppled platform in the East Cameron Artificial Reef Planning Area, hereafter the East Cameron (EC) site. This artificial reef is located within an area of high acoustic backscatter and increased bathymetric relief relative to surrounding areas, discovered during a side-scan survey of the Louisiana Artificial Reef Program (LARP) planning areas (Cowan et al. 2007). The extent of natural hard-bottom in the EC planning area is the largest observed among the Louisiana artificial reef planning areas (7,855 ha total). The local bathymetry is characterized by a gradual slope from 45-55 m, with the area of interest forming a shelf in the center approximately 4 m higher than the surrounding sediments. Though my video surveys showed no epifauna, bathymetric features associated with this site are assumed to be composed of slabs of lithified bottom sediment (Cowan et al. 2007).

SURVEY METHOD

The relative abundances of reef fish species at the study sites were estimated from BRUVS conducted between December 2012 and October 2013. Surveys were carried out twice quarterly, as weather permitted. Survey sites were selected to encompass as many habitat zones on each bank as possible during the study period, based on documented depth zones for each bank (Rezak et al. 1985, 1990, Schmahl et al. 2008). Up to two one-hour deployments, hereafter referred to as surveys, were conducted at a site during a single sampling trip, though never within the same habitat zone.

The BRUVS used high-definition stereo Canon VIXIA HF G10 camera arrays for all observations. The depth and scope of surveys precluded traditional SCUBA diver census techniques, while the camera arrays could be rapidly deployed to and retrieved from a wide variety of depths and sea conditions. The six-camera array consisted of a circular,

baited cage, within which two stereo camera pairs, and two single cameras were mounted orthogonally to one another at a height of 0.5 m affording a near 360° view (Figure 2.2), similar in arrangement to those used by the SEAMAP offshore reef survey (Gledhill 2001, Somerton and Gledhill 2005). Stereo cameras were separated by 70cm from their respective stereo partner to suit both the size of individuals observed and the average range of measurement, while being angled inward at 7 degrees, to maximize the overlapping area available for measurement. Prior to deployment, all stereo pairs were calibrated with a calibration cube (1m x 1m x 0.53m). Captured imagery was processed with the computer program Cal (SeaGIS Pty. Ltd.). Each video survey included a capture of a measurement bar of known length to check that appropriate calibration was obtained. Cameras were deployed for one hour of bottom time.

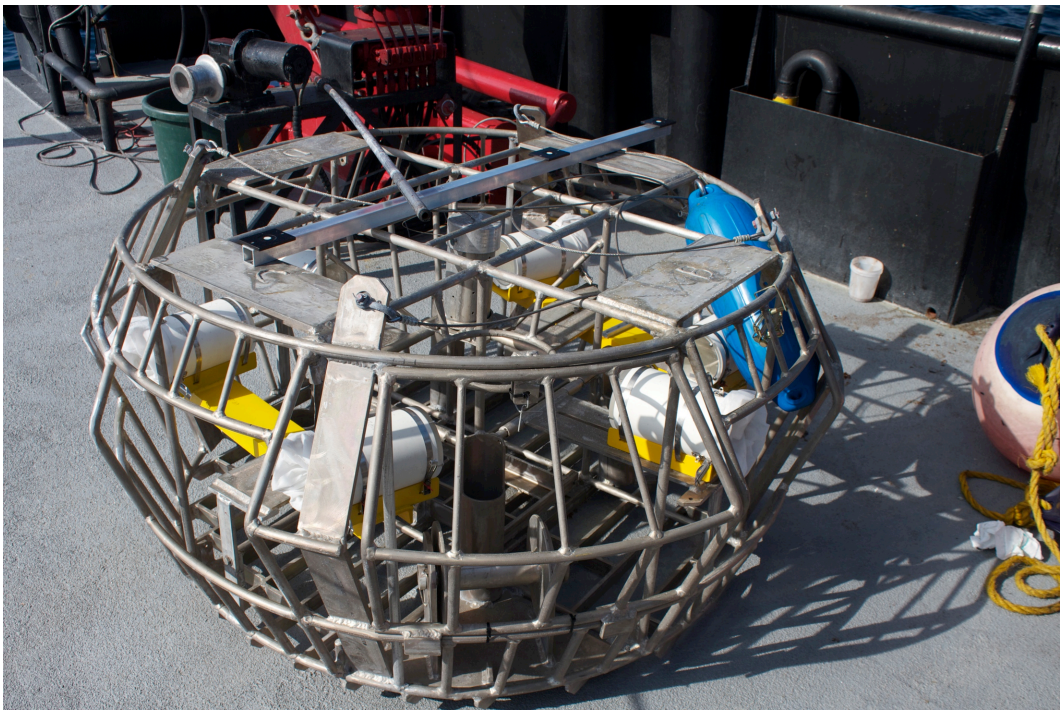

Figure 2.2. Camera array used to conduct video surveys. Composed of six cameras, two stereo pairs and two individual cameras positioned orthogonally to cover all directions around the cage.

Videos were reviewed in EventMeasure software (SeaGIS Pty. Ltd.) to identify and enumerate all species for the duration of the recording. Identifications were made to the lowest taxonomic level possible and enumerations were calculated in the form of MaxN (Priede et al. 1994). MaxN is the maximum number of individuals of a given species seen in a single video frame, a conservative estimator of the number of fish seen on a deployment (Priede et al. 1994). MaxN is used for stationary systems, rather than a running total typically used with transect-type surveys, because it is possible that individual fish might be counted repeatedly when leaving and then re-entering the field of view during video analysis, especially due to the centralized bait location relative to the camera layout (Kallayil et al. 2003). The use of two stereo-pairs in each camera array allowed for length measurements of many of the fish observed during the surveys. Adhering to the conservative MaxN principle, only the MaxN fish observed were measured to avoid measuring the same fish twice. Video surveys were used to determine the relative abundance and composition of reef fish species associated with the three shelf-edge banks and one artificial reef.

HABITAT CHARACTERIZATION

In addition to characterizing reef fish assemblages, the environments in which fish were observed were also characterized. For each camera deployment, a variety of environmental parameters were measured. Depth and position were obtained with a 123kHz Biosonics split-beam transducer and paired GPS. Water parameters including temperature, salinity, and dissolved oxygen (DO) were collected with a Seabird SBE 25 Sealogger CTD. However, due to a faulty DO sensor during some surveys, dissolved oxygen is not included in the analysis. Maximum relief, defined as the height of any geological or

biological structure in the field of view, was recorded for each camera direction. Substrate types were recorded as percent cover estimates within the field of view, similar to the procedure used by Gledhill (2001). Substrate types identified included rock, sand, mud, and rubble. The percent of live cover was recorded separately, as it was growing upon one of the previous substrate types, which were still identifiable. No physical sediment samples were taken, so substrate definition was solely based on visual examination and sediment behavior when the array landed on the bottom.

DATA ANALYSIS

The importance of both environmental variables and habitat characteristics in defining habitat zones and influencing assemblage structure was investigated with a permutational multivariate analysis of variance (PERMANOVA), principal components analysis (PCA), and distance-based linear models (DISTLM) in Plymouth Routines In Multivariate Ecological Research, Version Six (PRIMER 6). This progression of routines was chosen as a natural progression of specificity; a global PERMANOVA to test whether environmental variables and habitat characteristics differed significantly between habitat zones or sites, a PCA to determine which of these environmental or habitat variables were driving potential differences, and finally DISTLM to model how environmental variables and habitat characteristics related to the fish assemblages. Analytical methods involving the fish assemblage were restricted to observations made to the species level.

The individual camera data was combined from all four camera directions for each deployment, such that the highest MaxN observed for a given species on any camera was used as the MaxN for that survey. Individual camera information was combined at the survey level in an effort to preserve independence of observations and avoid pseudo-

replication (Hurlbert 1984). The species abundance data was square-root transformed, a moderate-strength pre-treatment procedure intended to down-weight the importance of highly abundant (and usually highly variable) species, so that future calculations were not overly influenced by only the most abundant species.

The environmental data was normalized to account for the different units of measurement of the various factors examined. A draftsman plot and correlation matrix were created to check for collinearity between environmental variables, an indication that two variables were providing redundant information and therefore one could be excluded from the analysis.

A PERMANOVA routine was performed to assess differences in the multivariate patterns of environmental variables and habitat characteristics among the habitat zones, testing the null hypothesis (H_0) that there were no differences in habitat characteristics between habitat zones or sites. Effects of habitat zone, study site, and the interaction between habitat and site were tested. The non-parametric PERMANOVA routine used is a permutational multivariate analog to Fisher's *F*-ratio and is calculated from a dissimilarity matrix, a matrix of pairwise dissimilarities between surveys (Anderson 2001, McArdle and Anderson 2001). For environmental data the dissimilarity between surveys, also known as distance, was calculated as the conventional Euclidian distance (Clarke and Gorley 2006). Further specifics about the PERMANOVA procedure can be found in Appendix B.

Given that this global test was significant ($\alpha=0.05$), pairwise tests were computed to determine which levels of habitat zone were statistically different ($\alpha=0.05$) from one another. The pairwise test statistic was calculated by taking each pair of levels, treating them like contrasts, and calculating a pseudo-*t* statistic as the square root of the pseudo-*F*.

P-values for all pairwise tests were obtained by comparing the observed pseudo-*t* against a distribution of simulated pseudo-*t* values generated by permuting labels. In the event that too few unique permutations were available to produce a meaningful test (<<999), constructed asymptotic permutation distributions were generated with Monte Carlo sampling and used to generate a more meaningful test statistic (Anderson and Robinson 2003, Anderson 2005).

A correlation-based PCA was conducted based on the normalized matrix of environmental variables and habitat characteristics both to ordinate surveys from an environmental perspective and to determine which characteristics best described habitat zonation patterns. Depth was excluded from the PCA routine as the draftsman plot and correlation matrix indicated potential redundancy with a number of the other variables. Five principle components (PC) were extracted in an effort to provide ample eigenvalues from which the meaningful components may be gleaned via the eigenvalue-one criterion (Kaiser 1960). The eigenvectors, or loadings, of the original variables were then examined for each PC to determine which variables were important in defining a particular component.

A multivariate multiple regression analysis, specifically the DISTLM procedure in PRIMER, was conducted to test relationships between the fish assemblages observed and the environmental and habitat variables measured. The procedure modeled the relationship between the normalized matrix of environmental and habitat variables versus the Bray-Curtis resemblance matrix of square-root transformed species abundance with a distance-based redundancy analysis approach (dbRDA; Legendre and Anderson 1999, McArdle and Anderson 2001). All possible combinations of explanatory variables were

modeled and the 20 models with the lowest corrected Akaike information criterion (AICc; Hurvich and Tsai 1989) and Bayesian information criterion (BIC; Schwarz 1978) scores were selected. AICc was chosen over AIC to avoid the potential overfitting of AIC due to the relatively small number of samples relative to predictors (Burnham and Anderson 2002, 2004). Models selected by both criteria were plotted in AICc/BIC space, from which the model that achieved the best balance between parsimony and fit was identified.

Two additional DISTLM procedures were run with fish datasets combined at the genus and family levels to determine whether the most important environmental or habitat characteristics differed when modeling coarser taxonomic levels. Species were pooled, by survey, at the genus and family levels, square root transformed, and entered into the same DISTLM routine as applied to the species-level data. Models were plotted in AICc/BIC space, as with the full species dataset, to determine the 'best' final model.

RESULTS

The permutational MANOVA (PERMANOVA) procedure indicated that the suite of environmental and habitat characteristic variables differed significantly between habitat zones (F_{pseudo}=6.8, p=0.001) (Table 2.2). Neither the site effect (F_{pseudo} =1.4, p=0.17) nor the site-by-habitat interaction were significant (F_{pseudo} =1.1, p=0.37). Post-hoc pairwise tests between habitat types indicated that the only habitat zones that did not differ significantly were the artificial zone versus coral community and deep coral zones (Table 2.3). Post-hoc tests were based on Monte Carlo p-values given the limited number of unique permutations available.

Table 2.2. Results of the global two-factor PERMANOVA performed on normalized environmental data. Asterisk (*) indicates a significant factor (α=0.05). Perms: number of permutations against which each effect was tested.

Effect	Df	Perms	Pseudo-F	p-value
Site	2	999	1.41	0.17
Habitat	2	999	6.79	0.001*
Site x Habitat	3	999	1.11	0.372

Table 2.3. Pairwise examination of the significant habitat effect from the global PERMANOVA performed on normalized environmental data. Asterisk (*) indicates a significant difference (α=0.05). CC: Coral Community, CAR: Coralline Algal Reef, DC: Deep Coral, Art: Artificial. P (perm): p-value obtained from the available permutations. P (Monte Carlo): p-value obtained from Mote Carlo estimation.

Pair	t	Perms	P (Perm)	P (Monte Carlo)
CC - CAR	2.76	60	0.09	0.002*
CC – DC	2.81	30	0.11	0.007*
CAR – DC	2.24	338	0.06	0.011*
Art – CC	3.04	3	0.001*	0.079
Art - CAR	2.97	24	0.11	0.011*
Art - DC	1.80	12	0.09	0.117

A draftsman plot and correlation matrix (Table 2.4) of all environmental and habitat characteristic variables were generated to look for highly skewed distributions and strong correlations between variables. Depth showed two moderate strength correlations relative to percent sand cover (corr=0.82) and temperature (corr=-0.65). After the removal of depth, the draftsman plot and correlation matrix (Table 2.5) showed no correlations

Table 2.4. Pairwise correlations between all environmental and habitat variables considered.

	Depth	Temp	Salinity	High relief	%rock	%sand	%mud	%rubble	%live cover
Depth									
Temp	-0.65								
Salinity	0.23	-0.11							
High relief	0.11	0.22	0.16						
%rock	-0.08	0.25	0.09	0.38					
%sand	0.82	-0.43	0.26	0.35	0.07				
%mud	-0.29	-0.03	-0.20	-0.64	-0.36	-0.40			
%rubble	-0.18	0.14	-0.02	0.18	-0.36	-0.29	-0.54		
%live cover	-0.35	0.40	0.08	0.57	0.46	-0.19	-0.60	0.43	

greater than 0.64. The rest of the analyses were run excluding the depth variable, though it is recognized that depth is likely an underlying factor behind the variation in many of the other variables used.

Table 2.5. Pairwise correlations between environmental and habitat variables, excluding depth.

	Temp	Salinity	High relief	%rock	%sand	%mud	%rubble	%live cover
Temp								
Salinity	-0.11							
High relief	0.22	0.16						
%rock	0.25	0.09	0.38					
%sand	-0.43	0.26	0.35	0.07				
%mud	-0.03	-0.20	-0.64	-0.36	-0.40			
%rubble	0.14	-0.02	0.18	-0.36	-0.29	-0.54		
%live cover	0.40	0.08	0.57	0.46	-0.19	-0.60	0.43	

Qualitatively, habitat zones grouped very consistently and discretely in the PCA ordination plot (Figure 2.3). Eigenvalues indicated that the first three components were important (Table 2.6), according to the eigenvalue-one criterion (Kaiser 1960), an indication that the component explained more variance in the original data than a single variable alone. The first three PCs cumulatively accounted for 75.8% of the total variation, a good representation of the original data (Clarke and Gorley 2006). Eigenvectors indicated the contribution of original variables to each component (Table 2.7), importance being defined at or above 0.4 (O'Rourke and Hatcher 2013). The first component (PC1) differentiated between artificial and natural habitat types and was most strongly associated with three variables, highest relief (-0.49), percent mud (0.51), and percent live cover (-0.51). The second (PC2) and third (PC3) components explained the differences between natural habitat zones. PC2 explained much of the difference between the deep

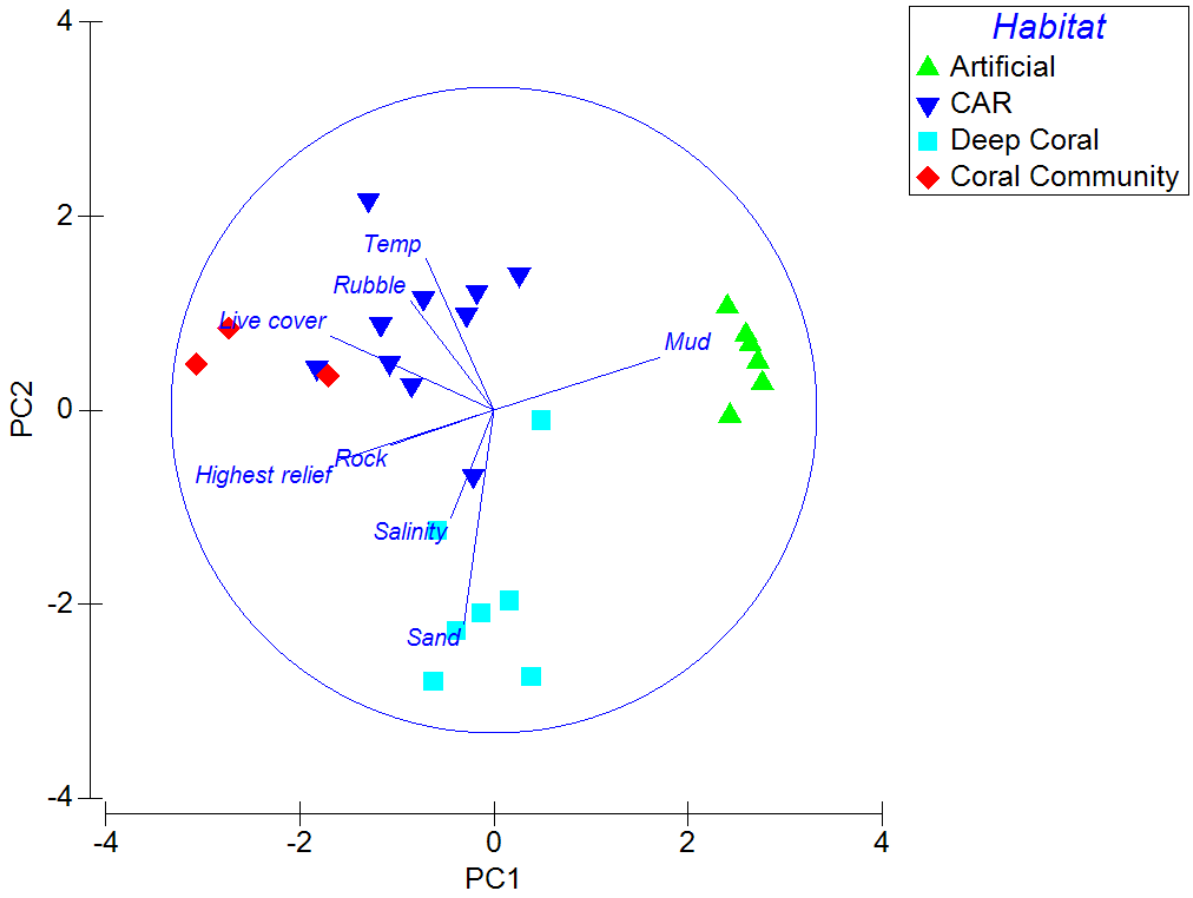

Figure 2.3. Two-dimensional PCA of individual survey events based on environmental and habitat characteristics. Colored symbols represent the habitat zone within which a survey was conducted. CAR: Coralline Algal Reef.

Table 2.6. Eigenvalues of the first five principle components generated by the PCA of environmental and habitat variables, excluding depth. Also included are the percent of total variation accounted for by each components, as well as the cumulative variation. Asterisk (*) indicates a meaningful component (Eigenvalue>1).

PC	Eigenvalues	%Variation	Cum.%Variation
1	2.82*	35.3	35.3
2	1.84*	23	58.3
3	1.4*	17.5	75.8
4	0.85	10.7	86.5
5	0.56	7.1	93.5

coral habitat and the two other natural zones and was most strongly associated with two variables, temperature (0.47) and percent sand (-0.66). Finally, to differentiate between

the coral community and coralline algal reef habitats, percent rock (-0.62) and percent rubble (0.64) were the most important factors in defining the PC3. Salinity is the only original variable that was not an 'important' factor in the first three PCs.

Table 2.7. Eigenvectors indicating the contribution of the original environmental and habitat variables to the first three principle components. Asterisk (*) indicates an important variable (Eigenvector>0.4).

Variable	PC1	PC2	PC3
Temp	-0.21	0.47*	-0.34
Salinity	-0.13	-0.33	0.07
Highest relief	-0.49*	-0.16	-0.04
%Rock	-0.32	-0.11	-0.62*
%Sand	-0.09	-0.66*	0.08
%Mud	0.51*	0.16	-0.26
%Rubble	-0.26	0.34	0.64*
%Live cover	-0.51*	0.23	-0.06

SPECIES-LEVEL ANALYSIS

The DISTLM showed that together, all eight environmental and habitat variables explained 49% of the total variation in the multivariate species assemblage data. Marginal tests of the environmental and habitat variables indicated that all, except salinity (F_{pseudo} =1.12, p=0.28), individually explained a significant amount of the total variation (Table 2.8). Two variables stood out in the marginal tests, percent mud and live cover, explaining roughly twice the total variation than others at 16%.

Table 2.8. Marginal tests of environmental and habitat variables, based on species-level data. Prop: proportion of the total variance accounted for by a variable alone. Asterisk (*) indicates significant factor (α=0.05).

Variable	Pseudo-F	P-value	Prop.
Temp	2.2533	0.009*	0.09
Salinity	1.1227	0.282	0.04
Highest relief	2.4588	0.004*	0.09
Rock	2.6141	0.004*	0.10
%Sand	2.2644	0.015*	0.09
%Mud	4.6728	0.001*	0.16
%Rubble	2.1783	0.022*	0.08
%Live cover	4.6442	0.001*	0.16

Seven models were mutually selected in the top 10 'best' models based on both AICc and BIC selection methods and subsequently plotted in AICc-BIC space to determine the overall 'best' model (Figure 2.4). Low values of AICc and BIC represent high explanatory value with few variables, thus the ideal model was the mutually selected set of variables nearest the origin of AICc-BIC space. Model selection using AICc and BIC criteria from all possible combinations of explanatory variables led to the selection of a two-variable model including percent mud and live cover (R^2=0.27).

High percent cover of mud substrate associated strongly with assemblages observed at artificial reef habitat, while little or no mud substrate was associated with natural habitat assemblages (Figure 2.5b). Live cover displayed a gradient from low cover associated with assemblages in the deep coral habitat zones to high cover at the coral community zone (Figure 2.5c).

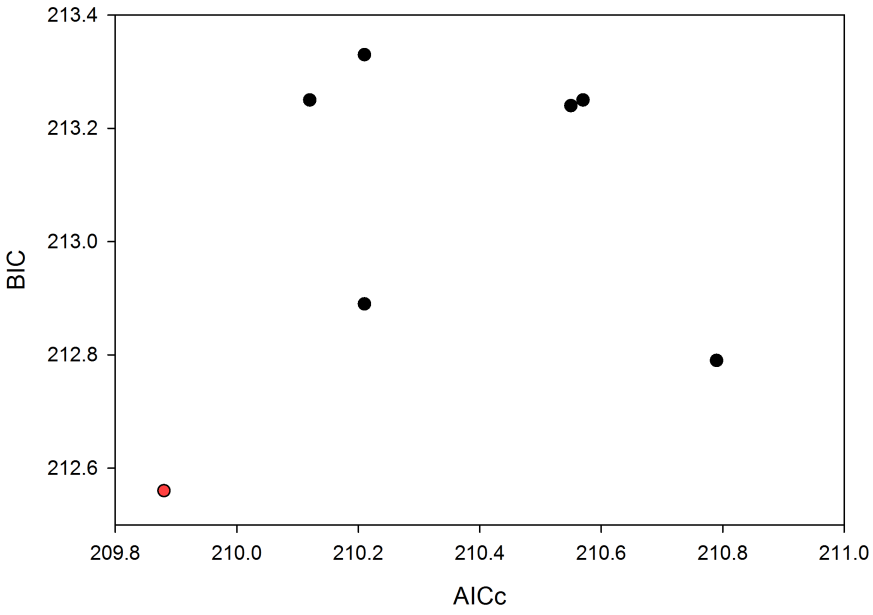

Figure 2.4. Scatterplot of mutually selected 'best' species-level models, based on AICc and BIC criteria. The red point represents the lowest mutual AICc and BIC scores, the 'best' model that includes percent mud and live cover.

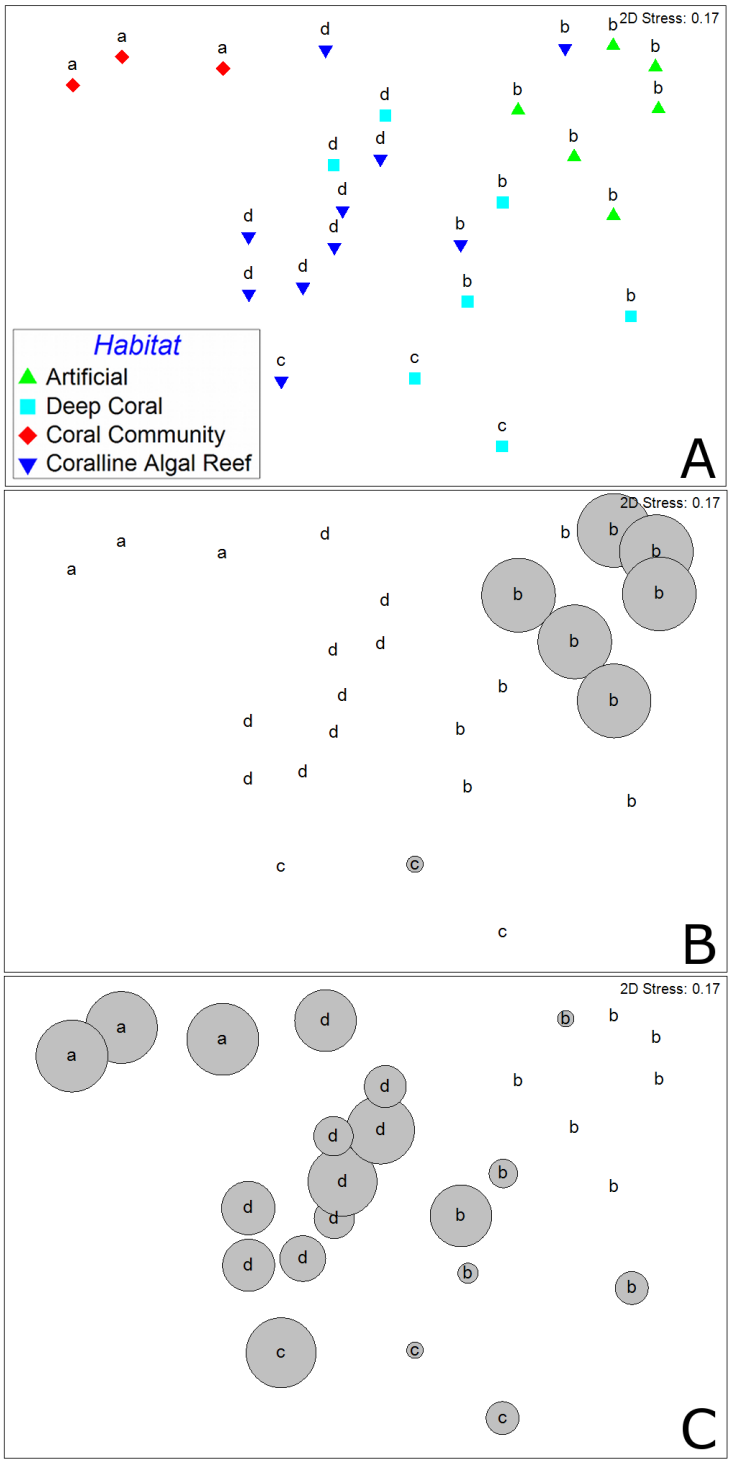

Figure 2.5. Non-metric multidimensional scaling (MDS) plots of surveys based on species-level assemblages (adapted from Chapter 1). Each point represents an individual survey, ordinated such that closer points have more similar fish assemblages. Letters indicate significantly different assemblages, based on cluster analysis. A) Symbols and shapes of points indicate the habitat zone within which each plotted survey was conducted. Bubbles represent the percent of mud substrate (B) and live cover (C). Larger bubbles represent a larger percentage.

GENUS-LEVEL ANALYSIS

When assemblage data was combined at the genus-level, all eight environmental and habitat variables together explained 51% of the total variation in the multivariate assemblage data. Marginal tests of individual variables showed that salinity was the only variable that did not explain a significant amount of the total variation (F_{pseudo} =1.06, p=0.37) when modeled alone (Table 2.9). Percent mud explained the largest proportion of total variation alone (0.19), followed by percent live cover (0.18) and percent rock (0.12).

Table 2.9. Marginal tests of environmental and habitat variables, based on genus-level data. Prop: proportion of the total variance accounted for by a variable alone. Asterisk (*) indicates significant factor (α=0.05).

Variable	Pseudo-F	P	Prop.
Temp	2.70	0.004*	0.10
Salinity	1.06	0.372	0.04
Highest relief	3.14	0.002*	0.12
Rock	3.23	0.001*	0.12
%Sand	2.13	0.018*	0.08
%Mud	5.51	0.001*	0.18
%Rubble	2.08	0.035*	0.08
%Live cover	5.20	0.001*	0.17

Six models were mutually selected in the top 10 best models based on both AICc and BIC selection methods, and subsequently plotted in AICc-BIC space to determine the 'best' model (Figure 2.6). The 'best' mutually AICc-BIC selected model was the same two-variable model as indicated by the species level data, including percent mud and live cover (R^2=0.29).

High percent cover of mud substrate associated strongly with assemblages observed at artificial reef habitat, while little or no mud substrate was associated with natural

habitat assemblages (Figure 2.7b). Live cover displayed a gradient from low cover associated with assemblages in the deep coral habitat zone to high cover at the coral community zone (Figure 2.7c).

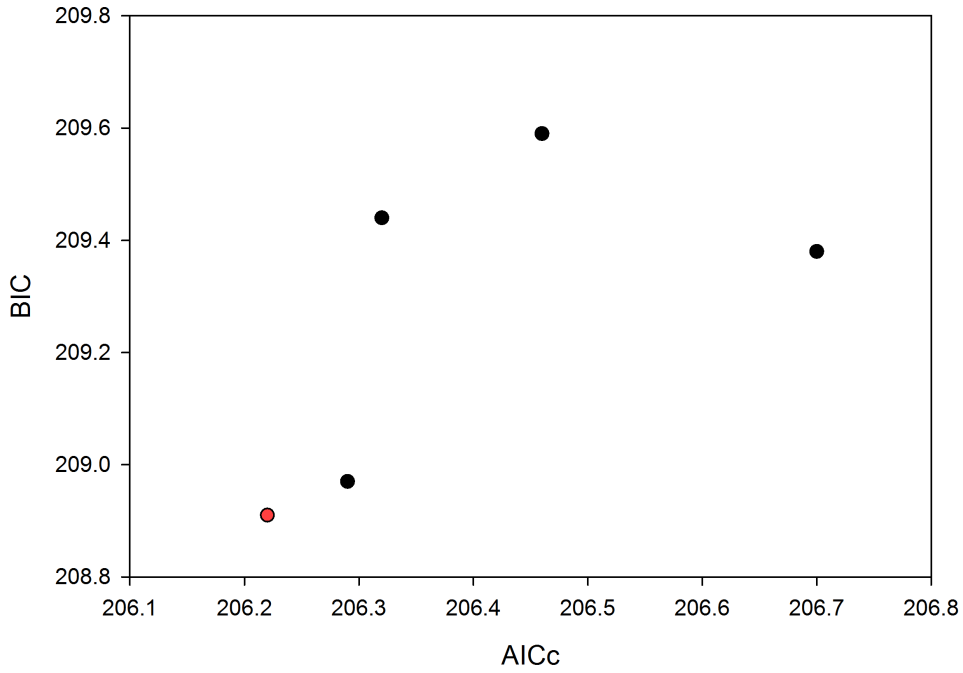

Figure 2.6. Scatterplot of mutually selected "best" genus-level models, based on AICc and BIC criteria. The red point represents the lowest mutual AICc and BIC scores, the "best" model that includes percent mud and live cover.

FAMILY-LEVEL ANALYSES

When assemblage data was combined at the family-level, all nine environmental and habitat variables explained 57% of the total variation in the multivariate assemblage data. Marginal tests of individual variables showed that salinity was the only variable that did not explain a significant amount of the total variation (F_{pseudo} =1.06, p=0.412) when modeled alone (Table 2.10). Percent mud explained the largest proportion of total variation alone (0.22), followed by percent live cover (0.20) and percent rock (0.17). Eight models were mutually selected in the top 10 best models based on both AICc and BIC selection methods, and subsequently plotted in AICc-BIC space to determine the 'best'

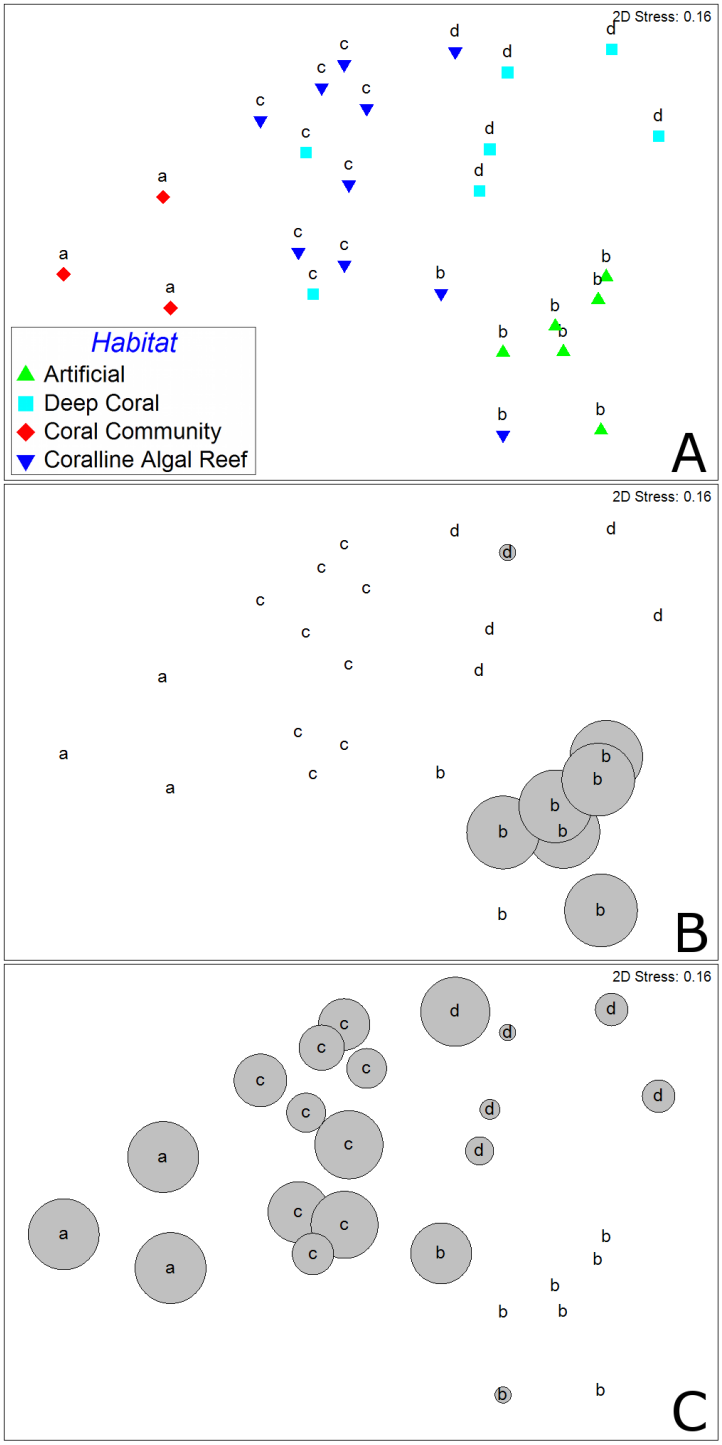

Figure 2.7. Non-metric multidimensional scaling (MDS) plots of surveys based on genus-level assemblages (adapted from Chapter 1). Each point represents an individual survey, ordinated such that closer points have more similar fish assemblages. Letters indicate significantly different assemblages, based on cluster analysis. A) Symbols and shapes of points indicate the habitat zone within which each plotted survey was conducted. Bubbles represent the percent of mud substrate (B) and live cover (C). Larger bubbles represent a larger percentage.

Table 2.10. Marginal tests of environmental and habitat variables, based on family-level data. Prop: proportion of the total variance accounted for by a variable alone. Asterisk (*) indicates significant factor (α=0.05).

Variable	Pseudo-F	P	Prop.
Temp	3.25	0.005*	0.12
Salinity	1.06	0.368	0.04
Highest relief	3.00	0.010*	0.11
Rock	4.75	0.001*	0.17
%Sand	2.72	0.015*	0.10
%Mud	6.91	0.001*	0.22
%Rubble	2.21	0.033*	0.08
%Live cover	6.05	0.001*	0.20

model (Figure 2.8). Contrary to the prior analyses, there was a five-way tie for 'best' model based on mutual AICc-BIC criteria. These were a four-variable model including percent rock, sand, mud and rubble and the four possible three-variable combinations of these four substrate variables. All five of these models achieved an R^2 value of 0.43.

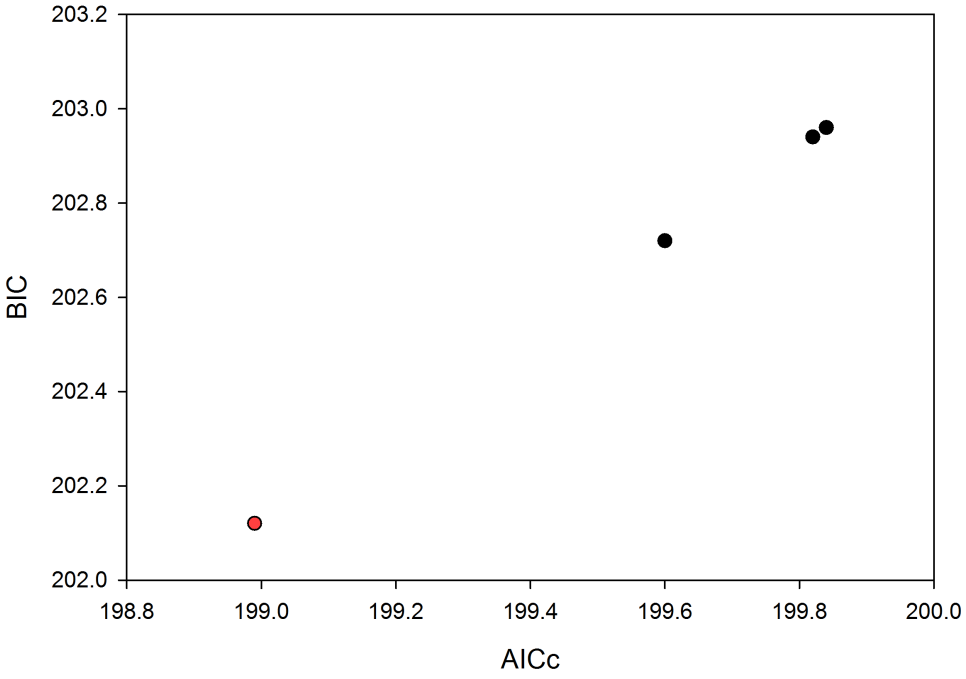

Figure 2.8. Scatterplot of mutually selected 'best' family-level models, based on AICc and BIC criteria. The red point represents the lowest mutual AICc and BIC scores, occupied by five separate variable combinations.

A high percentage of mud substrate coverage was associated with assemblages observed at the artificial reef site, and characterized one of the two significantly different family-level fish assemblages (Figure 2.9b). Percent coverage of sand, rubble, and rock varied among surveys conducted at the natural sites. High coverage of sandy substrate was most strongly associated with assemblages observed at the deep coral zone (Figure 2.9c). Larger grained rubble substrate was observed at every habitat zone, but the highest cover tended to occur in the coralline algal reef zone (Figure 2.9d). Finally, the highest cover of rock substrate was associated with assemblages from the shallow coral community zone and decreased with increasing habitat zone depth.

DISCUSSION

This study examined the relationship between fundamental habitat complexity characteristics and previously defined benthic habitat zones found at northwest Gulf shelf-edge banks, as well as their associated reef fish assemblages. Environmental and habitat characteristics differed significantly between habitat zones, but showed consistency within a given zone across multiple banks. Nearly all habitat characteristics were significantly related to the associated species assemblages, but substrate consistency and live cover showed the strongest correlation with reef fish assemblage structure.

Habitat complexity characteristics were observed to be significantly different between habitat zones, as defined by Schmahl et al. (2008). While this habitat zone classification scheme was not defined based on the specific environmental and habitat characteristics examined in this study, it is not surprising that such fundamental characteristics would differ between zones. The initial classification of northwest Gulf

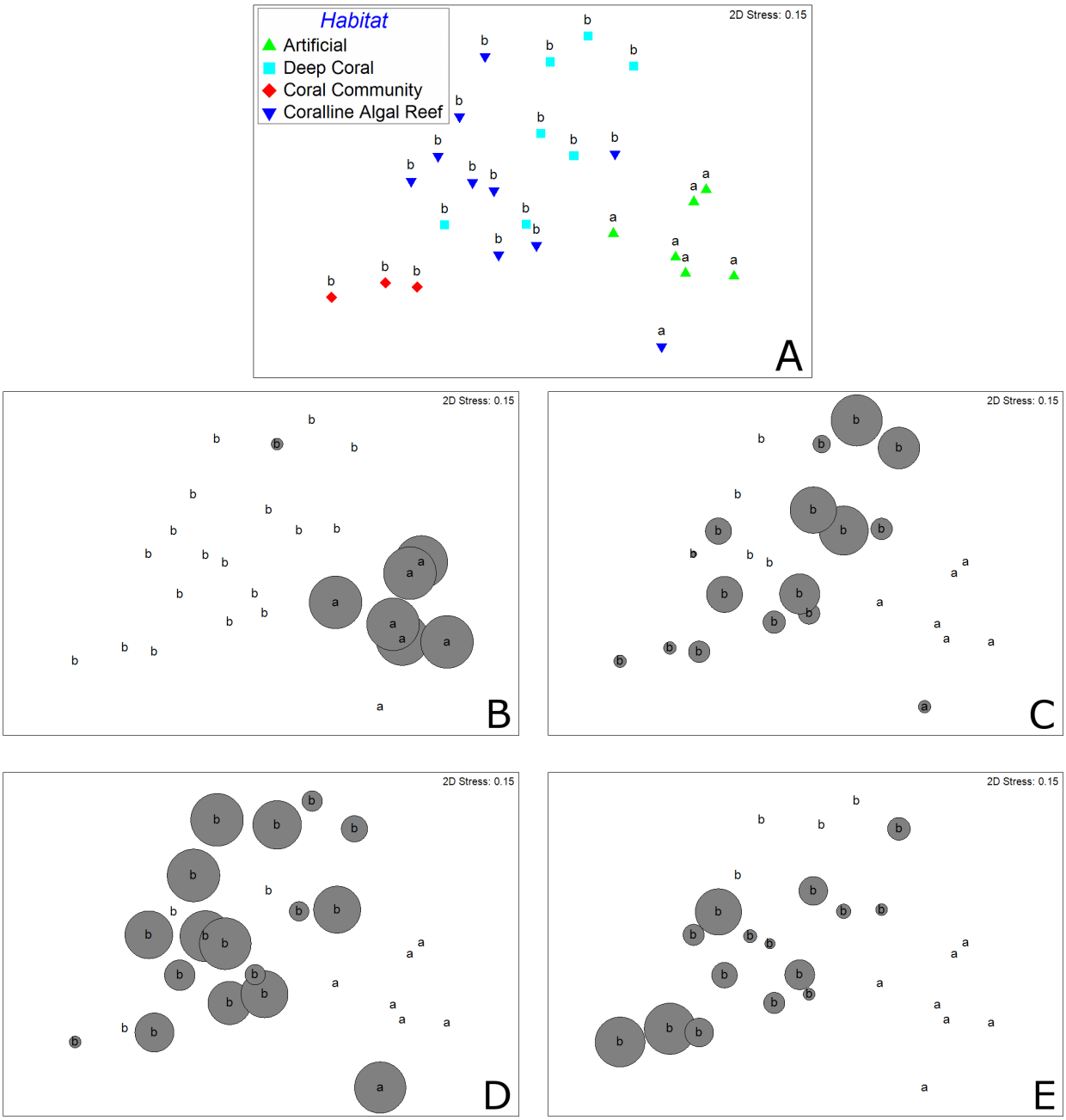

Figure 2.9. Non-metric multidimensional scaling (MDS) plots of surveys based on family-level assemblages (adapted from Chapter 1). Each point represents an individual survey, ordinated such that closer points have more similar fish assemblages. Letters indicate significantly different assemblages, based on cluster analysis. A) Symbols and shapes of points indicate the habitat zone within which each plotted survey was conducted. Bubbles represent the percent of mud (B), sand (C), rubble (D), and rock (E) substrate. Larger bubbles represent a larger percentage.

shelf-edge bank benthic habitat zones by Rezak et al. (1985) was based on the degree of reef-building activity and primary production, but zone descriptions often mentioned dominant epifauna and substrate characteristics. Schmahl et al. (2008) modified the earlier zonation classification to be characterized solely by 'broad biological zones', though descriptions of these modified zones still included descriptions of both dominant epifauna and substrate characteristics. Although habitat complexity characteristics were not the intended classification factors, such factors are inherently linked to the classification characteristics used to define "broad biological zones".

The suite of habitat characteristics used in this study was specifically chosen to represent recognized components of habitat complexity (Gratwicke and Speight 2005b), essentially breaking down the "broad biological zones" of Schmahl et al. (2008) into quantitative characteristics. While a significant habitat zone effect was observed based upon the suite of habitat characteristics, some post-hoc pairwise comparisons did not suggest strong differences between zones, particularly the comparisons between artificial habitat relative to the coral community and deep coral zones. One potential explanation may lie in the limited number of surveys available for comparison. The power of the permutational methodology used to test for these differences is limited by the number of permutations possible (Anderson 2005). Although Monte-Carlo estimates of the true p-value were used to account for the limited unique permutations available, these two comparisons had the lowest number of unique permutations available. Alternatively, it is possible that the suite of habitat complexity characteristics chosen may not represent the broader zonation pattern well. The habitat factors measured in this study were chosen as characteristics of habitat complexity, rather than to differentiate between the specific

habitat zones known to be present at northwest Gulf banks. Additional surveys would allow for more powerful tests of habitat characteristic differences between habitat zones, as well as better descriptions of the spatial distribution of previously classified habitat zones and the basic complexity characteristics targeted in this study.

The consistency of environmental and habitat characteristics across sites observed in this study is likely attributable to the manner in which the broader habitat zonation was initially described. The habitat classification scheme, and subsequent modification, initially generated from surveys at the East and West Flower Garden banks specifically noted the generality of the habitat zones to the northwest Gulf shelf-edge banks (Rezak et al. 1985, Schmahl et al. 2008). Subsequent and supplementary work has both confirmed the consistency of habitat zonation between features and refined habitat descriptions at additional banks, including the depths covered by specific zones and potential environmental controls driving the observed zonation patterns (Bright 1977, McGrail et al. 1982, Boland et al. 1983, Dennis and Bright 1988, Rezak et al. 1990, Pattengill et al. 1997, Schmahl and Hickerson 2006, Weaver et al. 2006, Hickerson et al. 2008, Wetmore and Rooker 2011). The consistency of complexity characteristics across sites in this study supports previous observations of consistent habitat zonation at features throughout the region.

The relationship between organisms and their environment is a fundamental focus of ecological studies (Howe and Westley 1988). One aspect of this environment is habitat structure or complexity, which has been related to distribution, abundance, diversity and richness of reef fishes through a wide variety of potential mechanisms (Gratwicke and Speight 2005b). The results of this study support the idea that complexity, specifically the

fundamental components of habitat complexity, is related to, if not driving, reef fish assemblage organization at northwest Gulf banks. The only measured habitat or environmental characteristic that did not explain a significant proportion of the species variation was salinity, likely because salinity differed very little between individual surveys.

The combination of percent mud substrate and live cover best explained the variation in the species assemblage data, which could indicate that these complexity characteristics are especially important in driving the presence and abundance of species at the shelf-edge banks. The variation these two factors between surveys indicated that together they could be acting as a proxy for habitat zone, which has already been shown to significantly relate to assemblage organization (Chapter 1).

Mud substrate was recorded almost exclusively at artificial habitat, thus is strongly associated with the assemblage differences observed between natural and artificial habitats. The artificial reef is composed of a toppled platform that was placed on the typical low-relief, mud sediments of the northern Gulf continental shelf, resulting in this defining sediment characteristic. However, this study was confined to benthic sampling and therefore was unable to examine the full vertical extent of the artificial reef structure and the associated assemblage, which is known to vary with depth and fouling complexity (Shinn 1974, Sonnier et al. 1976, Gallaway and Lewbel 1982, Rooker et al. 1997, Stanley and Wilson 2000, Wilson et al. 2003). The natural banks are located far enough offshore that they are not directly impacted by the Mississippi and Atchafalaya runoff, limiting the distribution of fine sediments to the bottom boundary layer (Rezak et al. 1990). Coupled with the fact that bottom currents flow around, rather than over the banks (Rezak et al.

1985), habitat zones shallower than the bottom nepheloid layer (approximately 80m) receive negligible amounts of fine, terrestrial sediments such as mud (Rezak et al. 1990).

Following the distinction between natural and artificial habitat zones by mud substrate, live cover was strongly correlated with the three natural habitats, with the lowest coverage at the deep coral zone and increasing through the coralline algal reef to a maximum in the shallow coral community zone. This gradient has previously been attributed to a number of interacting environmental controls such as depth, temperature, salinity, turbidity and sedimentation (Rezak et al. 1990). Light availability, controlled by depth and turbidity, is likely responsible for the species and extent of live benthic cover. Photosynthetic organisms are limited to depths that receive sufficient light for production, while turbidity attenuates light and the associated sedimentation can smother encrusting or sensitive epibenthos such as coral and sponges (Gittings et al. 1992). The increasingly hostile growth conditions with increasing depth may account for the changes in epibenthic communities observed (Rezak et al. 1985, Gittings et al. 1992, Schmahl et al. 2008), and drive the overall decrease in epifauna coverage. The present study did not break down live cover into contributions from particular species or types of organisms, though such an analysis may provide information about whether there is a functional relationship between particular types or species of epifauna and the associated fishes, such as a preferred refuge or food source (Wetmore and Rooker 2011), or if live cover is simply a convenient indicator of the more generalized large biotic zonation pattern.

Previous studies of the relationship between habitat characteristics and associated fish assemblages at northern Gulf banks have worked at a larger scale than this study, focusing on differences between banks, or even between groups of banks. Gledhill (2001)

found that depth, size, and distance of a bank from the Caribbean Sea were the most important factors influencing fish assemblage structure. Additionally, he showed that high substrate complexity was related to high taxonomic richness, while reef size and the proportion of sand-clay substrate were important in determining fish abundance. Wetmore and Rooker (2011) found that fish density, diversity, assemblage, and trophic guild density were all related to the degree of coral diversity at a bank, though surveys were limited to SCUBA-accessible depths. At the Pinnacles reefs in the northeastern Gulf, Weaver et al. (2002) found that species richness was likely related to the diversity of microhabitats, features such as rock outcrops, sand pockets, or complex benthic invertebrate structures. The variety of habitat characteristics examined across surveys, and specific methods of measurement, make direct comparisons of specific habitat characteristics between studies difficult (Gratwicke and Speight 2005b). Despite these difficulties, these studies echo the general importance of benthic structure characteristics and epifauna to reef fish assemblage organization that was observed in the present study, and suggest that such relationships exists across a variety of scales.

Beyond the work specific to northwestern Gulf banks, numerous studies have related the broadly-defined metric of reef complexity to fish assemblages (e.g. Risk 1972, Luckhurst and Luckhurst 1978, McClanahan 1994, Eklöv 1997, Kleypas et al. 2001, Charbonnel 2002, Almany 2004a, 2004b, Gratwicke and Speight 2005a, 2005b, Walker et al. 2009). The important habitat characteristics uncovered in the present study (live cover and substrate composition) agree with a number of studies that have shown relationships between reef fish assemblage structure and percent-cover variables of various substrates

and epifauna (Fitzpatrick et al. 2012), coral cover and richness (Komyakova et al. 2013), landscape metrics (Moore et al. 2011), environmental and physical habitat characteristics (Tuya et al. 2011), and biogenic cover (Cameron 2013).

Rugosity, or the ratio of actual surface area relative to linear surface area (Gratwicke and Speight 2005a), is a commonly cited habitat characteristic related to species richness, abundance, and assemblage patterns (eg. Gittings et al. 1992, McClanahan 1994, Friedlander and Parrish 1998, Weaver et al. 2002, Gratwicke and Speight 2005a, Walker et al. 2009). However, it was not directly measured in this study due to the difficulty of obtaining such a metric from video. The incorporation of substrate characteristics and live cover likely provided a reasonable proxy for rugosity as these two factors would be expected to influence actual surface area through various substrate grain sizes or growth forms (Gratwicke and Speight 2005b, Toohey 2007, Holmes et al. 2008, Pelletier et al. 2011). Despite limitations on comparing specific habitat characteristics between studies, the widespread documentation of significant fish assemblage-habitat relationships highlights the potential for more comprehensive spatial distribution information based on habitat descriptions that can be relatively easy to obtain, versus extensive biological surveys (Cameron 2013).

The characteristics most related to fish assemblage organization were not different at the species or genus level, however a wider range of characteristics were necessary to describe family-level assemblages. These differences, or lack of differences, may indicate a relatively low loss of resolution in habitat-assemblage relationships when combined at the genus level, but more dramatic changes at coarser classification. While species and genus-level assemblages showed grouping patterns related to habitat zonation, family groups

aligned more closely with the divide between artificial and natural habitat (Chapter 1). The similarity between assemblage patterns at the species and genus-level likely led to the similarity in important habitat characteristics. The broader habitat associations of family-level assemblages generated a shift in importance to those characteristics that best differentiated between artificial and natural structure, namely substrate characteristics. The multiple, mutually well-fitting combinations of substrate characteristics related to family-level assemblages may result from the fact that substrate coverage factors are necessarily correlated (must add up to 100%). For the family-level analyses especially, given the broad taxonomic resolution and interchangeability of important factors, it is more likely that factors identified as important are acting as representatives of a broader habitat distinction (artificial vs natural) than directly influencing the assemblages observed.

Whether the complexity characteristics identified in this study directly drive reef fish assemblage distributions or act as proxies of broader biological habitat zones, it is apparent that fish assemblages change with benthic habitat variations at northwest Gulf shelf-edge banks. A number of mechanisms have been proposed to explain the structuring of reef fish assemblages, the effects of which are intimately tied to habitat characteristics. Jones and Syms (1998) cite four widely examined models of reef fish population dynamics: recruitment rate, competition and competitively induced niche-diversification, Sale's (1977) lottery hypothesis, and predation.

If the assemblage patterns are primarily determined by recruitment, the assumption is made that recruitment does not saturate local resources and thus is a limiting factor (Caley and St John 1996, Hixon 1998). Settling fishes may evaluate potential settlement

areas based on structural, chemical, or tactile cues (Caley and St John 1996), all of which likely differ between the broad habitat zones at shelf-edge banks. Changes in fundamental complexity characteristics may also affect habitat selection, depending on the specific cues used to discriminate between habitats by a particular species. The shelf-edge banks likely receive recruits from a number of sources, both local and external. The paucity of species found at the banks compared to Caribbean reefs has been attributed to isolation from source populations in the Caribbean (Dennis and Bright 1988); however, Gulf circulation patterns suggest the potential for local larval retention and connectivity between banks as well (Lugo-Fernandez 1998, Gledhill 2001). Recruitment is not the only limiting factor and observed assemblages may result from differential survival of recruits post-settlement rather than being determined by habitat selection of settling fish alone (Caley 1993).

If competition is the major driver of assemblage structure, changes in resources resulting from changing habitat characteristics or biotic zonation will shift competitive advantages to species more suited to the new conditions. Complex, heterogeneous habitats are generally thought to support more diverse assemblages due to the abundance of resources provided, even allowing species with similar requirements to coexist (Hixon and Menge 1991). Competition is not limited to interspecies interactions, Boström-Einarsson et al. (2014) demonstrate a shift from interspecific to intraspecific competition with increased habitat degradation. Changes in habitat characteristics, due to degradation or movement between habitat zones, may be an important driver behind which species are able to coexist due to interspecific competition, as well as modify relative abundances through intraspecific competition.

If species have generalized and coincidental habitat requirements, then assemblages will be random subsets of a wide array of suitable inhabitants (Sale 1977). This is an unlikely mechanism in these shelf-edge systems given the consistency within, and distinctions between, assemblages based on both habitat zonation and characteristics across a variety of sites and studies.

If predation is a major influence on assemblage structure, changes in zonation or characteristics that provide shelter or refuge will influence whether certain species can effectively coexist. It has been suggested that increasingly complex habitats provide additional refuge and/or reduce predator efficiency (Jeffries and Lawton 1984, Nelson and Bonsdorff 1990, Almany 2004a, 2004b, Johnson 2006). In addition to physical habitat structure, turbidity has been shown to modify predation interactions (Abrahams and Kattenfeld 1997, Gregory and Levings 1998, Chivers et al. 2013, Lunt 2014) and the extent of exposure to turbid conditions may be one of the most influential environmental factors on fish assemblages at the shelf-edge banks (Dennis and Bright 1988).

As Hixon and Menge (1991) point out, these single process mechanisms do not act alone and likely modify the outcomes of one another, however all act to drive population dynamics through the four basic demographic rates of each species: birth, death, immigration, and emigration (Hixon 1998). Habitat plays a critical role in defining how these assemblage-structuring mechanisms operate and certainly underlay the observation of distinct reef-fish assemblages at the shelf-edge banks related to both broad zonation patterns and specific habitat characteristics.

The present study contributes to the call by resource managers for data at a scale relevant to individual banks (Schmahl et al. 2008). The information presented in this study

describes habitat use by reef fish at a level of detail and finer scale than previously available (Bright et al. 1985, Rezak et al. 1990, Gledhill 2001, Weaver et al. 2006, Wetmore and Rooker 2011), and provides managers with information about the reef fish assemblages that may be expected based on fundamental habitat characteristics or habitat zonation information. Such fundamental information can be used to estimate fisheries resources present at particular features based on habitat zone coverage or characteristics (Cameron 2013), or facilitate the inclusion of fish assemblage information in decisions regarding protective measures, such as the current proposal to expand the FGBNMS (USDOC et al. 2012).

Many of the northwest Gulf banks have been assigned BOEM No Activity Zone (NAZ) or NOAA Habitat Area of Particular Concern (HAPC) designations, but these measures do not directly protect the designated features. Rather, they prevent oil and gas operations within NAZ borders and require "special consideration" of these features in fishery management plans (Schmahl and Hickerson 2006). The expansion of the FGBNMS, which currently contains the East and West Flower Garden Banks and Stetson Bank, would extend the habitat protection measures and fishing limitations of the sanctuary to a proposed nine additional features, including two of the sites examined in this study: Bright and McGrail banks. The goal of the current sanctuary, and reasoning behind the proposed expansion, is to prevent or limit physical damage to sensitive benthic habitat present at many of the banks, as well as to maintain potential habitat and species connectivity within the larger northwestern Gulf bank ecosystem (USDOC et al. 2012). This study provides further support for the consistency of habitat zones, underlying characteristics, and species

assemblages across banks, suggesting that features may exhibit some connectivity and that sanctuary expansion is warranted to protect the ecological integrity of the larger connected system (Schmahl et al. 2008).

The results of this study indicate a significant relationship between fundamental habitat complexity characteristics and the associated reef fish communities present at shelf-edge banks in the northwestern Gulf. Characteristics differ between the broad habitat zones described by Schmahl et al. (2008) and explain significant variation among reef fish assemblages. This study adds to the extensive body of work describing the relationships between habitat complexity and underlying characteristics with reef fish assemblages and assemblage metrics. Important habitat-assemblage relationship factors were very similar at the species and genus levels, while family-level habitat factors were much less definitive, likely resulting from poorly defined assemblages at a coarse taxonomic resolution. Within the systems examined, habitat characteristics may directly determine reef fish assemblage structure by influencing the outcome of recruitment, competition, and predation processes (Jones and Syms 1998). Alternatively, characteristics may be defining the larger habitat zonation at the northwest Gulf shelf-edge banks, a factor known to be associated with distinctly different reef fish assemblages. Either way, this study provides valuable information about habitat-assemblage associations at a level of detail previously lacking at these unique habitats, providing a means to better describe spatial distributions of distinct reef fish assemblages and allow management or protective decisions to more easily incorporate such information in decision-making.

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CHAPTER 3: SPATIAL DISTRIBUTION OF FISHES AT SHELF-EDGE BANKS AND AN ARTIFICIAL REEF IN THE NORTHWEST GULF OF MEXICO

INTRODUCTION

The northwest Gulf of Mexico (Gulf) banks provide essential hard bottom habitat for diverse reef biota, acting as islands of hard substrate surrounded by expansive areas of mud and silt sediments (Bright 1977). Due to the uniqueness of, and habitat value provided by these features, the Bureau of Ocean Energy Management (BOEM) has designated many of the northwest Gulf banks as 'No Activity Zones' (NAZ). Fourteen of these banks have also received a Habitat Areas of Particular Concern (HAPC) classification from the Gulf of Mexico Fishery Management Council (GMFMC 2005) due to the important habitat and fisheries resources they support. The Flower Garden Banks National Marine Sanctuary (FGBNMS) affords additional protection to the East and West Flower Garden Banks and nearby Stetson Bank, in addition to maintaining a variety of thorough monitoring, mapping, and directed research projects (Hickerson 2009a, 2009b, Hickerson et al. 2011, 2012, FGBNMS 2012).

The recently renewed FGBNMS Final Management Plan (April 2012) proposes the inclusion of nine additional banks (Horseshoe, MacNeil, Rankin, Bright, 28 Fathom, Geyer, McGrail, Sonnier, and Alderdice) to the sanctuary, as well as an expansion of sanctuary boundaries around the two Flower Garden banks. The rationale behind sanctuary expansion is twofold: to provide a higher level of protection for additional unique features and habitats, and to maintain the habitat and species connectivity between banks, a recently recognized phenomenon and potentially critical means of preserving the ecological integrity of the entire bank system (FGBNMS 2012).

Understanding the spatial distribution of fish biomass and density associated with northwest Gulf banks, and how distributions are partitioned between different habitat zones, is central to quantitatively assessing the ecological functions of different habitats, as well as the banks themselves. Additionally, quantitative assessments of natural reef communities allow for direct comparisons to information from artificial structures, an important aspect in contrasting how each form of reef structure is used. The spatial distribution of reef-associated fishes has been examined at standing and toppled oil and gas structures in the northwest Gulf (Stanley and Wilson 1996, 1997, 1998, 2000a, 2000b, 2003, Boswell et al. 2010a, Harwell 2013, Simonsen 2013) and found to decrease exponentially with distance from structure. Fish biomass and abundance concentrate directly adjacent to the structure and decrease rapidly with distance (Simonsen 2013). Surveys at natural banks in the northwest Gulf are limited (Gledhill et al. 1996, Wilson et al. 2003, 2006, Clark et al. 2014), but have shown that higher biomass is associated with both low and high relief features, relative to areas distant from any vertical relief (Wilson et al. 2006). A survey of the West Flower Garden (WFG) bank by Wilson et al. (2003) showed depth to be an important factor in determining fish biomass, reporting a 35 to 100 times greater chance of finding fish over the shallowest area of the bank relative to deeper areas. Additionally, a significant 'habitat' effect was reported based on the division of the WFG bank structure into 'terraces', or distinct bathymetric breaks in the bank structure (Wilson et al. 2003). Wilson et al. (2006) reported a similar bathymetrically-defined habitat effect at Sonnier bank, with the highest biomass observed at high-relief pinnacle features versus

lower relief areas. Higher fish biomass and density have also been reported around standing platforms versus nearby artificial reefs (toppled platforms) or natural banks (Wilson et al. 2003, 2006).

A fundamental premise of ecology is relating the distribution of organisms to their biotic and abiotic environment, at any variety of spatial scales (Odum 1971). Habitat complexity, via a number of metrics, has been positively related to reef fish abundance and/or biomass (e.g. Risk 1972, Luckhurst and Luckhurst 1978, McClanahan 1994, Green 1996, Appeldoorn et al. 1997, Friedlander and Parrish 1998, Friedlander et al. 2003, Gratwicke and Speight 2005a, 2005b). Recently, the relationship between structural complexity, derived from bathymetry, and fish diversity and abundance in reef ecosystems has been used to inform predictive models with some success (Pittman et al. 2009, Walker et al. 2009, Pittman and Brown 2011, Costa et al. 2014). Accurate predictive models of abundance or biomass are valuable for meaningful decision-making both in resource management and in definition of marine protected areas (Miller et al. 2004), such as the FGBNMS expansion currently under consideration (FGBNMS 2012). Abiotic habitat factors and structural complexity may be important drivers of fish abundance and/or biomass associated with northwest Gulf banks given both the variety of substrates, relief, and complex topography that define the features (Bright et al. 1985) and the different reef fish assemblages reported between geomorphologically similar banks and benthic habitat zones (Dennis and Bright 1988, Gledhill 2001, Weaver et al. 2006). General visualization of reef fish biomass and density distributions have been mapped from single surveys of the

WFG bank (Wilson et al. 2003) and Sonnier bank (Wilson et al. 2006); however, no work has been done to develop a predictive model of reef fish presence or density based on seafloor structure or environmental variables.

The goal of this chapter is to describe the distribution of fish biomass and density at a site-specific scale and to examine the relative influence of a wide variety of environmental, seafloor structure, and spatial variables on the presence and density of fish. Hydroacoustics are a useful tool to assess fish distributions associated with a variety of habitats as they provide a noninvasive, rapid means of surveying a large area with high spatial resolution that may be inaccessible by more traditional means of sampling (Simonsen 2013). Hydroacoustics have been used extensively to examine spatial distributions of fishes ever since Sund (1935) examined cod spawning aggregations in waters near Norway, and have proven to be an effective tool for assessing spatial distributions of fish associated with natural and artificial structure in the Gulf (Gledhill et al. 1996, Stanley and Wilson 1996, 1997, 1998, 2000a, 2000b, 2003, Wilson et al. 2003, 2006, Boswell et al. 2010a, Harwell 2013, Simonsen 2013).

METHODS

I examined the spatial distribution of fishes associated with three shelf-edge banks and one artificial reef in the northwest Gulf. The three banks (Bright, McGrail, and Jakkula) are located on the Louisiana-Texas shelf edge, while the artificial reef is closer to shore on the Louisiana-Texas shelf in the Louisiana Artificial Reef Program (LARP) East Cameron Artificial Reef Planning Area (Figure 3.1).

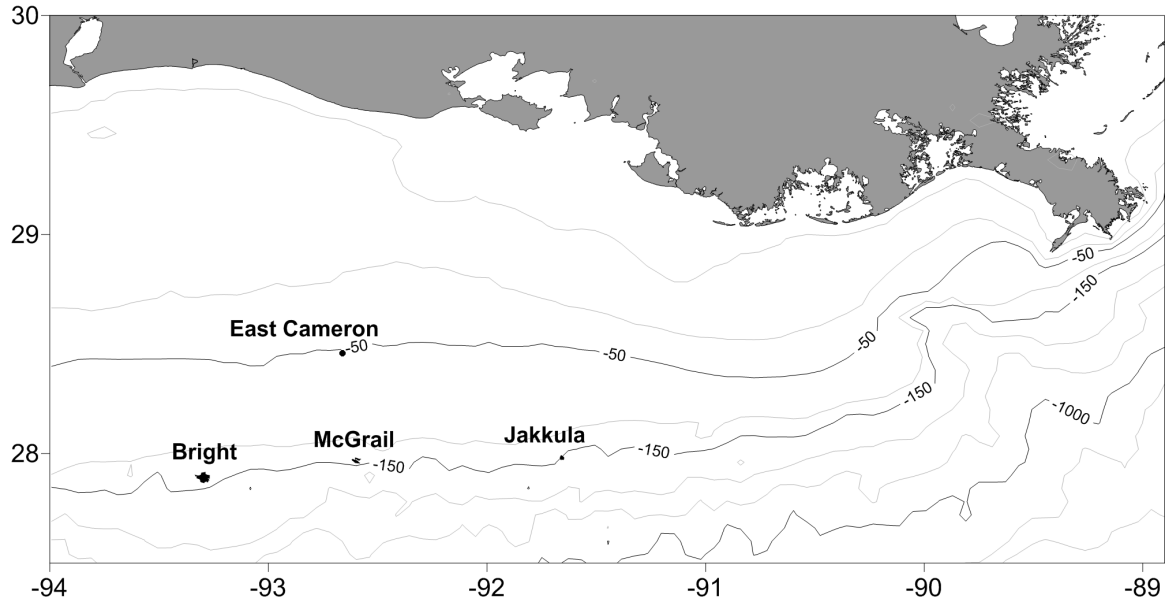

Figure 3.1. Sampling locations for mobile acoustic surveys at one artificial reef (East Cameron) and three shelf-edge banks in the northwest Gulf of Mexico.

STUDY AREA

The Louisiana-Texas shelf-edge banks are a result of diapiric salt intrusions uplifting bedrock that is subsequently capped by carbonate reef structure (Rezak and Bright 1983, Rezak et al. 1985, 1990, Dennis and Bright 1988). The banks used in this study rise from depths of 140-160 m, crest at depths of 30-50 m below the surface, and range in size from 4 to 20 km^2 (Appendix Table C.1). The three sites selected (Bright, McGrail, and Jakkula) were chosen to effectively sample throughout the East-West Texas-Louisiana shelf-edge bank track. The term 'reef' is often used to describe these features, in the sense that they represent underwater structure, though many do possess areas of biotic reef structure. This biotic reef structure was categorized into distinct depth-related benthic biotic habitats by extensive baseline biological and geological studies of the Louisiana-Texas shelf-edge banks (Rezak and Bright 1983, Rezak et al. 1990). Seven characteristic zones were identified and subsequently grouped into four general classifications based on the degree

of reef building and primary productivity: major reef-building activity and primary production, minor reef-building, transitional zones with minor to negligible reef-building, and no reef building. More recently, work by the Flower Garden Banks National Marine Sanctuary (FGBNMS) has modified and reorganized the zonation classification of Rezak et al. (1983) into a similar, but more generalized scheme based solely on five broad biological zones, within which there are multiple specific habitat types (Schmahl et al. 2008; Table 3.1). My acoustic surveys sampled all the habitat zones present at each site, up to five zones at a single bank.

Table 3.1. Summary of revised biological zones of NWGOM banks proposed by Schmahl et al. (2008).

Zone	Depth (m)	Biology	Previous classification per Rezak et al. (1985)
Coral Reef	16-52	*Montastraea* *Madracis* *Stephanocoenia* Coral sand	*Diploria-Montastraea-Porites* *Madracis* and Leafy Algae *Stephanocoenia -Millepora*
Coral Community	16-52	*Millepora*-sponge Low density coral Leafy algae Sponge	*Millepora*-Sponge
Coralline Algal Reef	45-98	Algal nodules Coralline algal reef Leafy algae	Algal-Sponge "Partly drowned reefs"
Deep Coral	50-200+	Antipatharian Octocoral Crinoid Stony coral	Antipatharian transitional Nepheloid "Drowned reefs"
Soft Bottom	16-200+	Sand Quartz Molluscan hash	Not defined as "hard bottom" so excluded from prior evaluations

The artificial reef site I examined consisted of a mid-shelf toppled platform in the East Cameron Artificial Reef Planning Area, hereafter the East Cameron (EC) site. This artificial reef is located within an area of high acoustic backscatter and increased bathymetric relief relative to surrounding areas, discovered during a side-scan survey of the Louisiana Artificial Reef Program (LARP) planning areas (Cowan et al. 2007). The extent of natural hard-bottom in the EC planning area is the largest observed among the Louisiana artificial reef planning areas (7,855 ha total). The local bathymetry is characterized by a gradual slope from 45-55 m, with the area of interest forming a shelf in the center approximately 4 m higher than the surrounding soft sediments, thought to be composed of slabs of lithified bottom sediment (Cowan et al. 2007).

SURVEY METHOD

Acoustic surveys were conducted at the four sites during twice-quarterly cruises between July 2011 and October 2013, as weather and scheduling permitted. The data collection system was composed of three downward-facing split beam transducers (70, 123, 206 kHz, Biosonics Inc.), a Biosonics DT-X scientific echosounder, and personal computer. The transducers were mounted 2 m below water level on a rotating arm attached to the vessel amidships to avoid surface disturbance and entrained bubbles. Transducers were calibrated periodically with the standard sphere method (Foote et al. 1987).

Surveys were run at an average vessel speed of 5 knots along pre-designated track lines. The survey pattern consists of ten intersecting lines at every 18° around a specified center point (Figure 3.2). The pattern was focused on the center of the sampling site with each line extending 1.5 km on either side of the center point (3 km per line), resulting in a

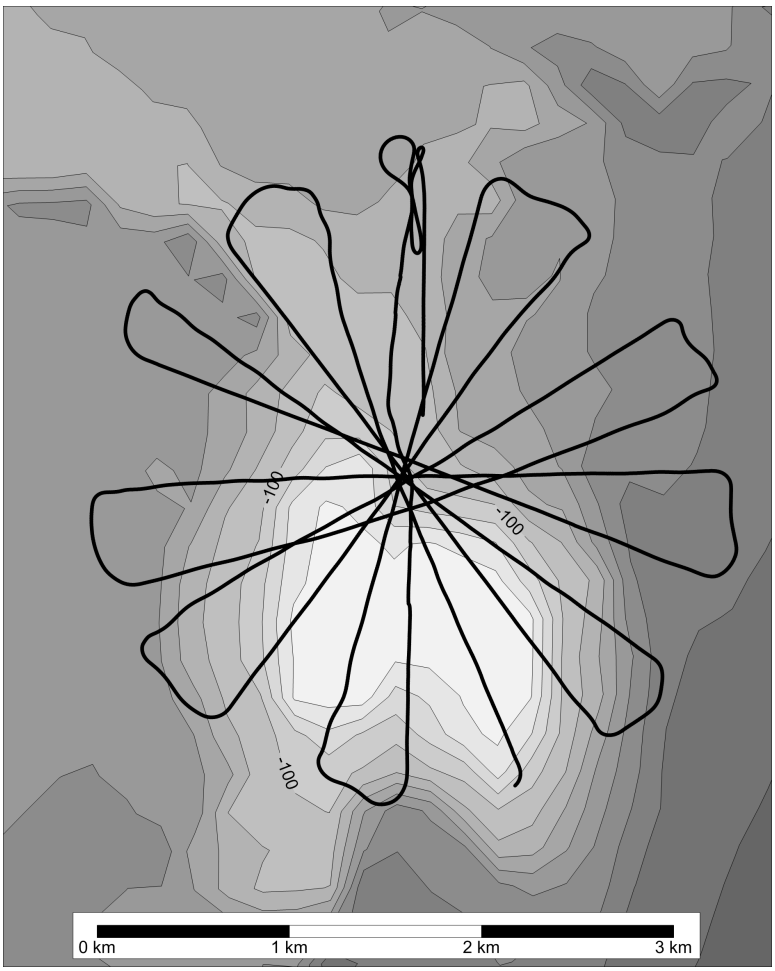

Figure 3.2. Example cruise track used during acoustic sampling, overlaid on bathymetry of Jakkula bank.

circular survey area of just over 7 km^2. Surveys were scheduled so that the hour surrounding both sunrise and sunset (30 mins before, 30 mins after) was avoided, an effort to reduce the effects of potential diel movements of fish communities. Acoustic data and time-synchronized GPS coordinates were visualized and recorded with Visual Acquisition 6.0 (Biosonics, Inc.). Data were collected at a pulse duration of 1.0 millisecond at varying rates, depending on survey depth. Active pinging was recorded during the main survey lines, while passive listening was recorded between lines to obtain a baseline background noise level of the survey environment and ship.

A Seabird SBE 25 Sealogger CTD was deployed at each sampling station prior to the acoustic survey to record a surface-to-bottom profile of conductivity, temperature, pressure, depth, and salinity, necessary for sound speed correction during analysis. The CTD was acclimated at the surface for three minutes before descent and was deployed vertically at approximately 1 m/s. Both descent and ascent data were collected for mutual validation. Profiles were conducted at the deepest point of the survey pattern in order to cover all depths sampled with the acoustics.

DATA PROCESSING

Acoustic backscatter data from the 123 kHz transducer (Table 3.2) were post-processed with Echoview v. 5.3 (Myriax Pty. Ltd., Hobart, Tasmania, Australia) to obtain values of both mean volume backscattering strength (MVBS; S_v, dB) and fish density (fish $m^{-3)}$. Environmental data from the CTD casts were used to correct the speed of sound for the effects of temperature and salinity during each survey. Echograms were visually inspected to exclude regions of bad data (signal loss, bubble interference, excess noise, etc.). Data within 5 m of the surface was excluded to avoid effects of surface noise and the near field area of the transducers. The 'best bottom candidate' bottom detection algorithm, with a 0.5 m backstep (Table 3.3), was applied to exclude the seafloor and reef structures, and manually edited as necessary. Each natural bank site echogram was divided into

Table 3.2. Echosounder properties.

Frequency	123.00 kHz
Receive sensitivity	-51.1 dB
Source level	221.3 dB
Major axis beam width	7.5°
Minor axis beam width	7.5°
Pulse length	1.000 ms

Table 3.3. Bottom line pick algorithm settings. S_v: Volume backscatter

Line pick algorithm	Best bottom candidate
Basic Settings	
Start depth	20.00m
Stop depth	1000.00m
Minimum Sv for good pick	-70.00dB
Backstep settings	
Discrimination level	-55.00 dB
Backstep range	-0.50m
Advanced Settings	
Peak threshold	-50.00 dB
Maximum dropout	2 samples
Window radius	10 samples
Minimum peak asymmetry	-1.00

regions corresponding to the expected habitat zone at given depths, as described by Schmahl et al. (2008) (Appendix Table C.1). Habitat zones for the artificial sites were defined according to distance from the structure. An 'artificial reef' zone was defined to be within 250 m of the structure, an estimate of the area of influence of the structure (Shipley and Cowan Jr. 2010), beyond which habitat was designated as 'mud'.

A standardized dataflow was applied to each echogram to remove either unwanted or background noise, export MVBS from the 'cleaned' data, and compute mean fish densities (Figure 3.3). Background noise was filtered out with the background noise removal operator (Robertis and Higginbottom 2007; Table 3.4). Intermittent noise was cleaned when necessary with an algorithm similar to that described by Anderson et al. (2005, Figure 3.4). Finally, the echogram was gridded into 10 m depth by 20 m distance analysis cells.

Figure 3.3. Schematic of the Echoview dataflow used in processing of acoustic data. S_v: Volume backscatter; TS: target strength; MVBS: mean volume backscattering strength.

Table 3.4. Background noise removal algorithm settings (DeRobertis and Higgenbottom 2007). SNR: signal-to-noise ratio

Averaging Cell	
Horizontal extent	20 pings
Vertical units	Meters
Vertical extent	5.00m
Vertical overlap	10%
Thresholds	
Maximum noise	-100.00 dB
Minimum SNR	6.00

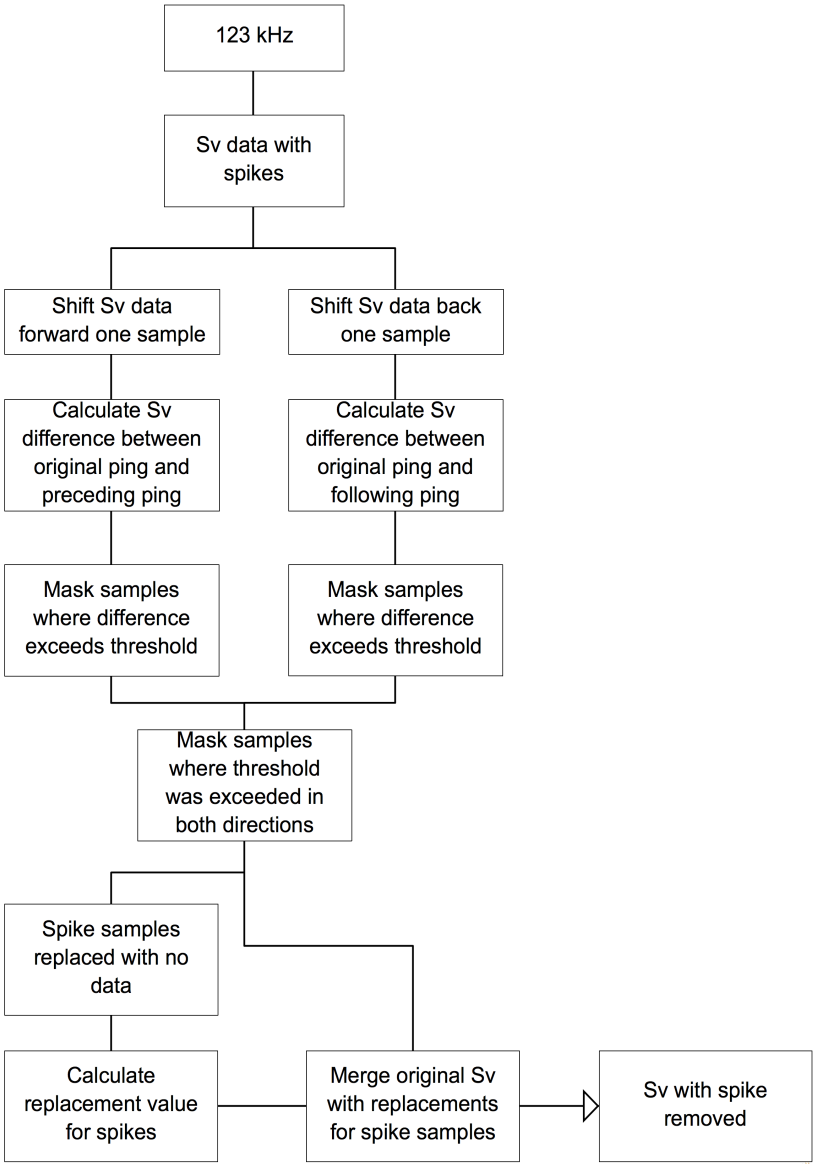

Figure 3.4**.** Schematic of the Echoview dataflow used to remove spike noise when present, adapted from Anderson et al. (2005). S_v: volume backscattering strength.

The volume backscattering coefficient (s_v) was integrated over each depth-by-distance cell to obtain mean volume backscattering strength (MVBS; S_v, dB) according to the relationship:

$$S_v = 10 \log_{10}(s_v)$$

which was exported for analysis of spatial distribution (Maclennan et al. 2002). Density (FPCM, fish m^{-3}) was calculated for each analysis cell by scaling MVBS by mean single-target target strengths (TS) following MacLennan et al. (2002):

$$\mathrm{FPCM}_{\mathrm{cell}} = 10^{(\mathrm{MVBS}/10)} / 10^{(\mathrm{TS}/10)}$$

Both MVBS and density were exported in a by-region, by-cell manner, meaning that estimates were obtained for each individual analysis cell on a region-by-region basis. This allowed for each cell to be linked to a particular region, in this case habitat zone designations, for statistical analysis purposes.

PREDICTOR DEFINITION

A variety of predictors were either measured or calculated to inform the modeling procedures used to interpret the fish biomass and density information gathered during acoustic surveys. For all surveys, a suite of basic identifying information was paired with each analysis cell, including site, habitat, season, depth, and GPS location. Additionally, the offset of a given cell from the bottom was defined as the difference between the mean depth of that cell and the mean bottom depth below it. The environmental data obtained via CTD casts was binned and averaged over the same depth intervals as the analysis cells and merged with the exported MVBS and density estimates.

For surveys conducted at the natural bank sites, 24 additional predictors related to bathymetry and spatial orientation were calculated (Table 3.5). Distance to the shallowest point on the bank, defined with high-resolution multibeam bathymetric surveys (Gardner and Beaudoin 2005), was calculated using the 'GEODIST' function in SAS v. 9.3. The angular

Table 3.5. Predictors and their sources used in the machine learning modeling procedures.

Predictor	Source
Site	Sample design
Season	Sample design
Year	Sample design
Habitat	Rezak et al. (1985) and Schmahl et al. (2008)
Temperature	CTD
Salinity	CTD
Relief	Split-beam echosounder
Offset	Split-beam echosounder
Distance to shallow	SAS 9.3, "GEODIST"
Bearing to center	SAS 9.3
Cell Depth	Split-beam echosounder
Depth*	Multibeam bathymetry (Gardner and Beaudoin 2005)
Standard deviation of depth*	ArcGIS Spatial Analyst: focal statistic function
Curvature *	ArcGIS Spatial Analyst: curvature function
Rugosity*	DEM Surface Toolbox: Surface Area and Ratio
Slope of the slope*	ArcGIS Spatial Analyst: Slope function

* Included at three additional spatial scales, averaged over radii of 25, 50, and 100 meters.

direction of each cell from the bank center was calculated as its initial bearing (θ), given the short distances being considered (<3 km):

$$\theta = \text{atan2}\big(\sin(\Delta\lambda)\cos(\varphi_2), \cos(\varphi_1)\sin(\varphi_2) - \sin(\varphi_1)\cos(\varphi_2)\cos(\Delta\lambda)\big)$$

where $\Delta\lambda$ was the radian difference in longitude between the center point and the cell, and φ_1 and φ_2 were the radian latitude of the center point and the cell, respectively. Initial bearing (θ) was then converted back into decimal degrees for use by the models.

A variety of seafloor characteristics were calculated with both the split-beam data and multibeam bathymetric data (Gardner and Beaudoin 2005). From the split-beam data, an estimate of benthic relief was calculated as the difference between the maximum and minimum depth of the bottom beneath a given cell. Five parameters with demonstrated utility for predicting reef fish abundances and distributions (Pittman et al. 2009, Pittman and Brown 2011) were derived from multibeam surveys of the natural sites: depth,

standard deviation of depth, curvature, rugosity, and slope of the slope. Each parameter was calculated at the base multibeam survey resolution (5x5 m), as well as at three broader spatial scales (mean values within a radius of 25, 50, and 100 m) to examine the relative importance of scale. All surfaces were generated using the Spatial Analyst and DEM Surface toolboxes in ArcGIS and paired with acoustic data cells according to GPS position.

DATA ANALYSIS

The spatial distribution of reef fishes at three natural banks and one artificial reef was examined with generalized linear mixed models and two machine learning (ML) techniques: boosted regression tree (BRT) and random forest (RF).

TRADITIONAL STATISTICS

MVBS was linearized and compared between study sites, habitat zones, and seasons with a generalized linear mixed model (GLIMMIX, SAS v. 9.3), with MVBS as the dependent variable in the model. Mean depth and offset from the bottom were included in the model as potentially significant covariates. A random effect for year was included to account for variability between years that may exist.

Due to the nature of both acoustic data and fish distributions, a large proportion of fish density estimates are either zero or exceedingly small, a distribution that would tend to violate assumptions of traditional statistical analyses such as the normality of residuals, even when biased transformations (i.e., log(x+1)) are applied or exotic distributions are assumed. To address this, density data were examined with two models. The first modeled the presence or absence of fish, while the second modeled fish density, given that individuals were present.

The original data were used to create two new datasets: 1) the first consisted of a binomial response that indicated either presence or absence of a density value, the 'presence data' and 2) the other was a subset of the original dataset containing only the cells in which a non-zero density was recorded, the 'density data'. The two datasets were then modeled separately using GLIMMIX models. The presence model assumed a binomial response, while the density model assumed a gamma distribution, the preferred option versus lognormal for fisheries density data (Myers and Pepin 1990), since the majority of density estimates were small even after the exclusion of zeros.

Both models were fit with GLIMMIX (SAS 9.3) with either presence or density as the dependent variable and logit or log links, respectively. Mean depth and offset from the bottom were included in the models as potentially significant covariates. As with the MVBS model, a random effect for year was included. Because the presence and density models included continuous predictors, default goodness-of-fit (GOF) metrics, such as the ratio of the generalized chi-square to model degrees of freedom, were unreliable. The fullest model, based on the predictors of interest, was fit in an effort to maximize GOF for both the presence and density models.

Machine Learning Techniques

Two ML techniques, BRT and RF, were employed to complement the traditional analyses with variable importance measures, as well as to provide the potential for more flexible and accurate predictive capabilities. These models were developed with data from the natural sites only because many of the predictors of interest (Table 3.5) were unavailable at the artificial site, precluding their use in these analyses. Both techniques were used to model the divided data as created for the conditional model, the binomial

'presence' dataset and the non-zero 'density' dataset. The density data was converted to a four-class categorical response using head/tail breaks (Jiang 2013) for modeling with ML techniques to simplify the modeling procedure and predictions of the models. All 31 predictors were used to develop the four ML models: BRT presence, BRT density, RF presence, and RF density. BRT models were constructed in R with the 'dismo' and 'gbm' packages in R (version 3.1.2), while RF models were generated using the 'randomForest' package.

Boosted regression trees

BRT are able to model complex, non-linear relationships between organisms and their environment, producing both accurate predictions and interpretable models (De'ath 2007, Elith et al. 2008). BRT develop many simple classification tree models based on random subsets of the data, which are subsequently combined linearly to produce a final aggregate model. 'Boosted' refers to the optimization technique of minimizing a loss function, in this case predictive deviance, at each step of tree addition. Each new tree is fitted to the residuals of the trees already in the model in stagewise fashion, meaning trees in the model are not changed as it grows. The final BRT model is a linear combination of the trees, similar to a regression model where each term is a tree. BRT was used to model both the binomial presence data and the non-zero density data.

The presence BRT was trained on a random subset of 50,000 observations from the entire acoustic survey dataset (474,339 data points) with the cross-validation (CV) method described in Elith et al. (2008) using the 'gbm' package in R. Learning rate (lr), the contribution of each tree to the growing model, was specified as 0.005 and tree complexity (tc), the number of nodes in a single tree, was set at 5. The CV method developed 10 BRT

simultaneously on a unique half of the available data. After every 50 new trees, the predictive performance of each model, quantified as predictive deviance, was evaluated with the withheld half of the data. The optimal number of trees (nt) for the BRT was defined by a minimum in predictive deviance, beyond which models were 'over fitting' their subset of the data and losing predictive generality.

The construction of the multiclass non-zero density BRT differed slightly from that for the presence model. The density BRT was trained on a random 30,000 of the 64,881 cells where a non-zero density was observed. The model was built using an lr of 0.005 and a tc of 5, assuming a multinomial response. As with the presence model, 10-fold CV was used to determine the optimal number of trees to include in the final model.

Once the optimal presence and density BRT models were defined, two common model interpretation methods were conducted. Relative variable importance was estimated according to Friedman (2001), a method that incorporates how often a variable was selected for splitting and model improvement as a result of the split. Partial dependence plots were created to examine the marginal effect of the high-influence predictors on the response, after accounting for the average of all other variables in the model.

True predictive performance of the BRT models was evaluated with the data subset completely excluded from model development (424,339 obs for presence, 34,881 obs for density). Before prediction, spatially autocorrelated points were removed to avoid violating the assumption of independence and biasing statistical tests through essentially pseudoreplication. Spatially autocorrelated points were defined according to Costa et al.

(2014), which led to a variogram model with a range of 110 m. Points in the data to be used for prediction closer than 110 m were assumed to be spatially correlated and were removed.

Predictions were generated from the remaining 6129 presence observations and 5199 non-zero density observations with the appropriate BRT model. Predictions from the BRT models were expressed as the probability of a given observation being either a 1 (present) or belonging to a particular density class, depending on the model. To provide an absolute classification from the non-zero density BRT, each observation was assigned to the class with the highest probability.

Random Forest

The RF procedure is another ensemble tree-based ML method that has been growing in popularity within the ecological community recently for classification procedures. In the simplest terms, RF fits multiple classification trees to the data and combines the predictions from all trees. As with BRT, the data were split into two sets: one indicating the presence/absence of a density value, and the other with only the cells in which a density was observed, coded into four categories based on head/tail breaks (Jiang 2013). The same subsets of the presence and non-zero density data that were used to train the BRT models were used to train the RF models (50,000 presence obs, 30,000 non-zero obs), while the remainder was reserved for the predictive aspect of the analysis.

The RF algorithm selected 5000 bootstrap samples from the training data for each dataset, presence and density. For each bootstrap sample, an unpruned classification tree was grown. Rather than considering all predictors in the model at each split, a random sample of five of the predictors was selected at each node and the best split from among

those predictors was used. The error rate for this procedure was estimated by predicting out-of-bag (OOB) data, the data in the training set, but not selected to grow a particular tree. These predictions were aggregated as the forest was grown, after which an OOB estimate of the error rate was calculated versus the observed data to judge model performance.

Variable importance and partial dependence plots were generated from the presence and non-zero density RF models to examine which predictors were the most influential and how they affected prediction outcomes. Variable importance was estimated by examining how much prediction error increased when OOB data for a given variable was permuted while all others were left unchanged, a procedure carried out tree by tree as the forest was constructed. Partial dependence plots were produced to depict the marginal effects of the high-influence variables on classification of presence and density class.

A true test of prediction was run with the presence and density RF to predict the data withheld from any model development. As with BRT, these verification datasets had spatially autocorrelated points removed to satisfy assumptions of independence. RF predictions were made by majority vote. Each tree in the forest made a prediction for each observation such that the final predicted value was determined with a 'majority vote' from the individual trees within the forest. Probability of membership in each density class was generated for each observation in order to inform model performance metrics that used soft classifiers.

Near-Bottom Analysis

Because the main focus of this study as a whole relates to reef fishes, the four models described (2 RF, 2 BRT) were run on a subset of the data that included only those

analysis cells within 20m of the bottom. This cutoff was determined through preliminary observations of raw echograms and the results of the ML models fit using data from the full water column. These bottom-focused models were defined and run in the exact same manner as those including the full water column, with one exception. Density classes were re-defined based on the densities present in the near-bottom data subset using the same head/tail breaks method (Jiang 2013) as used with the full dataset.

Model Performance

A variety of metrics were calculated both to quantify predictive performance and to provide a means by which to compare between ML methods. The reliability of the models was evaluated with mean absolute error (MAE) and root mean square error (RMSE). MAE is simply the average of the magnitude of predictive errors, while RMSE is a weighted average where larger errors receive more influence. For the binomial presence models, the other performance metric used was a receiver operating characteristic (ROC) curve, a depiction of relative tradeoffs between sensitivity and specificity (Fawcett 2006). ROC curves are independent of arbitrary classification break points, in this case a probability threshold defining presence, and describe the model's performance over the entire range of predicted values. The area under the curve (AUC) statistic was calculated to describe model performance versus a random guess. A randomly generated model would produce a linear y=x ROC curve and an AUC value of 0.5; a model-generated curve above this line, and thus a greater AUC value, would indicate a model performing better than a random model.

The theory behind ROC curves extends to multiclass problems (Srinivasan 1999); however, practical implementation is limited by computational complexity and interpretability (Ferri et al. 2003). Methods have been developed to calculate multiclass

AUC values (Mossman 1999, Provost and Domingos 2000, Hand and Till 2001, Landgrebe and Duin 2007), which estimate the true volume under the ROC surface (VUS) with an average, weighted or otherwise, of pairwise or one-to all AUC values. For the non-zero density models, Hand and Till's (2001) version of the multiclass AUC was calculated for the density models as a simple point of comparison between BRT and RF, though interpretability of the value itself as performance metric is limited (Ferri et al. 2003). To supplement multiclass AUC, the Adjusted Rand Index (ARI), a commonly used metric to assess classifier performance (Santos and Embrechts 2009), was calculated to evaluate and compare the multiclass model performances.

RESULTS

A total of 574,068 individual analysis cells were defined from 45 separate acoustic surveys, conducted at the four survey sites between July 2011 and October 2013. A non-zero density was observed in 13.7% of the total defined cells. Data were split relatively evenly between sites, 21.9% from Bright, 15.4% from East Cameron, 31.5% from Jakkula, and 31.1% from McGrail. Data were not balanced between habitat zones, the relative frequencies of which were dictated both by survey design and habitat prevalence. The deep coral zone characterized the largest proportion of cells (33.8%), followed by coralline algal reef (26.7%), soft bottom (17.1%), mud (13%), coral community (6.9%), and artificial (2.4%). Similarly, data were not equally partitioned between seasons, particularly due to weather-limited sampling ability during the later months in the year, with 35.8% of data collected in spring, 27.4% in summer, 20.9% in fall, and 15.9% in winter.

MIXED MODELS

Results of the MVBS mixed model indicated a significant three-factor interaction between site, season, and habitat zone ($p<0.0001$, Table 3.6). The model also indicated that the covariates, depth and offset, explained a significant portion of the variation in MVBS observed ($p<0.0001$, Table 3.6). LSMean MVBS values ranged from a low of -76 dB in the coralline algal reef habitat at Jakkula in winter to a high of -63.2 dB at the artificial reef in fall. Note that a less-negative MVBS value indicates a higher relative acoustic biomass.

Table 3.6. Mixed model results indicating the significance of various effects and interactions on observed mean volume backscatter (MVBS).

Effect	Numerator df	Denominator df	F Value	p-value
Habitat Zone	4	5.74E5	83.3	<0.0001
Site	2	5.74E5	1.1	0.321
Season	3	5.74E5	1.7	0.17
Depth	1	5.74E5	64.8	<0.0001
Offset	1	5.74E5	902.5	<0.0001
Habitat*Site	6	5.74E5	56.0	<0.0001
Habitat*Season	12	5.74E5	224.2	<0.0001
Site*Season	6	5.74E5	3.0	0.006
Habitat*Site*Season	14	5.74E5	84.4	<0.0001

MVBS values at the artificial reef site tended to be similar to the highest natural habitat values in all seasons except fall, where MVBS was much greater within both habitats at the East Cameron site. At the East Cameron site, MVBS within 250m of the artificial structure was consistently higher than above the surrounding mud, significantly higher in spring, summer, and winter ($p<0.0001$).

Limited consistent relationships were observed at the natural sites. MVBS generally declined with increasing habitat depth in summer, however Jakkula and Bright displayed the complete opposite pattern in winter. Overall, the LSMean MVBS of each three-factor interaction combination did not show any truly consistent patterns of MVBS between sites,

habitats or seasons (Figure 3.5). The presence of a significant three-way interaction and limited consistent patterns among model LSMeans suggests that MVBS is highly variable within each of the effects considered.

The density presence/absence model indicated a significant three-factor interaction between site, season, and habitat zone ($p<0.0001$, Table 3.7). Depth and offset appeared to be significant covariates with respect to the probability of a density value ($p<0.0001$, Table 3.7). LSMean probability of fish presence ranged between 0.016 at the soft bottom habitat

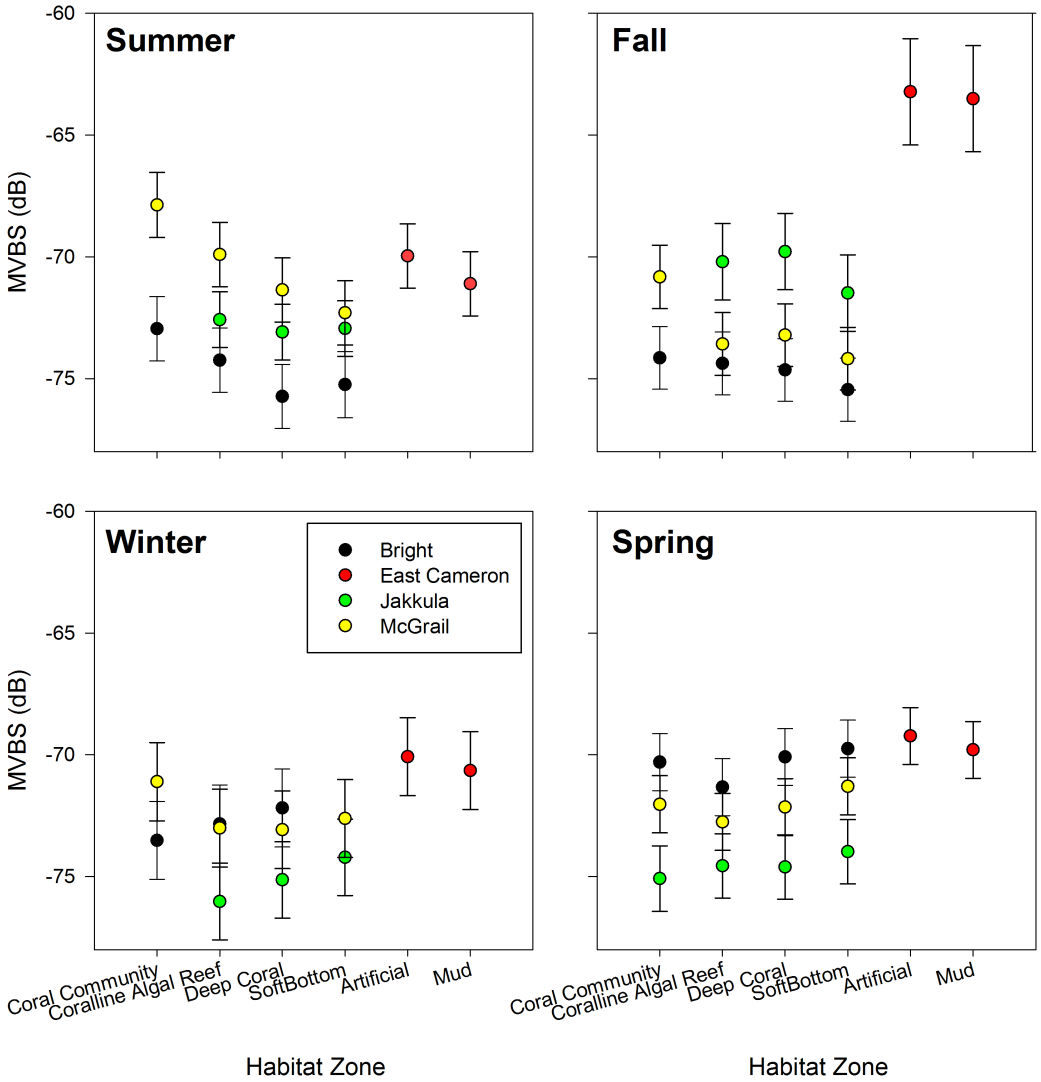

Figure 3.5. LSMean mean volume backscatter (MVBS) values corresponding to the significant three-factor interaction of habitat, site, and season. Error bars indicate standard error.

Table 3.7. Mixed model results indicating the significance of various effects and interactions on observed presence of a density value.

Effect	Numerator df	Denominator df	F value	p-value
Habitat Zone	4	563E3	33.2	<0.0001
Site	2	563E3	0.4	0.68
Season	3	563E3	2.8	0.04
Depth	1	563E3	959.0	<0.0001
Offset	1	563E3	1412.7	<0.0001
Habitat*Site	6	563E3	95.4	<0.0001
Habitat*Season	12	563E3	65.8	<0.0001
Site*Season	6	563E3	3.4	0.002
Habitat*Site*Season	14	563E3	35.1	<0.0001

on Bright in summer, to 0.31 at the deep coral habitat on Bright in winter (Figure 3.6). At the artificial site, LSMean probability of presence was significantly higher directly adjacent to the structure in all seasons except fall ($p<0.0001$). In spring and winter Bright showed the highest probability of presence across habitats, contrary to summer where Bright had the lowest probability across habitats. Over all natural habitats, the probability of presence declined with increasing habitat depth in summer, though the opposite was observed at Bright in winter. Overall, the probability of presence showed few consistent relationships between habitats, sites, or seasons, though the relative positioning of values loosely resembled the MVBS data. As with MVBS, the fact that a significant three-way interaction was found and the lack of consistent habitat, site, or season relationships suggests that the probability of fish presence is highly variable across the effects examined.

Results of the continuous density model, constructed with only those observations with a non-zero density value, indicated a significant three-way interaction between site, season, and habitat zone ($p=0.0001$, Table 3.8). Season appeared to be a highly influential

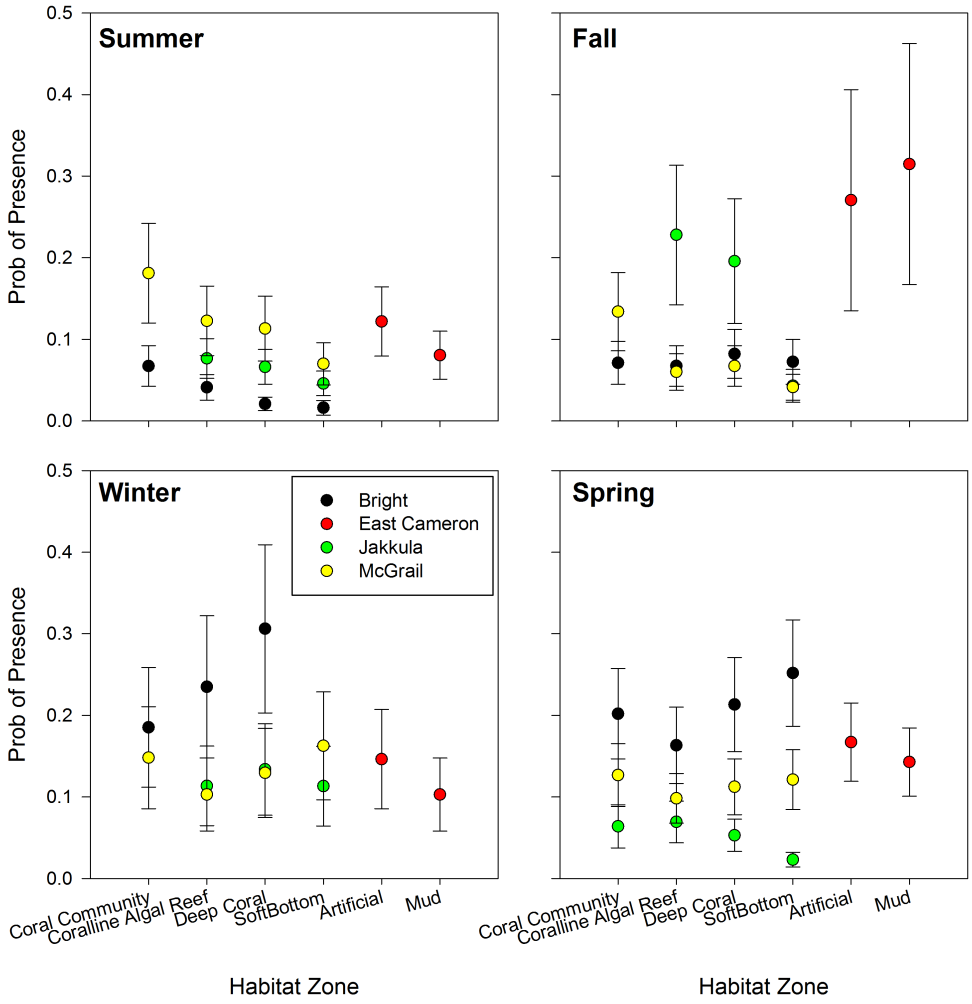

Figure 3.6. LSMean probability of presence corresponding to the significant three-factor interaction of habitat, site, and season. Error bars indicate standard error.

Table 3.8. Mixed model results indicating the significance of various effects and interactions on observed fish density.

Effect	Numerator df	Denominator df	F value	P value
Habitat Zone	4	80130	0.14	0.97
Site	2	80130	1.06	0.34
Season	3	80130	7.99	<0.0001
Depth	1	80130	134.07	<0.0001
Offset	1	80130	2.23	0.14
Habitat*Site	6	80130	1.44	0.19
Habitat*Season	12	80130	2.19	0.01
Site*Season	6	80130	2.28	0.03
Habitat*Site*Season	14	80130	3.00	0.0001

effect in this model, as only the terms including season were found to be significant (Table 3.8). Depth was shown to be a significant covariate, while offset did not appear to significantly relate to density values.

LSMean density values of site-by-season-by-habitat zone combinations ranged from a high of 0.0187 fish m^{-3} on the mud habitat at East Cameron in fall to a low of 0.0029 fish m^{-3} at the coralline algal reef habitat on Jakkula in winter (Figure 3.7). Across all sites and

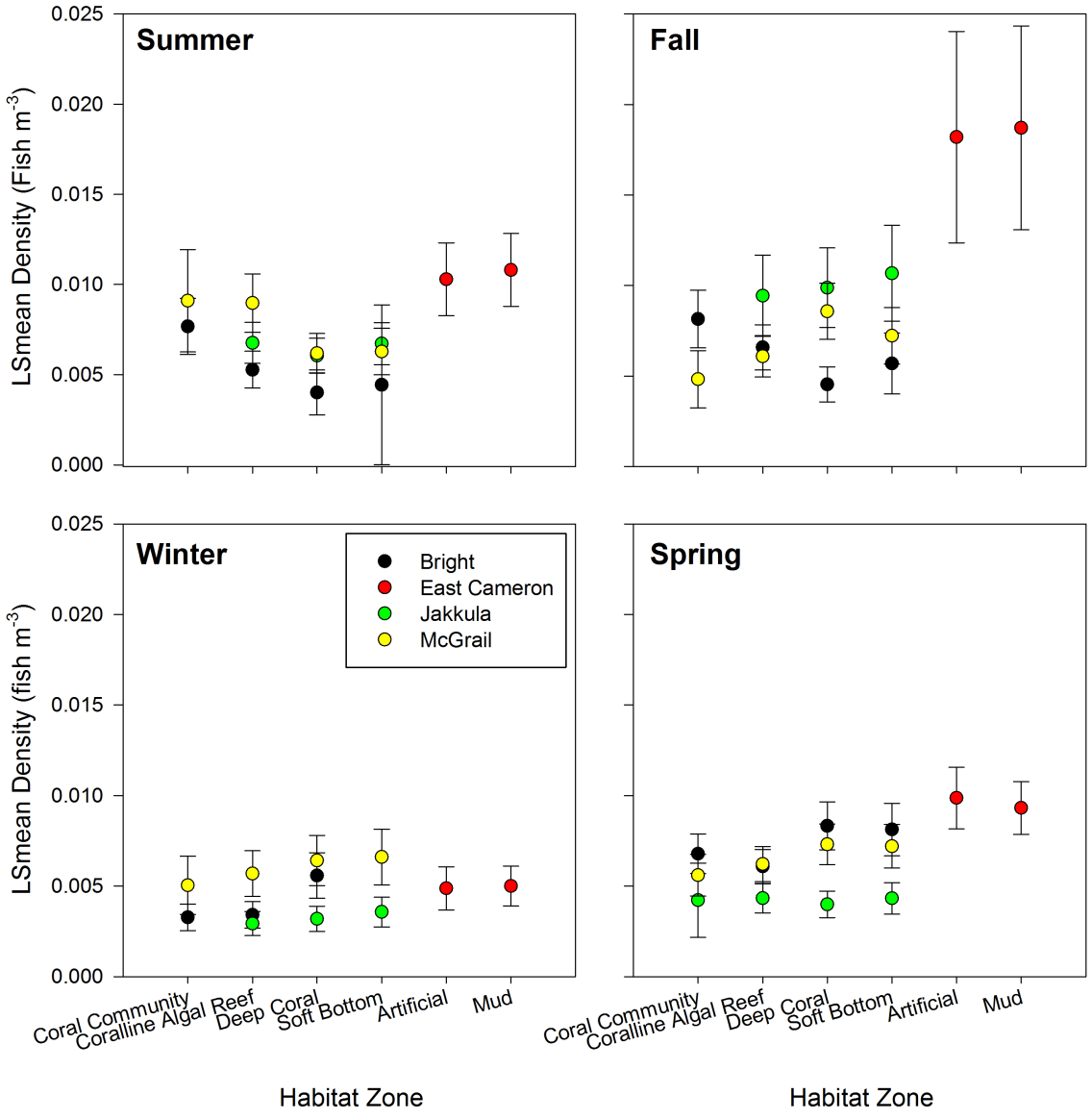

Figure 3.7. LSMean fish density (fish per m^{-3}) corresponding to the significant three-factor interaction of habitat, site, and season. Error bars indicate standard error.

habitats, density was generally lower in the winter relative to other seasons. At a given site, densities in spring and winter were relatively constant across habitat zones, and Jakkula had consistently lower densities at a given habitat zone. In summer, density tended to be highest in the shallowest habitat zone, coral community, and decreased with increasing habitat zone depth. Excluding winter, densities observed at East Cameron were higher than at any habitats at the natural sites, especially in fall. The complex interaction structure indicated by the model and limited consistency of site, habitat, or seasonal effects with respect to density, suggested that density is a highly variable property within the effects examined.

Fish assemblage data (Chapters 1 and 2) indicated that habitat zone was the main driver behind differences in species distributions and abundances. To examine whether this assemblage difference translated into larger distribution differences the main effect of habitat was examined alone, over all sites and seasons. Significant differences in MVBS, probability of presence, and density were observed between habitat zones (Figure 3.8).

MVBS was higher at both artificial reef site habitats than any of the natural bank habitats (Figure 3.8a). MVBS was highest directly adjacent to the structure, significantly greater than above the surround sediments. At the natural habitats, the shallowest coral community habitat showed a significantly higher MVBS than the deeper three zones, which did not differ.

The probability of presence, based on habitat zone alone, was significantly higher directly adjacent to the artificial reef structure than any other habitat (Figure 3.8b). The

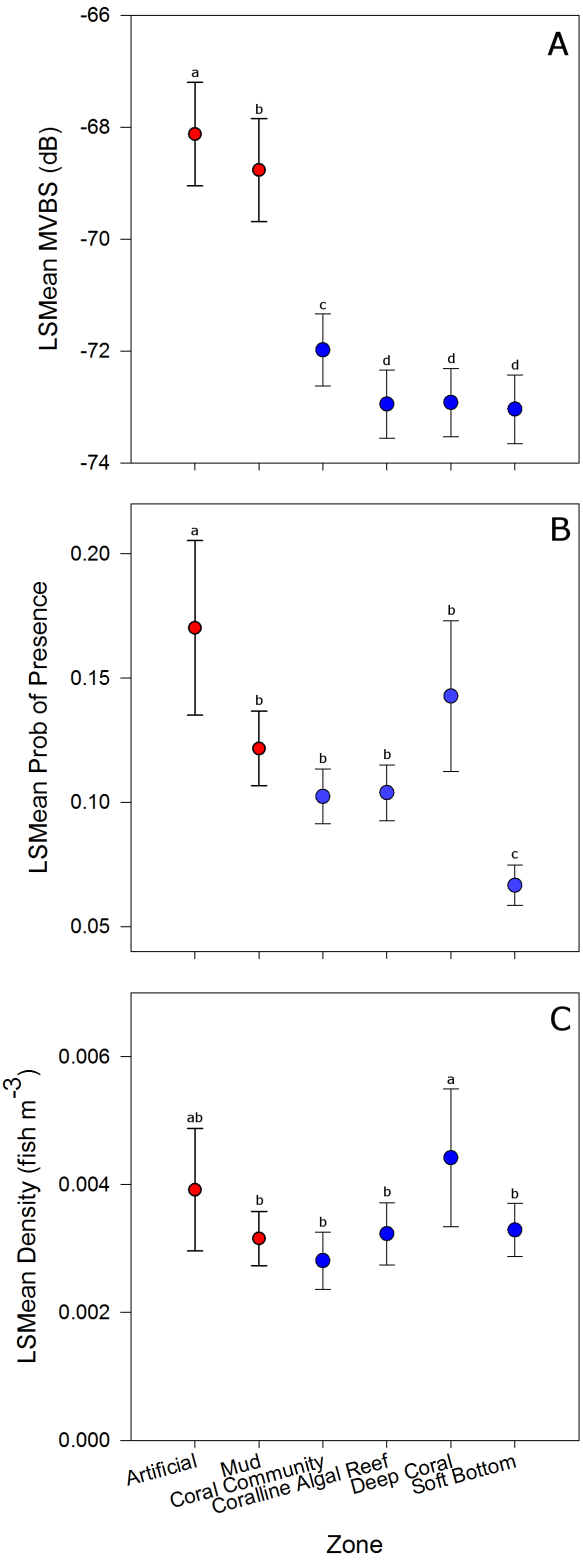

Figure 3.8. LSMean estimates of (A) mean volume backscatter, (B) probability of presence, and (C) fish density by habitat zone. Red symbols indicate the habitats at the artificial reef site. Blue symbols indicate habitats at the natural bank sites. Error bars represent standard error.

three shallowest natural bank habitats did not differ significantly from one another or the sediments surrounding the artificial structure. The lowest probability of presence was observed above soft bottom habitat, significantly lower than other zones.

The deep coral habitat zone showed the highest average fish density, significantly higher than the other natural habitat zones and the area surrounding the artificial structure, which did not differ significantly from one another (Figure 3.8c). The habitat zone directly adjacent to the artificial structure showed a moderate value, not significantly different from either group.

MACHINE LEARNING MODELS

ML models were built and validated using data from natural sites only, a dataset comprised of 474,339 presence/absence observations and 64,881 observations with a non-zero density. Each model used a suite of 31 predictors (Table 3.5) to explain variation in either the presence of fish ('presence' models) or the density of fish when present ('density' models).

PRESENCE MODELS

The presence BRT model used an optimal 6850 trees to achieve an AUC value of 0.85, an indication of 'excellent' model performance (Figure 3.9). The average difference between the predicted and observed probability of occurrence was MAE=0.18 and RMSE=0.29. The majority of errors were positive (86.4%) and less than MAE, meaning that the model frequently overestimated the probability of presence. Negative errors were less frequent (13.5%) but their magnitude tended to be larger, 98% of the negative errors were greater than MAE.

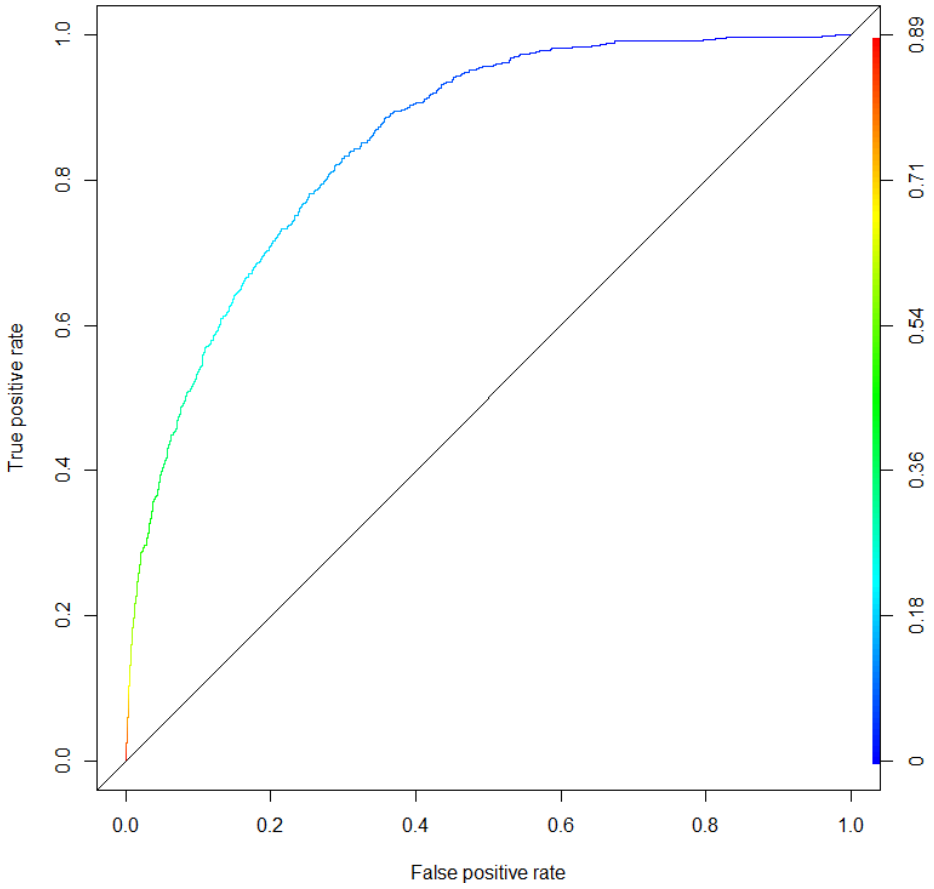

Figure 3.9. Receiver operating characteristic (ROC) curve for the 'presence' boosted regression tree (BRT) model. Color indicates the binary classification threshold value that yields the true/false positive rate at a given point along the line.

Variable importance analysis indicated that analysis cell depth was the most important predictor, followed by offset and salinity (Figure 3.10). The predictors prioritized for mixed model analysis, site, season, and habitat, varied in their relative importance. Season and site were moderately important, ranking in positions 5 and 6 respectively, however habitat zone ranked last. Marginal plots of the three most important predictors, depth, offset, and salinity, showed that the probability of occurrence increased with depth until approximately 75m and was highest at low offset values, indicating the analysis cell was near the seafloor (Figure 3.11). The salinity predictor indicated higher

probability of presence at higher salinities, especially around 35.5 ppt, though this effect may be overemphasized due to the limited range of salinities encountered during sampling (Appendix Figure C.1).

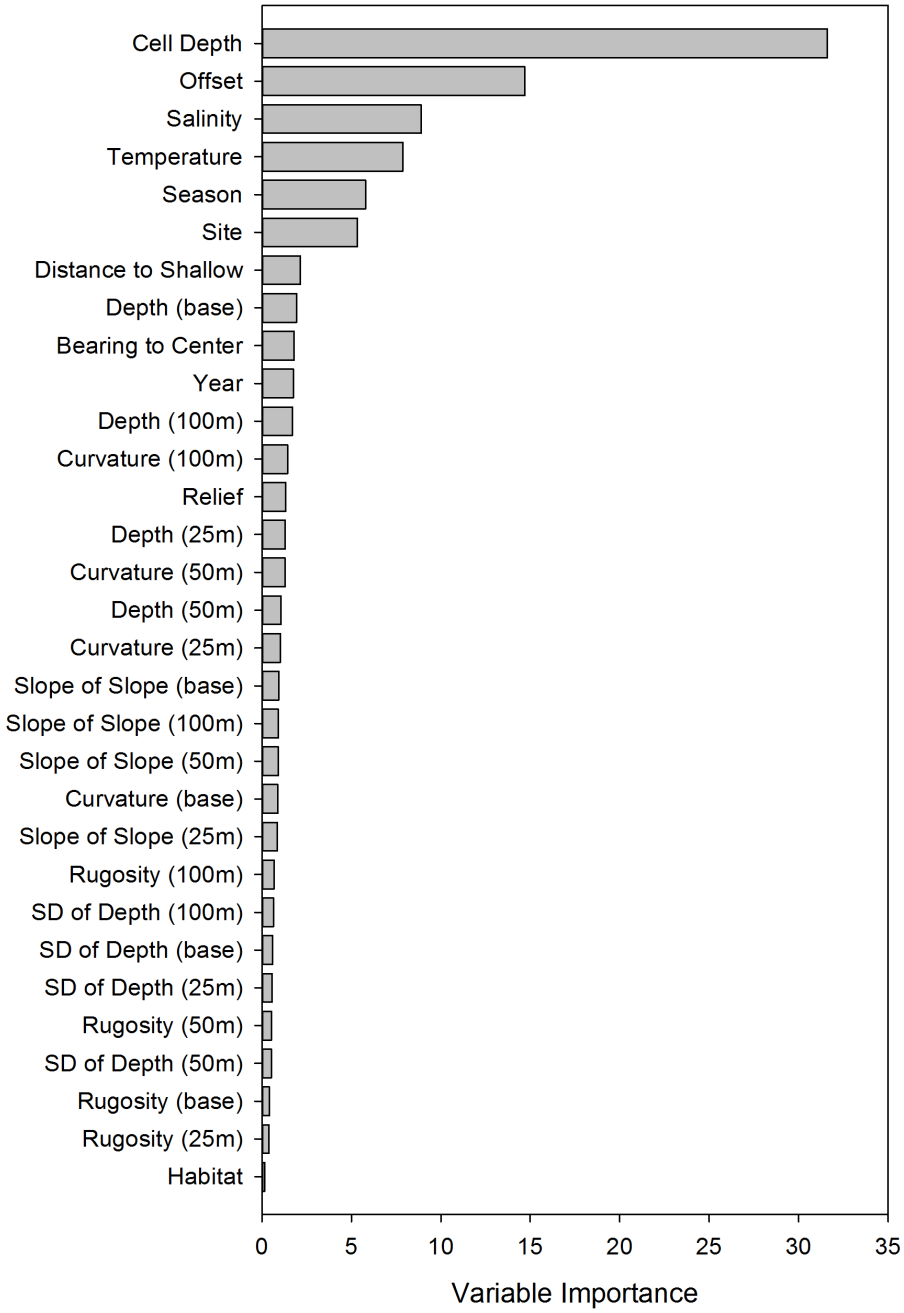

Figure 3.10. Relative variable importance for predictors in the presence boosted regression tree (BRT) model. Variables are defined in Table 3.5.

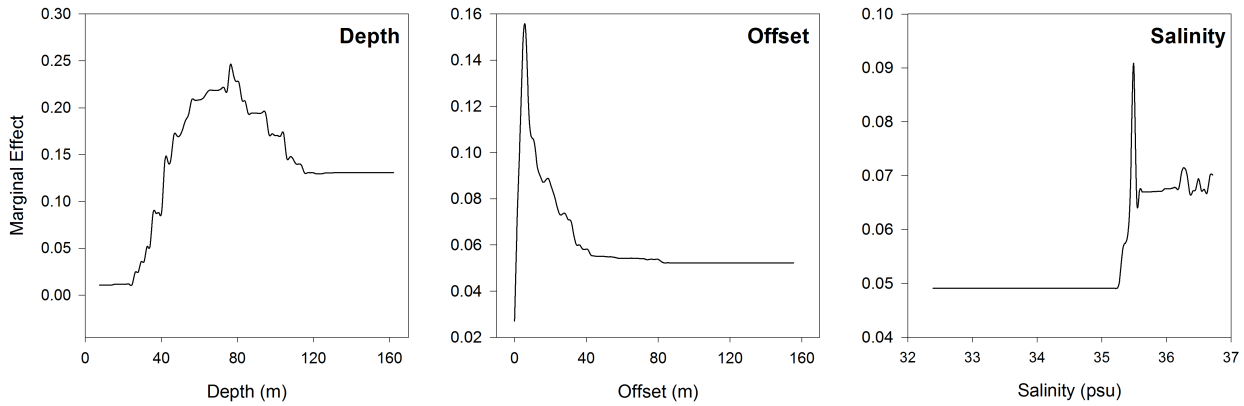

Figure 3.11. Partial plots displaying the marginal effect of the top three most influential variables from the presence boosted regression tree (BRT): cell depth, offset, and salinity. Marginal effect is a relative measure, with higher values indicating a higher probability of presence.

The presence RF model achieved a comparable AUC to the BRT method, 0.87, indicating it also achieved 'excellent' performance (Figure 3.12). The average difference between the predicted and observed probability of occurrence was MAE=0.27 and

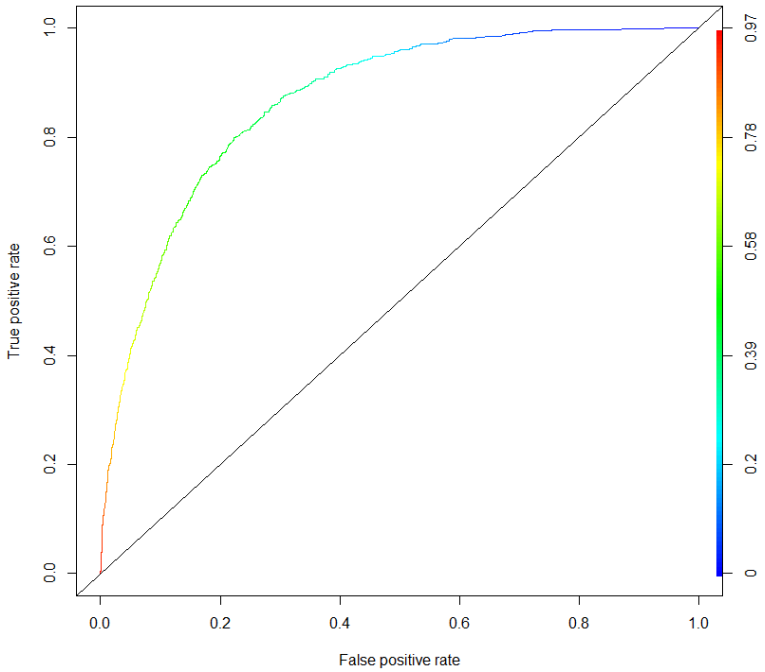

Figure 3.12. Receiver operating characteristic (ROC) curve for the presence random forest (RF) model. Color indicates the binary classification threshold value that yields the true/false positive rate at a given point along the line.

RMSE=0.89. The majority of errors were positive (85.5%) and less than MSE, meaning that the RF model more commonly over-predicted the probability of occurrence. The majority of the less-frequent negative errors were greater than MSE (64%). Variable importance analysis of the presence RF model indicated cell depth was the most important predictor, followed by offset and temperature (Figure 3.13).

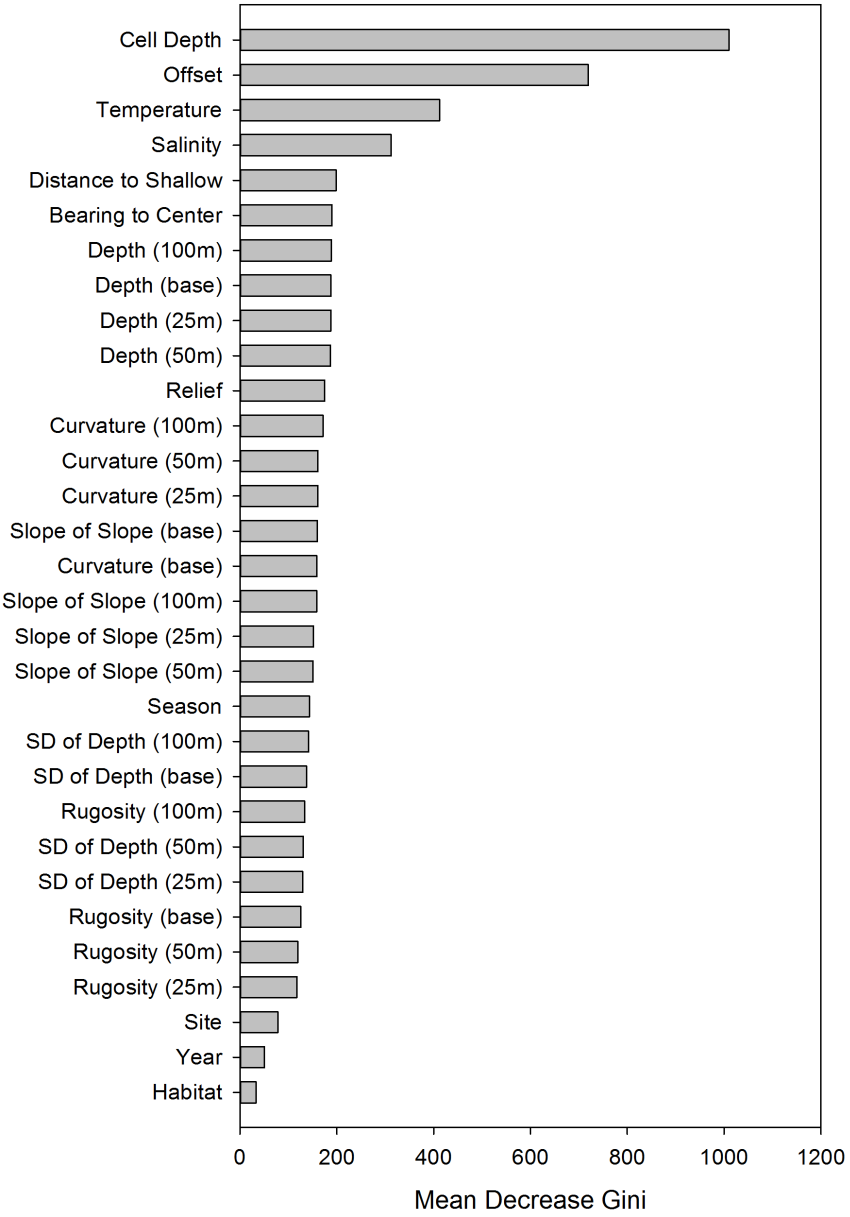

Figure 3.13. Relative variable importance for predictors in the presence random forest (RF) model. Variables are defined in Table 3.5.

Site and habitat were two of the three least important predictors for the RF presence model, while season was marginally more important, ranking 20th out of the 31 predictors. Marginal plots of the three most important variables, depth, offset, and temperature strongly agreed with those produced by the BRT model (Figure 3.14). Probability of presence increased to a depth of approximately 75 m, then decreased slightly. Low offset values showed the highest probability of presence, followed by a steady decline beyond approximately 10 m. Finally, the probability of presence appeared to generally decline with increasing temperature.

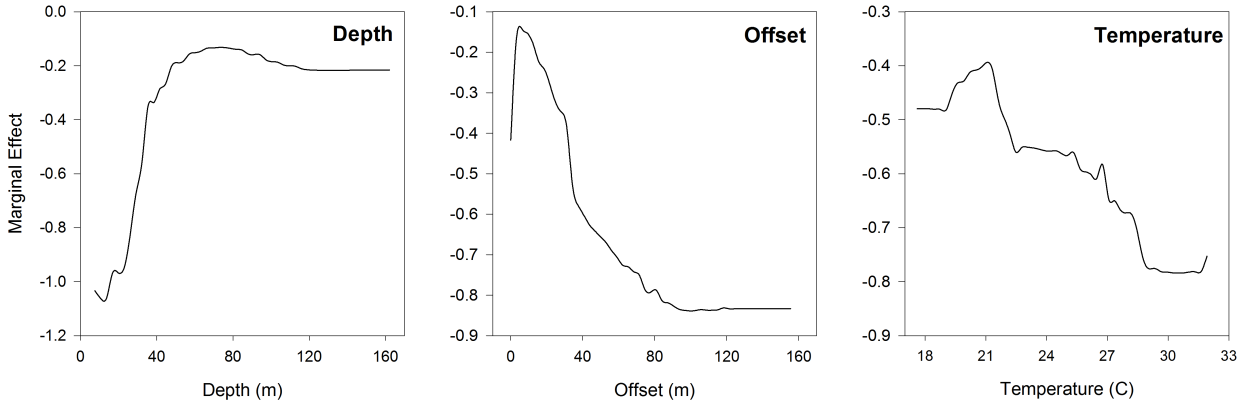

Figure 3.14. Partial plots displaying the marginal effect of the top three most influential variables from the presence random forest (RF): cell depth, offset, and temperature. Marginal effect is a relative measure, with higher values indicating a higher probability of presence.

Density Models

Observations with a non-zero density made up 13.7% of the total dataset collected at the natural sites. When classified into four classes based on the head/tails scheme, 67.2% had 'very low' density, 24.3% 'low', 6.8% 'medium', and 1.7% 'high' density (Table 3.9). It should be noted that classification cutoffs were not biologically based, rather solely defined by the data structure.

Table 3.9. Breakdown of the four density classes derived from the 'head/tails' classification procedure used for both density ML models. Percentage refers to the percent of cells with a density value recorded at the natural sites.

Class	Density (fish m^{-3})	Number	Percent of Observations
Very Low	<0.006	43,606	67.2
Low	0.006-0.014	15,767	24.3
Medium	0.014-0.026	4,436	6.8
High	>0.025	1,072	1.7

The multi-class density BRT used an optimal 3,331 trees to achieve a classification error rate of 28.6%, a multiclass AUC of 0.55, and an adjusted Rand index (ARI) of 0.16. Both the AUC and ARI suggested poor model performance. The average difference between the predicted and observed density class was MAE=0.36 and RMSE=0.73. The majority of prediction errors were negative (88%), meaning the model tended to predict low density classes. Two of the top three most important variables were the same as the presence BRT model, depth and offset (Figure 3.15). Temperature was the second most important variable. Of the variables examined with mixed models, season was the most important. Due to the poor model performance, marginal plots were not generated. At best, the marginal plots would be of little use because the variables provided a limited explanation of the variation in fish density, and at worst could provide inaccurate information or lead to misleading interpretations.

The multi-class density RF achieved a classification error rate of 48%, an ARI of 0.13, and a multiclass AUC of 0.68. Together, these model performance measures suggested poor model performance. The average difference between the predicted and observed density class was MAE=0.78 and RMSE=1.24. Contrary to the density BRT, the majority of prediction errors for this model were positive, meaning the model tended to predict higher density classes than observed. Variable importance analysis indicated a more balanced

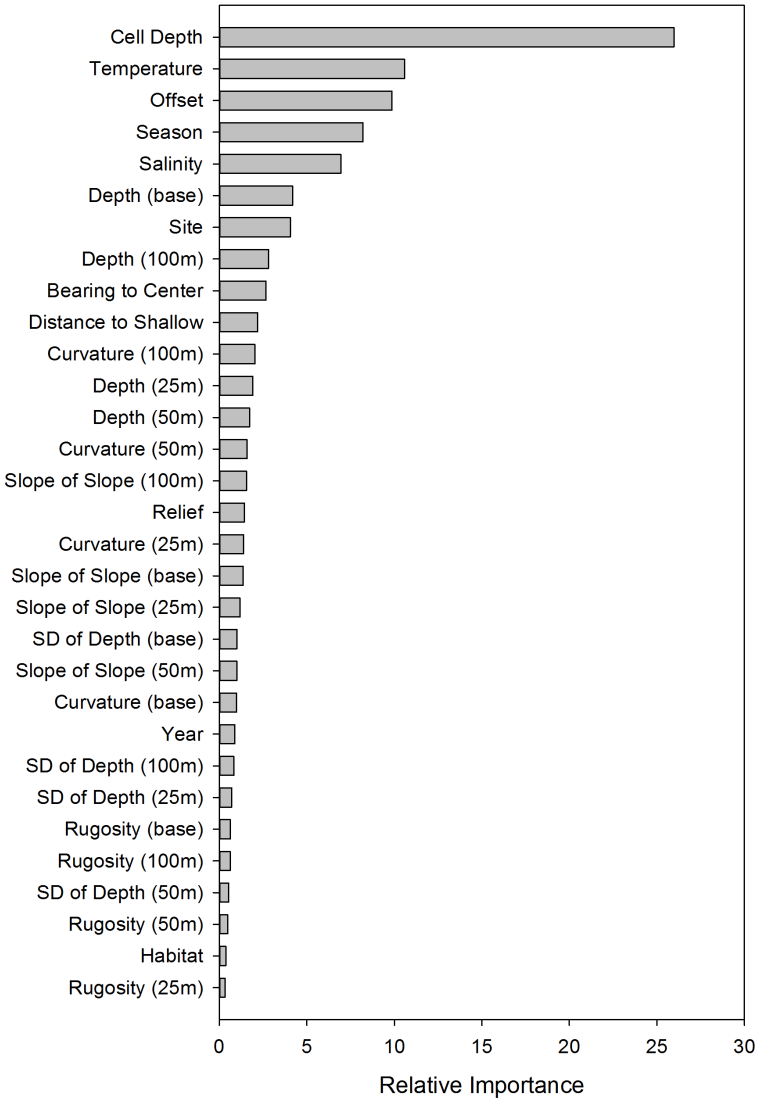

Figure 3.15. Relative variable importance for predictors in the density boosted regression tree (BRT) model. Variables are defined in Table 3.5.

influence of predictors, however the most influential were cell depth, offset, and the distance to the shallowest point on the bank (Figure 3.16). Site, season, and habitat zone were some of the least important predictors to the model, all located within the five least important predictors. Marginal plots were not generated due to the poor model performance.

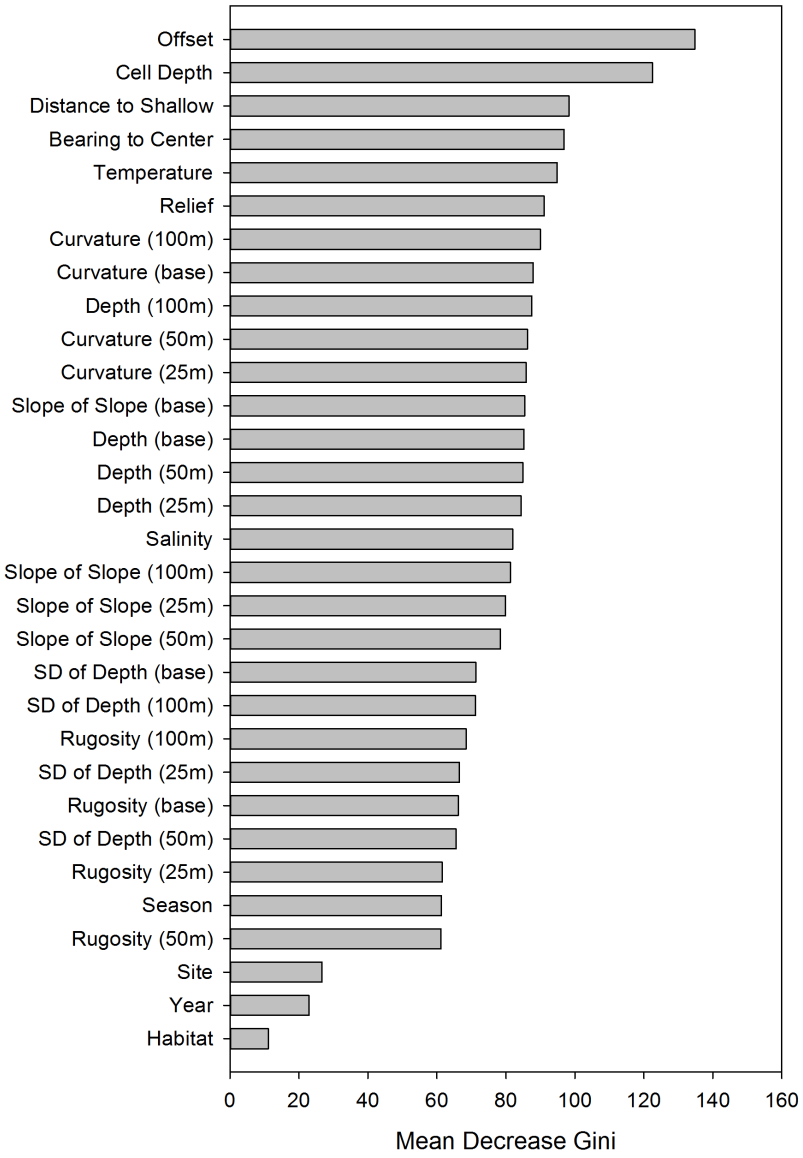

Figure 3.16. Relative variable importance for predictors in the density random forest (RF) model. Variables are defined in Table 3.5.

Near-Bottom Analysis

The near-bottom cells within 20 m of the seafloor accounted for 29% of the 474,339-presence/absence observations from natural sites and 56% of the 64,881 non-zero density observations. Density classes were redefined based on these near-bottom cells (Table 3.10). As before, the density classifications were defined based upon data structure,

not biological reference points. The same suite of 31 predictors as used with the full water column ML models was used to model the presence and magnitude of near-bottom density (Table 3.5).

Table 3.10. Breakdown of the four density classes derived from the "head/tails" classification procedure used for both near-bottom "density" ML models, based on cells located within 20 m of the seafloor.

Class	Density (fish m^{-3})	Number	Percent of Observations
Very Low	<0.010	31,936	87.3
Low	0.010-0.026	3,878	9.4
Medium	0.026-0.203	751	2.0
High	>0.203	24	0.06

Based on AUC, the RF model performed marginally better for the presence/absence of a density value within 20m of the seafloor, though both achieved good predictive performance (Table 3.11). However, the other model evaluation parameters, MAE, RMSE, and error rate, were marginally worse for the presence RF model relative to the presence BRT model. Offset and temperature were the two most important variables in both models. Both models tended to overestimate the presence of a density value (74% of errors), but the majority of these errors were smaller than the MAE.

Table 3.11. Model evaluation metrics for the four bottom-focused ML models, fit using only data within 20m of the seafloor. MAE: mean absolute error. RMSE: root mean square error. AUC: area under the receiver operating characteristic curve (presence models) or the multi-class version (Hand and Till 2001) for density models. ARI: adjusted Rand index.

Response	Method	MAE	RMSE	Error Rate	AUC	ARI
Presence	BRT	0.299	0.382	0.206	0.799	-
	RF	0.355	0.403	0.221	0.826	-
Density	BRT	0.139	0.423	0.118	0.499	0.014
	RF	0.159	0.447	0.140	0.494	0.114

Based on all but one of the various summary statistics for the multiclass density models, the BRT model was superior (Table 3.11). However, the ARI was very low (0.01) and a closer examination of model predictions revealed that the model was extremely biased towards predicting the lowest density class (99.6% of model predictions). Though somewhat complicated by the multi-class generalizations, the AUC values for both near-bottom density models indicated poor performance on par with random chance.

DISCUSSION

Hydroacoustic studies centered on reef fishes in the northwest Gulf have predominantly focused on the distribution of biomass associated with artificial structures, both standing and toppled oil and gas platforms (Stanley and Wilson 1996, 1997, 2000a, 2000b, 2003, Wilson et al. 2003, 2006, Boswell et al. 2010b, Harwell 2013, Simonsen 2013). Natural hard-bottom reef habitat has received considerably less attention even though it has been shown that fish exhibit very different distributions at natural banks relative to artificial structures (Wilson et al. 2003, 2006, Clark et al. 2014). This study found that mean volume backscatter (MVBS), probability of presence, and fish density all differed based on the interactive effects of study site, season, and habitat zone. However, these three factors were shown to generally be less important than water column position or physical factors for presence or biomass prediction purposes.

To my knowledge, this study represents the first fishery acoustics surveys of Bright, McGrail, and Jakkula banks, though extensive acoustic surveys have been conducted in the northwest Gulf at the Flower Garden banks (FGB; Wilson et al. 2003, Clark et al. 2014) and Sonnier bank (Wilson et al. 2006). MVBS values reported from Sonnier bank depended on

depth, but generally agreed with average values observed at natural banks during this study (Wilson et al. 2006). Similarly, average fish densities recorded during previous studies at the FGB were similar to those observed during this study, around 0.005 fish m^{-3}, depending on habitat (Wilson et al. 2003, Clark et al. 2014). It is encouraging to see that the sites surveyed during this study show similar fish densities and acoustic biomass to "one of the least impacted, thriving coral reef ecosystems in the western Atlantic and Caribbean region" (Clark et al. 2014). The relative inaccessibility of the Louisiana-Texas shelf edge banks, a product of their far offshore location and relatively deep structure, may contribute to the limited direct impacts to these features.

Both Wilson et al. (2003) and Clark et al. (2014) reported decreasing fish densities with increasing habitat zone depth (called 'terraces' by Wilson et al. (2003)). However, I found higher densities associated with a deeper habitat, the deep coral zone, relative to the other natural habitats. Interestingly, this deep coral zone was the second-most dense recorded by Clark et al. (2014) at the FGB. This discrepancy may be due to differences in habitat zones found at the FGB relative to the banks surveyed in this study. Both FGB possess much more developed coral reef habitat than the sites in this study (Bright, McGrail, and Jakkula) due their shallower crests (Schmahl et al. 2008). The crests of the FGB are characterized by the coral reef habitat zone (not to be confused with the coral community zone), which is not found at Bright, McGrail, and Jakkula. Therefore, the fact that the shallowest habitat zone did not display the highest density of fishes in this study may simply be due to the fact that the shallow coral reef habitat, with which high densities were associated, does not exist at the sites I surveyed.

The interacting effects of site and habitat zone with respect to MVBS, probability of presence, and density are not without precedent. Clark et al. (2014) reported significant fish density differences between the East and West FGB overall and within habitats, but do not discuss potential explanations. As reported in this study, within-habitat differences between banks may be further complicated by seasonal differences as well. While this statistically significant three-factor interaction was consistently observed, the results must also be considered with regard to biological significance. The sheer number of observations involved in testing these effects (574,068 for MVBS and presence, 80,213 for density) mean that the power of the tests are very high, allowing small differences to be very significant. Therefore the specific significance relationships between sites, habitats, and seasons must be interpreted with care, keeping in mind the bigger biological picture. The high inherent variability of acoustic data (Simmonds and MacLennan 2005) and patchy nature of fish distributions suggest that general data trends may provide more reliable interpretive opportunities.

A general pattern that emerged from this study was that MVBS and density tended to be as high, or higher, at the artificial reef habitats than the natural habitats. Additionally, the area directly adjacent to an artificial reef structure generally showed higher MVBS, probability of presence, and fish density than the surrounding sediments. Similar relationships of higher MVBS and fish density at artificial structures were observed in two previous studies that specifically compared standing and toppled platform structures to natural reef habitats (Wilson et al. 2003, 2006). The differences in fish distribution parameters between artificial and natural banks may be due to the way relief is expressed at each reef type. While the natural banks examined in this study exhibit up to 75 m of

vertical relief, this relief is spread out over multiple square kilometers (Gardner and Beaudoin 2005). Conversely, artificial reefs formed from production platforms produce vertical relief with a very small footprint and no gradient, leading to a structure that is essentially vertical. This means that fish at natural banks are able to spread out along the reef surface, while those at artificial structures concentrate around the central structure and distribute vertically. Basically, the 'structure loving' reef fish distribute according to the distribution of hard substrate, horizontally at the broad natural banks, or vertically along the extent of artificial structure. The concentration of fishes around a central structure leads to a rapid decline in fish density and biomass with distance from standing and toppled platforms and artificial reef structures, a phenomenon that has been well documented (Stanley and Wilson 1996, 1997, 2000a, 2000b, 2003, Wilson et al. 2006, 2003, Boswell et al. 2010b, Shipley and Cowan Jr 2010, Harwell 2013, Simonsen 2013). In fact, the assumed horizontal area of influence of the artificial reef in this study of 250 m was generous, distances reported on the order of tens-of-meters are not uncommon (Stanley and Wilson 1997, Wilson et al. 2006, Boswell et al. 2010b). The small footprint and high relief of the artificial reef examined may induce higher local biomass and densities, therefore contributing to the discrepancy in MVBS and density observed between the artificial structure and natural banks in this and previous studies.

The different distribution of fish in the water column, based on reef type, has important implications with regard to the acoustic sampling method used. When an acoustic pulse is transmitted, the wavefront propagates in a spherical manner. When the pulse reaches a boundary, such as the seafloor, the spherical propagation pattern means that as the center of the beam interacts with the boundary, there will be an unsampled area

between the wavefront and the boundary that increases in size towards the edges of the acoustic beam. This near-bottom area is termed the 'acoustic dead zone' (Ona and Mitson 1996), the extent of which depends on the seafloor depth, acoustic pulse duration, sound speed, and transducer beam width (Mello and Rose 2009). In this study, the dead zone was on the order or 0.5 to 1 m. Based on the previous discussion of fish distribution throughout the water column, the fact that reef fish are generally found directly associated with, or close to the seafloor at the natural banks means that a large proportion of fish biomass may be missed or underestimated during acoustic surveys in these systems. This near-bottom bias could also contribute to the discrepancy in MVBS and density observed between the artificial structure and natural banks in this study.

The predictive models based on acoustic surveys from the natural banks indicated that variables associated with water column position, offset and analysis cell depth, were generally the most important for determining fish presence and density. As expected, fish were much more likely to be present near the seafloor, and thus the reef structure, with maximum likelihood at approximately 10 m. The increase in probability of occurrence to a depth of approximately 75 m is likely due to the depths covered by the bank bathymetry. Deeper analysis cell depths were more likely to be close to the bank surface, leading to the higher probability of presence associated with a low offset. Previous acoustic surveys of natural banks in the northern Gulf agree that depth has a significant relationship with fish presence and density (Wilson et al. 2003, 2006, Clark et al. 2014). Additionally, these surveys supported the finding that fish biomass is concentrated near the seafloor, with Clark et al. (2014) reporting up to 90% of fishes observed within 10 m of coral reef habitat.

Given that the fish assemblages present at these features are primarily reef-associated, a close relationship with benthic habitat is expected given their affinity for structured substrate as opposed to the unstructured pelagic environment.

The two ensemble modeling methods used, boosted regression tree (BRT) and random forest (RF), did not show dramatic differences with regard to model performance; both performed well when modeling fish presence and subpar with density. The relative importance of variables did differ slightly between the two methods, though most differences were associated with low-importance variables. Differences in variable importance are likely due to the different way each model is assembled, as the final marginal effects of important variables were very similar between both model types.

Predictive models in this study performed much better for fish presence than densities. This is in contrast to a study by Costa et al. (2014) that developed similar models that achieved good predictive performance for the density of large fish, but poorer performance for the occurrence of large fish. Costa et al. (2014) divided fish records into size classes, something that may have improved the performance of models in this study by allowing different relationships between variables and fish depending on fish size. Fish distributions are well known to be patchy and densities to be positively skewed (Simmonds and MacLennan 2005, Woillez et al. 2009). These factors make prediction difficult by introducing high inherent variability and limiting the occurrences of valuable high-density observations to learn from. Nevertheless, these models demonstrate a step towards potentially providing managers with basic fisheries information at sites or features where

the seafloor has been mapped, but fish distribution information is lacking. Such information could help guide future survey efforts, identify areas of potential conservation value, or predict changes in fisheries resources given habitat changes.

The results of this study provide an assessment of fish biomass and density distributions at natural banks in the northern Gulf that has not previously been described. Fish biomass, occurrence, and density varied significantly in accordance with the interactive effects of site, season, and habitat zone. However, predictive models indicated that these factors were not as important as water column position for determining the presence or density of fishes. In accordance with previous studies that compared fish biomass and density between natural and artificial reefs (Wilson et al. 2003, 2006), equal or higher localized densities and biomass were observed adjacent to artificial structure as opposed to natural banks, likely due to the orientation of reef structure.

Hydroacoustics provide a powerful tool to survey and monitor these valuable, but largely inaccessible, reef systems. The acoustic biomass values and fish densities observed at the three shelf-edge banks during this study were comparable to those described at the East and West FGB, both in magnitude and basic distribution. This is important given the proposed expansion of the Flower Garden Banks Nation Marine Sanctuary (FGBNMS) to additional features in the northwest Gulf (USDOC et al. 2012). The results of this study and the video surveys previously discussed (Chapters 1 and 2) suggest that these presently unprotected habitats support very similar fish assemblages at comparable densities to the currently protected FGB, warranting their inclusion into the FGBNMS.

Future standardized surveys of additional natural banks in the area would allow for broader conclusions to be drawn about the fisheries resources present at these features, as

well as allow for further development of predictive models for the region that could be used for both resource management and conservation purposes. Comprehensive, high resolution habitat and substrate maps, such as those available at the FGB, would be especially useful for interpreting fish distribution surveys at additional banks and provide a better understanding of whether habitat associations are consistent between banks. The lower relief hard-bottom ridges and rocky outcroppings located between banks may be of particular interest for future surveys because it has been proposed that these areas act as 'habitat highways', linking the seemingly isolated banks to one another (Schmahl et al. 2008, USDOC et al. 2012). Longer-term monitoring of features of interest would be beneficial to document the effect of management actions, protective measures such as the proposed expansion of the FGBNMS, and natural or anthropogenic disasters such as hurricanes or oil spills.

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CHAPTER 4: STABLE ISOTOPE ECOLOGY OF RED SNAPPER (*LUTJANUS CAMPECHANUS*) AT NORTHWEST GULF OF MEXICO BANKS

INTRODUCTION

The shelf-edge banks in the northwest Gulf of Mexico (Gulf) host unique reef ecosystems in an area otherwise dominated by low relief terrigenous silt, mud, and sand sediments (Wilson et al. 2006). Natural hard bottom habitat is estimated to cover approximately 2700 km^2 in the northwest Gulf (Parker Jr. et al. 1983). However, this natural hard substrate has been supplemented by the addition of artificial hard substrate and structured habitat in the form of standing, toppled, and cut platforms since 1947, minimally increasing hard substrate surface area, but drastically altering the availability of structured habitat throughout the water column (Stanley and Wilson 1990, 1991, 1997). Though few studies have directly compared fish assemblage characteristics between the two reef types (natural and artificial), both have been shown to support a large associated fish biomass. While both reef types may support high numbers of reef fish, differences in absolute abundances, spatial distributions, and fish assemblages have been reported between the two types (Rooker et al. 1997, Wilson et al. 2003, 2006). Characteristic reef fish assemblages have also been described within a given reef type, with assemblage zonation at the natural banks determined primarily by depth and benthic habitat type (Boland et al. 1983, Dennis and Bright 1988) and zonation at artificial structures driven by the bottom depth where the structure is located (Gallaway et al. 1981, Gallaway and Lewbel 1982, Stanley and Wilson 2000). Many of the reef fish species that associate with

both types of habitat are valuable commercial and recreational species, including but not limited to: red snapper (*Lutjanus campechanus*), greater amberjack (*Seriola dumerili*), and a variety of grouper species (*Mycteroperca spp.*).

With two radically different reef types utilized by many managed reef fish species in the northwest Gulf, it is important to both evaluate the functional role of the two reef types in the life history of these valuable species and to incorporate any differences into the management process. Given the recent progression of fisheries management from single-species based to ecosystems-based methods, understanding the biological and environmental interactions of target species within a system is of utmost importance (Pikitch et al. 2004). A key aspect of these interactions is the trophic ecology of the target species, which provides insight into energy flow through a system and the niche a particular species fills (Layman et al. 2007b). For example, Simonsen (2013) reported a high overlap in the diets of red snapper between geographically similar natural and artificial reefs, with less than 5% of total diets exclusive to a particular reef type. Similarly, neither the trophic niche breadth defined by stable isotopes, nor nutritional condition based on tissue caloric density, differed between natural and artificial reefs, suggesting that red snapper biomass accumulations at artificial structures were not driven by unique trophic opportunities, a finding consistent with other red snapper diet analyses (McCawley et al. 2006, McCawley and Cowan 2007, Wells et al. 2008b). However, a concurrent study to this one found that diets of red snapper did differ between natural and artificial reefs, with diets at natural banks composed primarily of reef-dependent prey species, while diets at artificial reefs were either pelagic or soft-bottom associated organisms (Schwartzkopf 2014).

Stable isotope analysis is a widely used method to analyze the structure of food webs and to provide a useful means of examining temporal and spatial integrated trophic relationships between individuals or communities (Layman et al. 2012). The most commonly employed elements in marine food-web analysis are nitrogen (N), carbon (C), and occasionally sulfur (S). The ratio of ^{15}N to ^{14}N (denoted relative to a standard as $\delta^{15}N$) provides information about the trophic level of an organism due to the stepwise enrichment of $\delta^{15}N$ at each trophic transfer (Minagawa and Wada 1984, Peterson and Fry 1987, Post 2002, Fry 2006). The ratio of ^{13}C to ^{12}C ($\delta^{13}C$) can be used to identify basal carbon sources of a system, as $\delta^{13}C$ varies among primary producers, but undergoes minimal fractionation through trophic transfers (DeNiro and Epstein 1981, Peterson and Fry 1987, Post 2002, Fry 2006). Individuals or species in isotope analyses are most often plotted in a bivariate fashion based on their $\delta^{15}N$ and $\delta^{13}C$ values, a representation referred to as isotope space, niche space, trophic space, or isotopic niche (Layman et al. 2007a, 2012). By comparing the relative position of members in this isotope space, one is able to make inferences about food web structure. However, stable isotopes do not provide direct information about functional relationships or feeding pathways between individuals; rather they provide a sum representation of all energy pathways leading to an organism (Paine 1980, Layman et al. 2007a, 2012). As such, isotopic variation of a consumer is not necessarily representative of dietary variation; food items may also show isotopic variation in space or time (Araújo et al. 2007). Therefore, stomach content analyses are recommended to complement isotopic information to provide more comprehensive and more definitive interpretations (Peterson 1999, Layman and Post 2008, Layman et al. 2012).

Isotope analyses began with largely qualitative analyses of relative isotopic values (Haines and Montague 1979); however, a variety of new analytical methods allow for increasingly quantitative examinations of a variety of fundamental ecological concepts, such as defining the trophic position of an organism, the resource pools of a food web, the degree of trophic variability within a population, and relative positioning of consumers within a food web (Layman et al. 2012). Bearhop et al. (2004) and Layman et al. (2007a, 2007b) expanded the traditional isotopic analysis procedures of examining mean δ-values to an examination of isotopic variation within a species or community, operating under the assumption that greater variation in isotopic signatures was related to a more complex food web. Layman et al. (2007a) proposed several quantitative metrics related to the extent and positioning of individuals or species in isotope space that could be related to fundamental aspects of trophic structure. To address several caveats associated with these community and niche metrics, such as sensitivity to sample size and lack of variability propagation, Jackson et al. (2011) developed modified versions using standard ellipses and Bayesian methodology, termed stable isotope Bayesian ellipses in R (SIBER), as an effective means of examining trophic variability.

The goal of this chapter is to evaluate the relative position and extent of red snapper isotopic niches at three natural banks and one artificial reef in the northwest Gulf, specifically to evaluate the effect of habitat type and availability on red snapper trophic ecology. Additionally, this work seeks to supplement a concurrent diet study (Schwartzkopf 2014) and to evaluate the relationship between traditional short-term diet information with longer-term isotope information. It is hypothesized that fishes at sites with a larger

variety of habitats available will have a wider variety of prey options, thus exhibit a greater isotopic niche extent. Predominant diet items are expected to influence relative isotopic position, with higher trophic-level diets leading to higher trophic-level consumers.

METHODS

I examined the stable isotope composition of red snapper associated with three shelf-edge banks and one artificial reef in the northwestern Gulf of Mexico. The three banks (Bright, McGrail, and Jakkula) are located on the Louisiana-Texas shelf edge, while the artificial reef is closer to shore on the Louisiana-Texas shelf in the East Cameron Artificial Reef Planning Area (Figure 4.1).

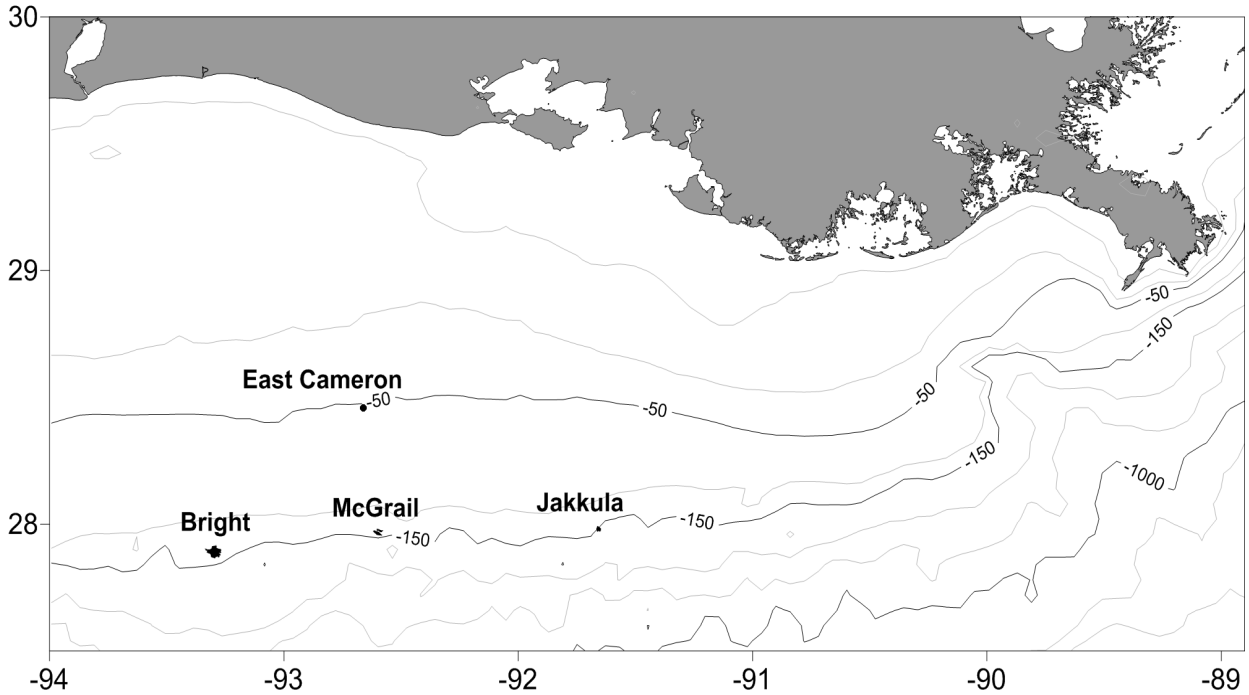

Figure 4.1: Sampling locations for fish collection at one artificial reef (East Cameron) and three shelf-edge banks in the northwestern Gulf of Mexico.

STUDY AREA

The Louisiana-Texas shelf-edge banks are a result of diapiric salt intrusions uplifting bedrock that is subsequently capped by carbonate reef structure (Rezak and Bright 1983, Dennis and Bright 1988, Rezak et al. 1990). The banks used in this study rise from depths of 140-160 m, crest at depths of 30-50 m below the surface, and range in size from 4 to 20 km^2. The three sites selected (Bright, McGrail, and Jakkula) were chosen to effectively sample throughout the East-West Texas-Louisiana shelf-edge bank track. The term 'reef' is often used to describe these features in the sense that they represent underwater structure, though many do possess areas of biotic reef structure as well.

The artificial reef site I examined consisted of a mid-shelf toppled platform in the Louisiana Artificial Reef Program (LARP) East Cameron Artificial Reef Planning Area, hereafter the East Cameron (EC) site, located within an area of high acoustic backscatter and increased bathymetric relief relative to surrounding areas, discovered during a side-scan survey of the LARP planning areas (Cowan et al. 2007). The extent of natural hard-bottom in the EC planning area is the largest observed among the LARP areas (7,855 ha total). The local bathymetry is characterized by a gradual slope from 45-55 m, with the site of interest forming a shelf in the center approximately 4 m higher than the surrounding soft sediments, thought to be composed of slabs of lithified bottom sediment (Cowan et al. 2007).

SAMPLING PROTOCOL

Sampling was conducted twice quarterly between September 2011 and October 2013, as weather and scheduling permitted. Fishing sites were selected at semi-random points within each study site, with some assistance being provided by visual examination of hydroacoustic data as to the presence of fish.

Two types of gear were used during each sampling effort: vertical long lines and traditional single hook poles. Vertical long lines consisted of ten hooks, spaced approximately 0.5 m apart, extending on leads from a weighted main line. Each rig was composed of alternating size 6 and 9 circle hooks. Single pole rigs utilized a single hook, leader, and sliding egg weight. Bait for both types of gear consisted of squid (*Loligo sp.*) and/or chub mackerel (*Scomber japonicas*) pieces. The time of day at which fishing was conducted varied by site and sampling trip due to other sampling requirements and convenience. Two vertical long lines and up to four single poles were deployed at a time and fished for approximately two hours per site either until fifty fish were collected, or as weather and scheduling allowed. All individuals caught, excluding sharks, were tagged, numbered, and placed on ice until processed on board the vessel.

On-board fish processing for stable isotope purposes involved taking a small muscle tissue sample using a stainless steel scalpel, rinsed with deionized (DI) water between each individual. Epaxial muscle tissue was sampled from the left flank, above the pectoral fin of each fish and retained for analysis. Tissue samples were stored in sterile 20 ml glass scintillation vials at -18°C until return to the laboratory, where they were stored at -80°C. Tissue samples were dried at 60°C for 24 hours in a drying oven (model DX600; Yamato), and then homogenized with a ball-mill grinder. A sample of each individual ground tissue weighing between 1.0 and 1.5 mg dry weight was placed in a tin capsule, per the sample preparation guidelines supplied by the University of California, Davis Stable Isotope Facility (UCD-SIF). Samples were then sent to the UCD-SIF and analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). During analysis,

samples were interspersed with several replicates of at least two different laboratory standards selected to be compositionally similar to the tissue samples. The long-term standard deviation at the facility was 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$. Final isotopic ratios were reported relative to international standards, Vienna PeeDee Belemnite (V-PDB) for $\delta^{13}C$ and standard atmospheric N_2 for $\delta^{15}N$, calculated as:

$$\delta_{\text{sample}}(‰) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000$$

where R represents the ratio of heavy to light isotope.

DATA ANALYSIS

Stable isotope ratios were analyzed with both linear mixed models and the stable isotope Bayesian ellipses in R (SIBER) developed by Jackson et al. (2011). Given that fish size has the potential to confound stable isotope ratios, simple linear regressions of $\delta^{13}C$ and $\delta^{15}N$ on fish fork length were performed to examine whether such an effect existed for this dataset (Godley et al. 1998, Jennings et al. 2001, Sweeting et al. 2007a).

Values of $\delta^{13}C$ and $\delta^{15}N$ were compared between sites, seasons, and sexes with a multivariate analysis of variance (MANOVA) that included a fork-length covariate. MANOVA was chosen over multiple ANOVA procedures given the moderate correlation observed between $\delta^{13}C$ and $\delta^{15}N$ values during initial raw data examination. Seasons were defined as Winter (December, January, February), Spring (March, April, May), Summer (June, July, August), and Fall (September, October, November). All interactions were initially fit; however, the model was simplified through the removal of any effects that did not explain a significant portion of the variance. Least squares (LS) means were obtained

based on the 'reduced' model. Pairwise differences between LS means were examined for significance after Tukey-Kramer adjustment, given the multitude of potential comparisons being made.

The SIBER method (Jackson et al. 2011) was used to compute intraspecific isotope niche structure between sites, seasons, and size classes. Metrics of isotope niche structure based on the spread and extent of samples in $\delta^{13}C$-$\delta^{15}N$ space, such as those defined by Layman et al. (2007a), have frequently been used to compare between groups of an individual species or communities as a whole. However, these metrics are very sensitive to sample size and do not include any information about the natural variability within the observed system (Jackson et al. 2011). A similar area-based procedure, SIBER, has been shown to alleviate such shortcomings and thus was used to calculate descriptive metrics and statistically compare populations based on site, seasonal, and size class effects. Size classes were defined as seven 100 mm length bins based on fork length (FL) culminating in a 600 mm and greater category. This categorization scheme was chosen to facilitate comparison to a concurrent diet analysis (Schwartzkopf 2014).

SIBER is based on the standard ellipse, the bivariate analog to univariate standard deviation (Batschelet 1981). As compared to Layman's (2007a) convex hull area, defined by the most extreme values of a particular group and thus encompassing all group observations, the standard ellipse area (SEA) contains 40% of the data in a given group, regardless of sample size (Batschelet 1981). Ellipses can be rescaled to contain more or less of the data; however, relative size comparisons remain the same.

A corrected version of the SEA (SEA_c) has been shown to address the issue of population SEA underestimation from small sample sizes, while minimally influencing

large sample groups (Jackson et al. 2011). The SEA_c was calculated for each site, seasonal, or size class group (siar package, R) as defined relative to the SEA as:

$$SEA_c = -SEA(n-1)(n-2)^{-1}$$

In order to limit underestimation bias and maintain a sample size greater than 10 individuals per group (Jackson et al. 2011), site, season, and size class effects were analyzed separately (three, four-group analyses) rather than a cross-classified analysis.

A Bayesian approach was taken to identify significantly different groups in terms of SEA. The 'siber.ellipses' function in the R-package 'siar' was used to generate a distribution of Bayesian estimates for each site, season, and size class group, a procedure described in detail by Jackson et al. (2011). Essentially, a distribution of estimated SEA values for each group was generated that reflected the uncertainty associated with the sampling process, where larger uncertainty was associated with small sample sizes. Simulated values of group means (10^6) and covariance matrices were generated, from which the Bayesian standard ellipse area (SEA_B) was calculated. The estimated values were then plotted and compared probabilistically based on site, seasonal, and size class effects.

The relative positioning and extent of group SEA_c values were quantified by calculating the overlap between groups in a pairwise fashion. The area of overlap, in $‰^2$, was defined simply as the shared area encompassed by both standard ellipses being compared. To make this area more interpretable relative to the total area encompassed by the ellipses, the area of overlap was also presented as a percent of both standard ellipses being considered. Obviously, the degree to which ellipses overlapped depended on the proportion of the data they were scaled to contain. As mentioned prior, the SEA_c from

which overlap was calculated were not scaled and thus contained 40% of the data for their respective group, a consistent size used for all groups when examining site, seasonal, and size class effects.

RESULTS

A total of 636 red snapper (*Lutjanus campechanus*) tissue samples were collected and analyzed for $\delta^{13}C$ and $\delta^{15}N$ from four sites, three natural banks and one artificial reef. The most individuals were collected at the East Cameron artificial reef site (50.6%), followed by Bright bank (32.9%), Jakkula (12.4%), and McGrail (4.1%). Seasonally, the most individuals were collected during the summer months (42.7%), followed by spring (26.6%), winter (15.9%), and fall (14.8%). Sex ratios were almost equal between males (53.8%) and females (46.2%), however size class frequencies were dominated by the larger fish in size class 6 (>600mm, 41.2%), followed by size class 5 (400-500mm, 31.8%), class 4 (300-400mm, 19.8%), and finally class 3 (200-300mm, 7.2%). Size class frequencies were not consistent across sites. A higher proportion of size class 3 and 4 fish were caught at East Cameron and Bright relative to McGrail and Jakkula, which showed a higher proportion of size class 5 and 6 fish (Figure 4.2). There was no significant linear relationship between fish fork length and $\delta^{13}C$ ($p=0.98$) or $\delta^{15}N$ ($p=0.36$, Appendix D.1).

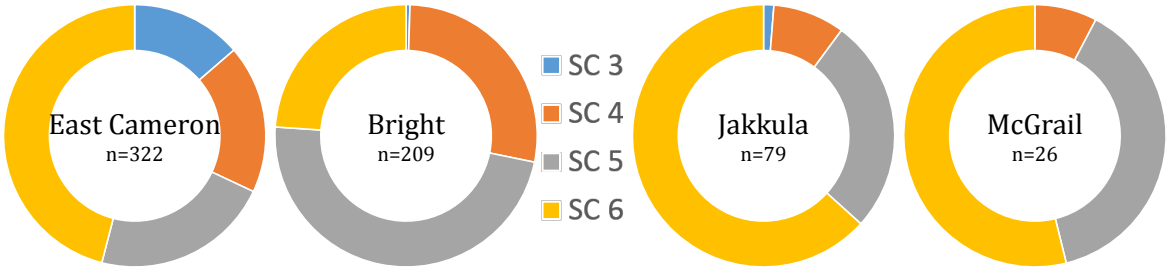

Figure 4.2. Size class (SC) frequency of red snapper, by site. Total number of fish sampled at each site is also noted.

When plotted in isotope space, the individual data points showed obvious site-related differences and a clear positive correlation between $\delta^{13}C$ and $\delta^{15}N$, overall and within site groups (Figure 4.3). Other potentially important factors, including year, season, and size class, showed less conclusive distribution patterns (Figure 4.4). Although a concurrent study indicated that the condition of these fish from varied by site, as defined by the Liver Somatic Index (LSI) and tissue caloric content (Schwartzkopf 2014), these indices did not appear to relate to either $\delta^{13}C$ or $\delta^{15}N$ values (Figure 4.5).

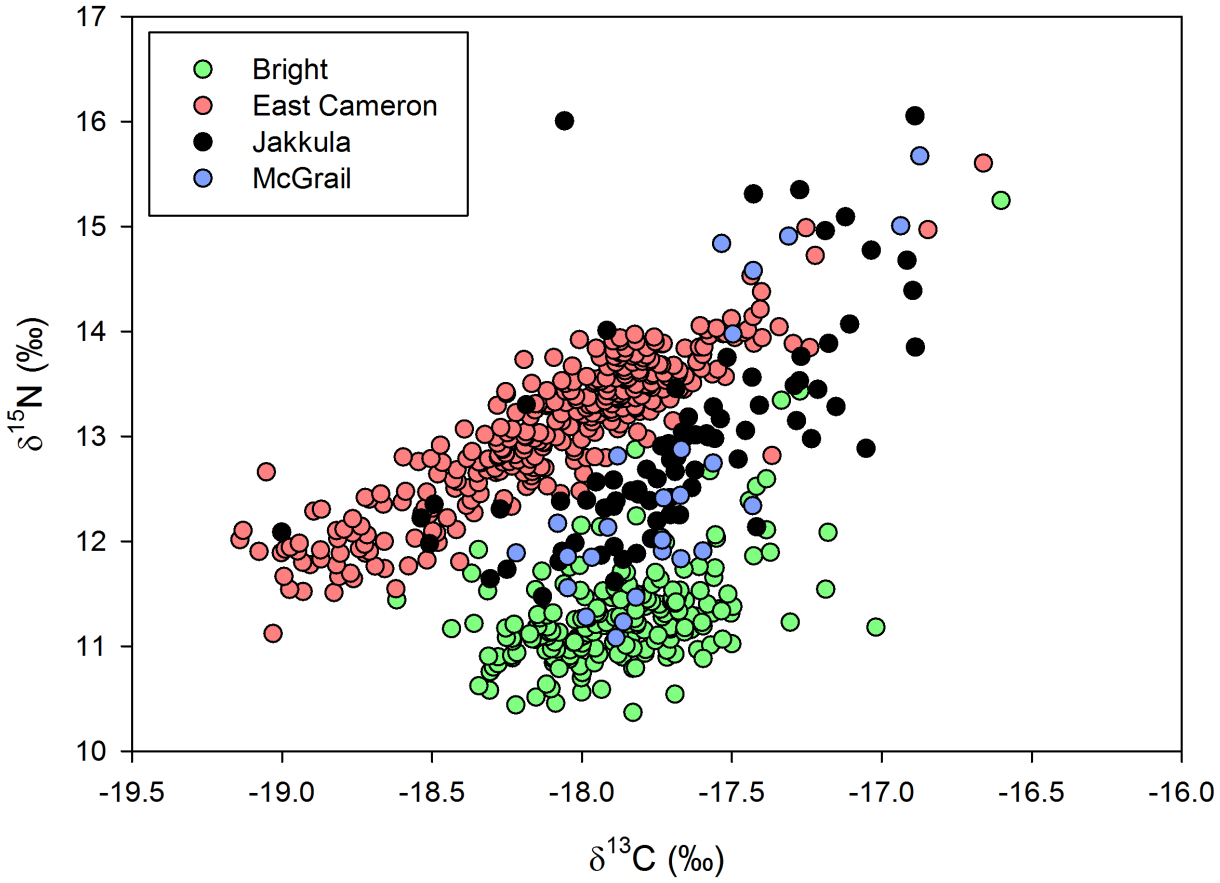

Figure 4.3. Individual red snapper plotted in isotope space, colored according to the site at which they were caught.

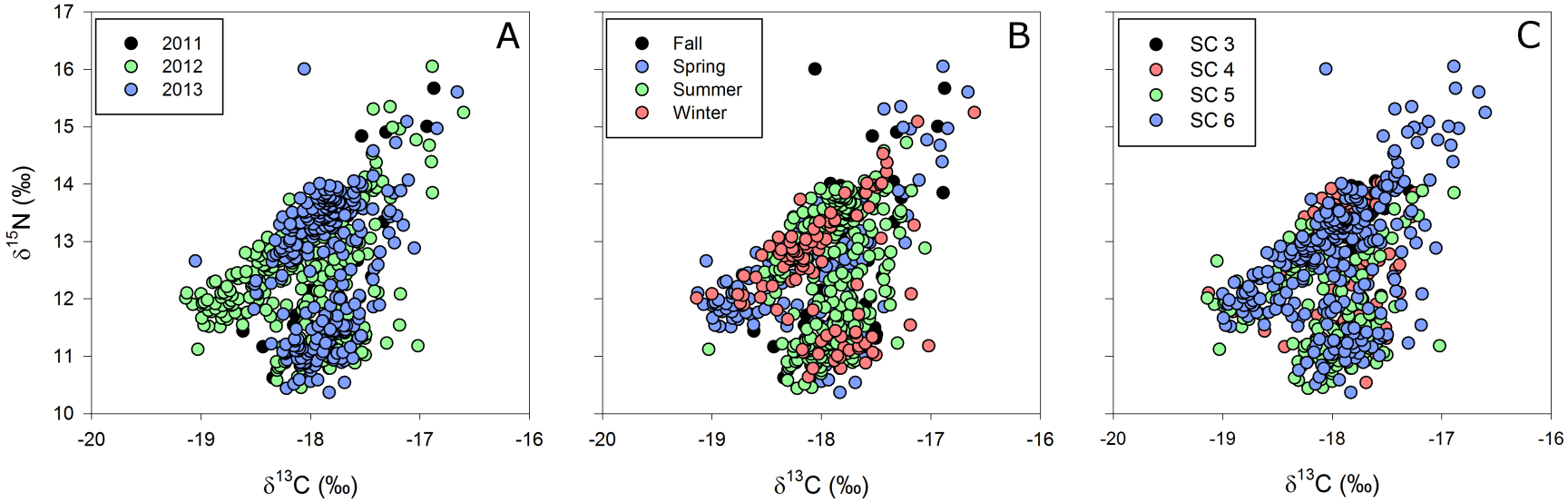

Figure 4.4. Plots of individual red snapper in isotope space, colored according to the (A) year and (B) season of capture, and (C) size class (SC) of the fish.

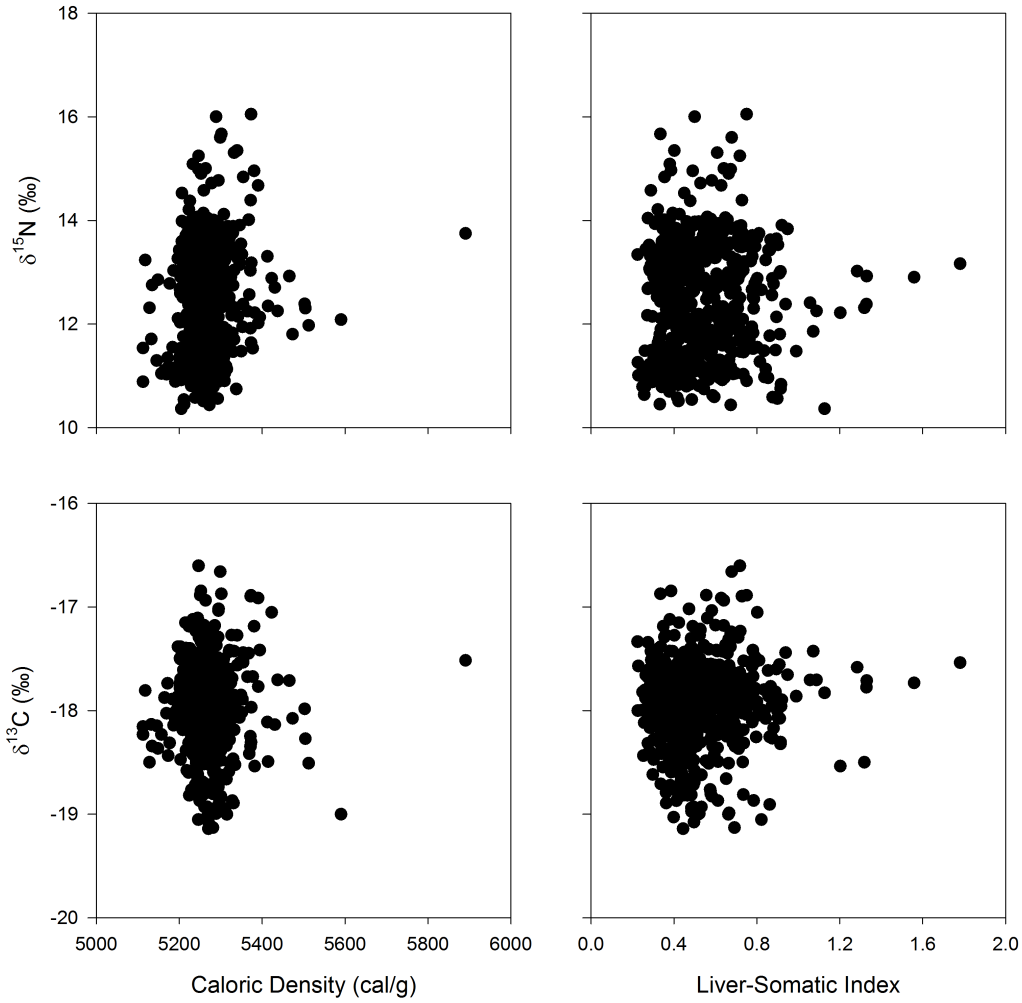

Figure 4.5. Plots of individual red snapper $\delta^{13}C$ and $\delta^{15}N$ relative to two condition indices, tissue caloric content and liver somatic index, obtained from a concurrent study (Schwartzkopf 2014).

MANOVA

The 'full' MANOVA model results indicated that all effects and interactions that did not include sex were significant (α=0.05, Table 4.1). After sex was removed from the model, the 'reduced' MANOVA showed that both the site and season main effects were significant, as was their interaction (Table 4.2).

Table 4.1. Results of 'full' MANOVA on $\delta^{13}C$ and $\delta^{15}N$. F-value and p-value reported correspond to the Wilks' Lambda statistic.

Effect	F Value	p-value
Site	230.00	<0.0001
Season	4.20	0.0003
Sex	0.45	0.64
Site*Season	4.80	<0.0001
Site*Sex	0.25	0.96
Season*Sex	1.79	0.097
Site*Season*Sex	1.62	0.067

Table 4.2. Results of 'reduced' MANOVA on $\delta^{13}C$ and $\delta^{15}N$ with the sex effect and appropriate interactions removed. F-value and p-value reported correspond to the Wilks' Lambda statistic.

Effect	F Value	p-value
Site	243.2	<0.0001
Season	5.00	<0.0001
Site*Season	5.09	<0.0001

Least square (LS) means from the site-by-season interaction showed that fish from Bright exhibited significantly lower mean $\delta^{15}N$ ($p<0.0001$) relative to the other sites in every season except spring, where fish from Bright and McGrail did not differ (Figure 4.6, Appendix Table D.1). Fish from East Cameron exhibited consistently lower mean $\delta^{13}C$ values across seasons, significantly different from both Bright ($p<0.0001$) and Jakkula ($p<0.0001$) in spring, McGrail ($p<0.0001$) and Jakkula ($p<0.0001$) in summer, McGrail in fall ($p=0.02$), and Bright in winter ($p<0.0001$, Figure 4.6). However, the differences observed between LSmean $\delta^{13}C$ values were very small, with the maximum $\delta^{13}C$ range observed in a given season at just 0.8‰ in spring (Figure 4.6, Spring).

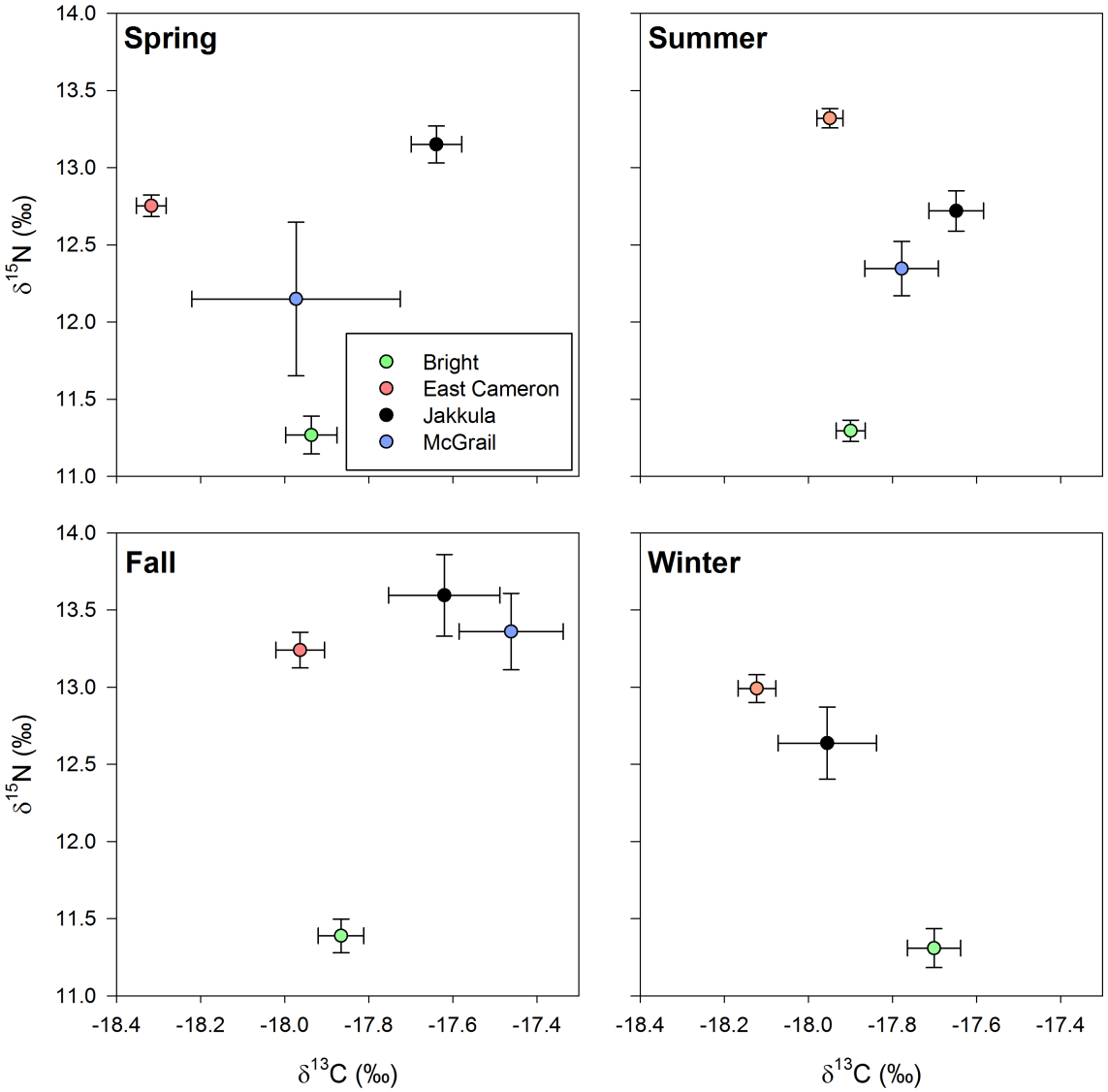

Figure 4.6. LSmean isotope values from the "reduced" MANOVA for each study location, by season. Error bars represent standard error.

The only site with fish that exhibited significant intrasite $\delta^{13}C$ or $\delta^{15}N$ differences among seasons was East Cameron. Pairwise comparisons of $\delta^{13}C$ at East Cameron indicated complex significance relationships (Table 4.3), however the range of $\delta^{13}C$ values was again very small (0.36‰). Pairwise comparisons of $\delta^{15}N$ values indicated fish at East Cameron were significantly less enriched during the spring season relative to fall ($p=0.027$) or summer ($p<0.0001$).

Table 4.3. Post-hoc pairwise Tukey significance groups of $\delta^{13}C$ values at East Cameron between seasons.

Season	LS Mean $\delta^{13}C$ (‰)	Standard Error	Significance Group
Spring	-18.31	0.035	A
Winter	-18.12	0.044	AB
Fall	-17.96	0.057	BC
Summer	-17.94	0.031	C

SIBER

The SIBER analysis indicated that red snapper exhibited significantly different isotope niche areas between sites, seasons, and size classes. Overlap between groups varied depending on the categorization factor, with seasonal and size class groups showing high overlap relative to the overlap between site groups.

BY SITE

When combined across seasons and size classes, fish from Bright and East Cameron produced significantly smaller Bayesian standard ellipse areas (SEA_B) than Jakkula and McGrail (Figure 4.7). The two smaller SEA groups, Bright and East Cameron, also exhibited far lower variability among SEA_B relative to the other sites due to the higher number of samples collected.

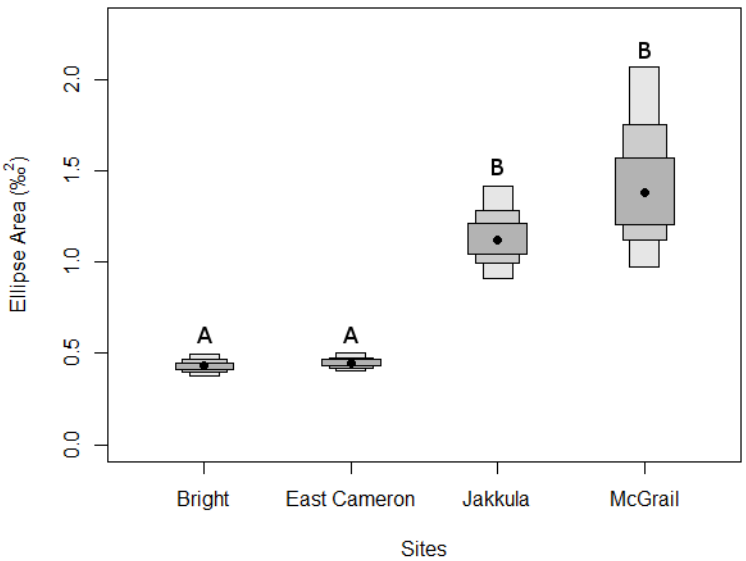

Figure 4.7. Bayesian standard ellipse area (SEA_B) distributions by site. The dot represents the most likely SEA and bars indicate the 50, 75, and 95 percent credible intervals. Letters indicate significantly different ellipse areas.

Site groups showed a relatively low degree of overlap, compared to seasonal or size groups, an indication that site groups were more distinct in C-N space relative to seasonal or size class groups (Figure 4.8). Jakkula and McGrail showed the highest degree of overlap between site ellipses (0.61‰^{2}). This overlap encompassed 60.6% of the total SEA_C of the Jakkula group and 75.9% of the McGrail group. Minor overlaps were also observed between Bright and McGrail (0.09‰^{2}, 22.2% of Bright, 10.6% of McGrail) and East Cameron with Jakkula (0.05‰^{2}, 12.7% of East Cameron, 6.2% of Jakkula).

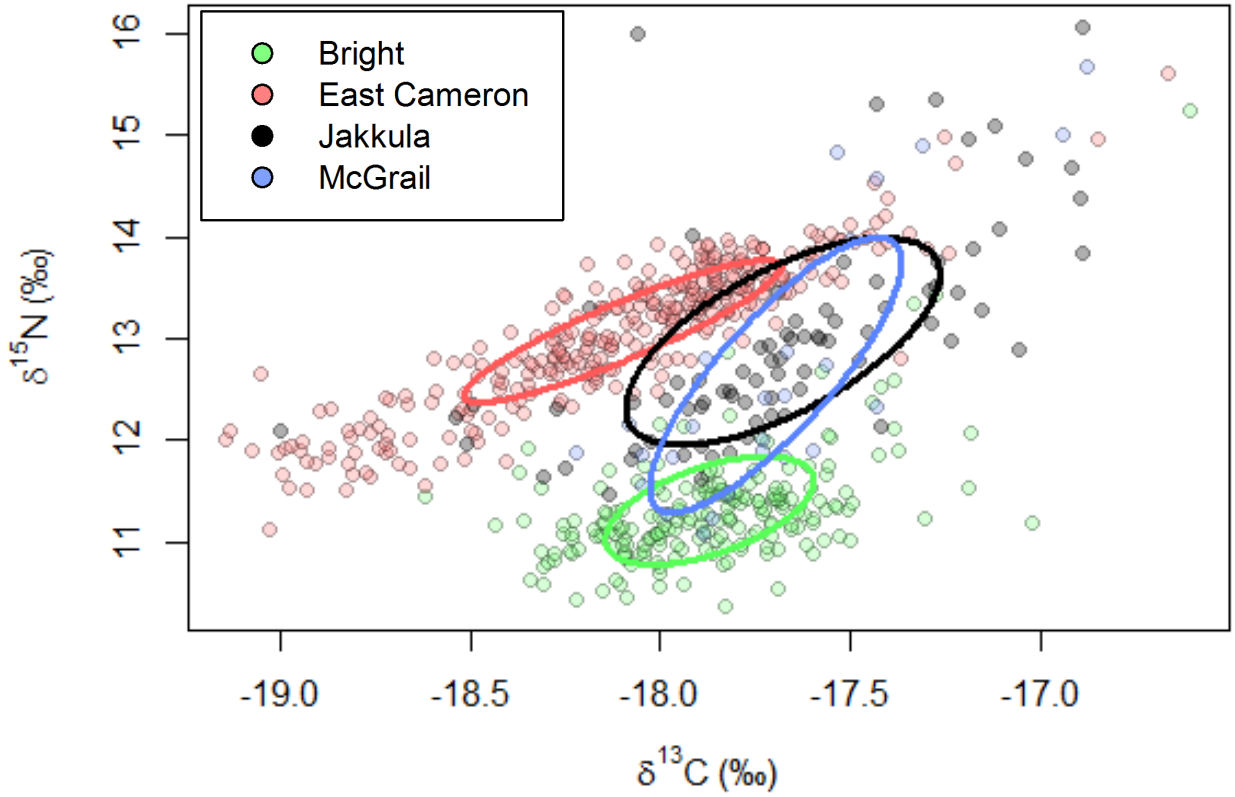

Figure 4.8. Plot of the individual red snapper isotope values, colored according to the site of capture, overlaid with their corresponding standard ellipse (SEA_C).

By Season

Combined across sites and size classes, the summer SEA_B was significantly smaller than all other seasons, which did not differ (Figure 4.9). The summer group also showed a narrower credible interval than other seasons due to the higher number of samples

collected during summer months. Standard ellipses defined by season showed a high degree of overlap, an indication that they were located similarly in $\delta^{13}C$ - $\delta^{15}N$ space relative to one another (Figure 4.10). All seasons overlapped with one another to some degree (Table 4.4), with the largest overlap observed between spring and winter groups (1.14‰^{2}) and the smallest overlap between spring and summer groups (0.68‰^{2}). The highest percentage of a seasonal SEA_C accounted for by an overlap involved the overlap between fall and summer, where 98% of the summer SEA_C overlapped with fall.

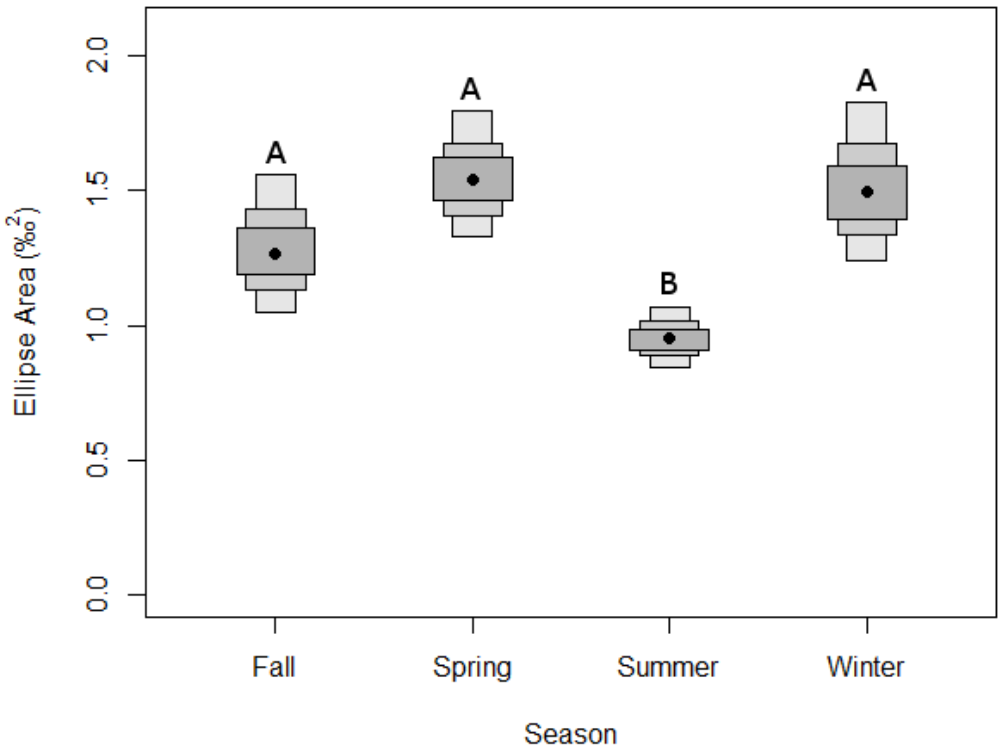

Figure 4.9. Bayesian standard ellipse area (SEA_B) distributions by season. The dot represents the most likely SEA and bars indicate the 50, 75, and 95 percent credible intervals. Letters indicate significantly different ellipse areas.

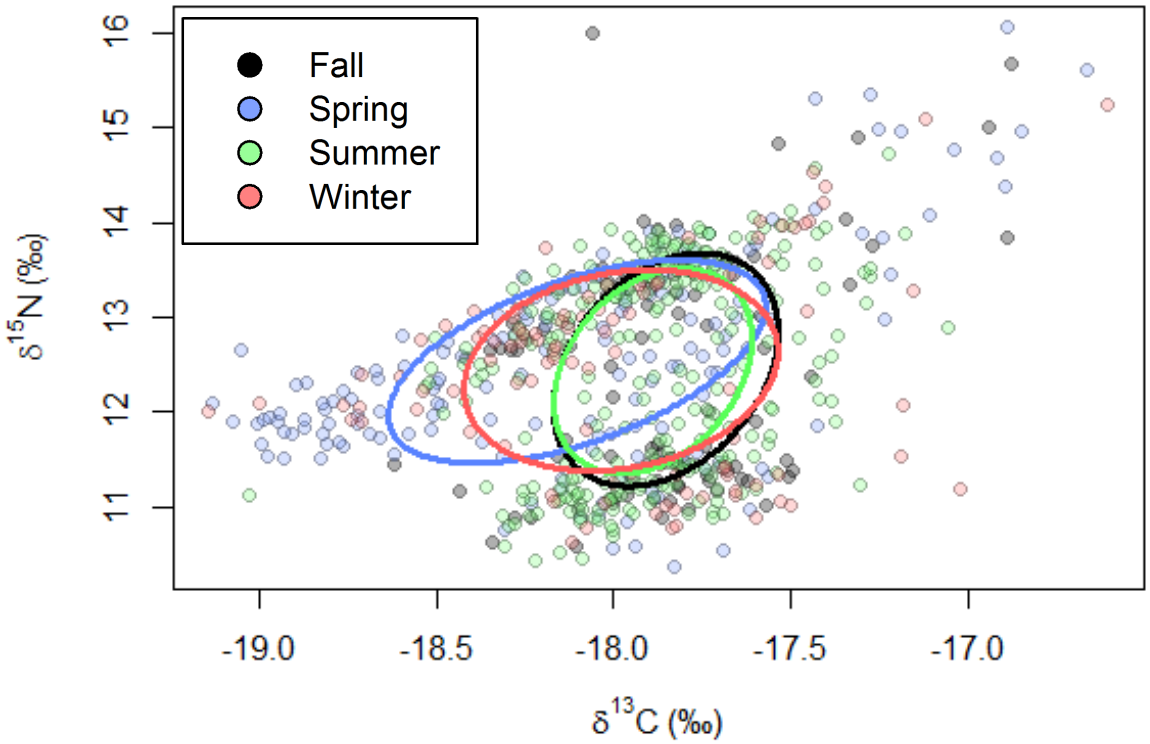

Figure 4.10. Plot of the individual red snapper isotope values, colored according to the season of capture, overlaid with their corresponding standard ellipse (SEA_C).

Table 4.4. The extent of overlap between seasonally defined groups of red snapper standard ellipse areas (SEA_C) in $\delta^{13}C$ - $\delta^{15}N$ space. In addition to actual overlap area, the percent of each seasons total SEA_C accounted for by the overlap is given, according to the order listed in the season pair.

Season Pair	Overlap (‰^{2})	Percent of Season 1	Percent of Season 2
Fall – Spring	0.76	65.4	50.2
Fall – Summer	0.90	77.8	98.0
Fall – Winter	1.00	86.2	68.9
Spring – Summer	0.68	45.2	74.2
Spring – Winter	1.14	75.5	78.6
Summer – Winter	0.89	96.3	61.1

By Size Class

When combined across all sites and seasons, size classes showed significantly different SEA_B values that increased with increasing fish size (Figure 4.11). Red snapper in size class 3 (<399mm) showed a significantly smaller SEA than any larger size class. Classes 4 and 5 (400-499mm and 500-599mm) did not differ in their SEA_B, but were significantly

smaller than size class 6 (>600mm). SEA_B variability within size classes was relatively consistent, though size class 3 showed a smaller credible interval than the large size classes despite the low number of individuals within this size class.

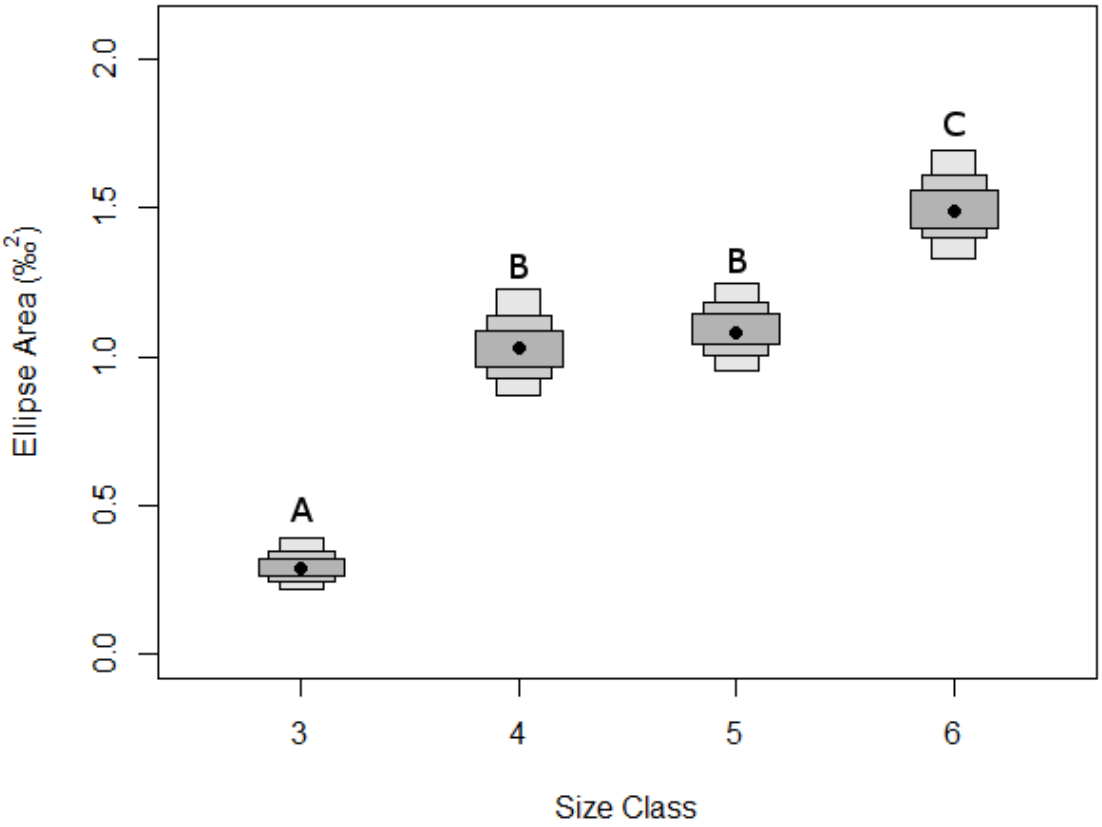

Figure 4.11. Bayesian standard ellipse area (SEA_B) distributions by size class. The dot represents the most likely SEA and bars indicate the 50, 75, and 95 percent credible intervals. Letters indicate significantly different ellipse areas.

As was observed for seasonal groups, size class groups showed a high degree of overlap between ellipses (Figure 4.12), with every size class standard ellipse overlapping with at least one other (Table 4.5). The only size classes that did not overlap were class 3 and class 5. Alternatively, the size class 3 standard ellipse was completely encompassed by the larger size class 6 ellipse, which also displayed large overlaps with size classes 4 (0.79‰², 83.7% of SC 4, 54.2% of SC 6) and 5 (0.63‰², 59.6% of SC 5, 43% of SC 6).

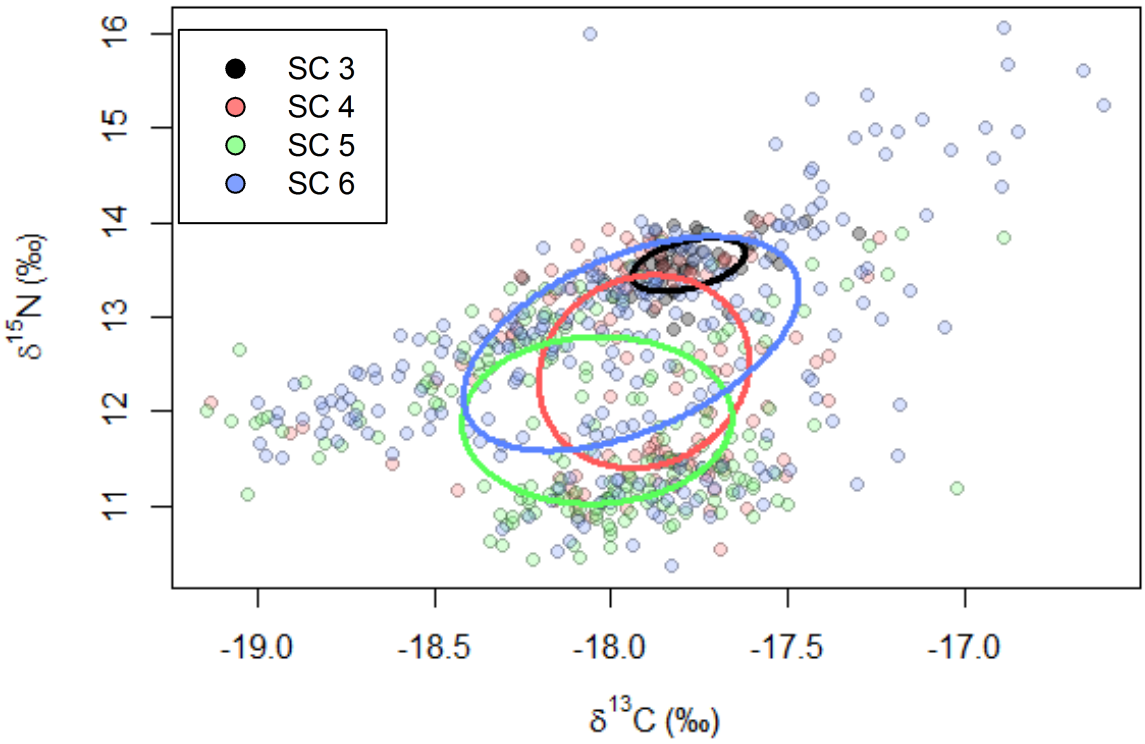

Figure 4.12. Plot of the individual red snapper isotope values, colored according to the size class (SC) of the individual, overlaid with their corresponding standard ellipse (SEA_C).

Table 4.5. The extent of overlap between size-class defined groups of red snapper standard ellipse areas (SEA_C) in $\delta^{13}C$ - $\delta^{15}N$ space. In addition to actual overlap area, the percent of each size-class total SEA_C accounted for by the overlap is given, according to the order listed in the size-class pair.

Size Classes	Overlap (‰²)	Percent of Size Class 1	Percent of Size Class 2
3 – 4	0.02	18.2	2.4
3 – 5	0	0	0
3 – 6	0.13	100	8.7
4 – 5	0.59	61.9	55.6
4 – 6	0.79	83.7	54.2
5 – 6	0.63	59.6	43.0

Because size classes were not evenly distributed across sites, the extent of isotopic variation by size class was examined within sites, though the limited number of replicates precluded SEA calculations or statistical comparisons. However, from a strictly qualitative perspective, the same relationship between size class and isotopic variability was

observed; larger size classes showed higher isotopic variation at every site (Figure 4.13). Variability was more pronounced in regards to $\delta^{15}N$, while $\delta^{13}C$ tended to be similar between size classes at a given site.

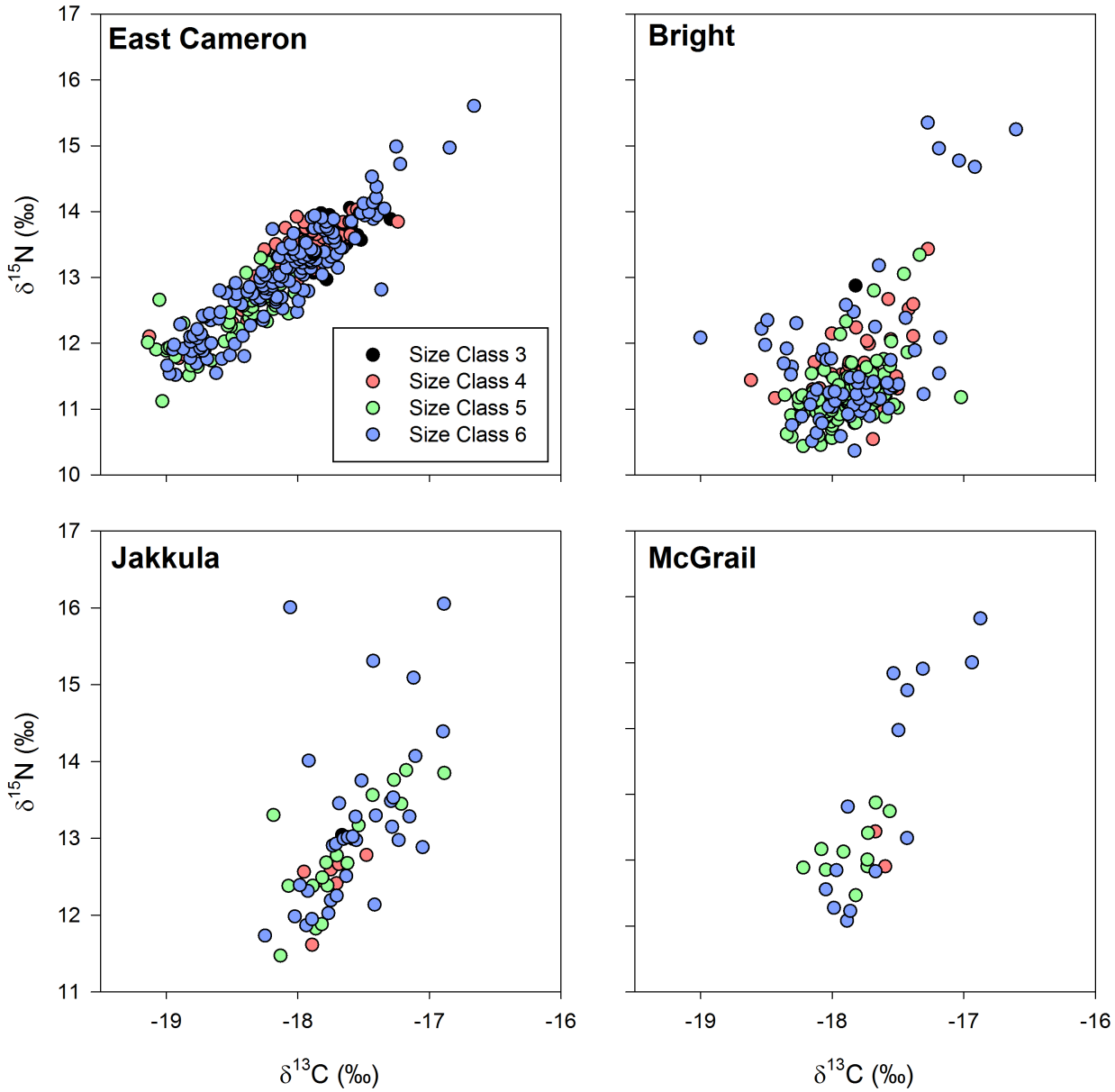

Figure 4.13. Plots of individual red snapper isotopic composition, separated by study site. Colors indicate the size class of each individual. Note that as size class increases, so does the range of values covered by individuals.

DISCUSSION

The present study examined the isotopic composition of red snapper at three natural shelf-edge banks and one artificial reef in the northwestern Gulf. Isotopic niche position and extent depended on fish size, site, and season of collection.

Sites were the most important factor in explaining isotopic variation. Fish from the two most highly sampled locations, Bright and East Cameron, showed no overlap of SEA_c, indicating relatively distinct isotopic compositions. There are two main drivers behind intraspecific isotope distinctions: diet and isotopic baselines. Two scenarios that represent the extremes of these drivers can be imagined: 1) fish are eating the same prey items everywhere, but the baseline differs between sites, or 2) the baseline does not differ between sites, but fish are eating different prey items at different locations. As with nearly every natural process, the truth likely lies somewhere along a continuum between these extremes.

Diet information from a concurrent study on the same fish did find significant differences in snapper prey items between natural and artificial reefs (Schwartzkopf 2014). Fish from the artificial reef ate a higher proportion of zooplankton prey relative to fish at natural habitats, whose diets were dominated by other fishes. However, diets of individuals at the natural sites, Bright and Jakkula, did not differ significantly. While Schwartzkopf (2014) did elucidate very detailed dietary variations in red snapper, these findings do not completely explain the isotopic data relationships. For example, the stomach contents data suggest similar diets at natural sites, yet isotope information indicates significantly different levels of variation between natural bank sites. Additionally, the predominance of lower trophic level prey at artificial reefs leads to the expectation that snapper would

exhibit lower $\delta^{15}N$ values, yet fish from the East Cameron site tended to be more enriched in $\delta^{15}N$ at given $\delta^{13}C$ value than fish from the natural sites. Given these discrepancies, baseline differences between sites, especially Bright and East Cameron, must also be considered as an important determinant of the observed relationship.

Different isotopic baselines between the artificial reef site and the natural bank sites likely contribute to the relative positioning of red snapper isotopic niche spaces observed in this study. The artificial reef site in this study was located mid-shelf in 50 m of water, as opposed to the shelf-edge location and deeper water (100 m+) from which the natural sites rise. This location in shallower water closer to shore makes the East Cameron site most susceptible to influences from the Mississippi River plume. Previous studies have shown enriched $\delta^{15}N$ values associated with the river water itself, particulate organic matter (POM), entrained plankton, and shrimp associated with the plume (Wissel and Fry 2005, Dorado et al. 2012). Additionally, increases in deep water coral $\delta^{15}N$ signatures have been attributed to increased nutrient loading of river waters, demonstrating both the extent of river influence and its effect on N isotopic compositions (Williams et al. 2007, Prouty et al. 2014). If this enriched N source were incorporated into the local food web at East Cameron, consumers such as red snapper would be expected to show enriched $\delta^{15}N$ values relative to snapper from areas where there is limited river influence.

Alternatively, particulate organic matter, pelagic fish larvae, and juvenile fish in oceanic Gulf of Mexico environments have been shown to have especially depleted $\delta^{15}N$ values (Wells and Rooker 2009, Dorado et al. 2012). These depleted values are attributed to the incorporation of N compounds derived from the production of, and N_2 fixation by, the cyanobacteria *Trichodesmium* which produces depleted $\delta^{15}N$ (Dorado et al. 2012). The

depleted $\delta^{15}N$ of an entire coastal food web, Guanabara Bay in Brazil, relative to similar systems nearby was also attributed to a substantial contribution of atmospheric nitrogen fixation by cyanobacteria (Bisi et al. 2012). Therefore, the lower relative $\delta^{15}N$ found in snapper at the natural banks may be a result of N derived from *Trichodesmium* being incorporated into the shelf-edge bank food webs.

The higher $\delta^{15}N$ observed at the artificial reef site in this study could be attributed to exposure to the enriched Mississippi River plume, lower $\delta^{15}N$ at the shelf-edge sites due to depleted N sourced from diazotrophy, or some combination of both effects. Unfortunately, baseline compositions were not collected so definitive attribution to such differences is not possible. Future studies comparing basal resource composition between natural and artificial habitat, or individual sites within either habitat type, would provide useful information about the relative importance of various nutrient sources to red snapper populations.

Two levels of individual variation within sites were observed, with Bright and East Cameron showing a significantly smaller isotopic niche width than McGrail and Jakkula. One driver of this variation difference between sites could be a difference in the variety of prey items being consumed between sites. However, diet analysis showed that there were more unique prey items and higher diversity diets consumed by snapper at East Cameron and Bright, the small isotopic niches sites (Schwartzkopf 2014), though this result could be biased by the limited number of individuals sampled from McGrail and Jakkula. Such a bias shouldn't be a factor for the isotopic analyses however, as the definition of SEA values and the methods of comparison were specifically designed to be insensitive to bias associated with sample size (Jackson et al. 2011).

Size class distributions between sites may better explain the differences in isotope niche width observed. A greater proportion of small fish were caught at Bright and East Cameron, the small isotopic niche width sites, relative to Jakkula and McGrail. This difference, coupled with the observation that larger fish tended to show more variability in both $\delta^{13}C$ and $\delta^{15}N$, likely contributed to the larger niche widths observed at Jakkula and McGrail.

The increasing isotopic variability with increasing fish size could be attributed to a number of factors, including a changing or more variable diet and movement. Size-related changes in diet were reported for these fish, with larger size-class individuals consuming a wider variety of prey items (Schwartzkopf 2014). Many studies of red snapper diet have shown changes in diet as fish grow, often documenting a shift in predominant prey items from invertebrates and zooplankton at smaller sizes to fish at larger sizes (Mosely 1966, Bradley and Bryan 1975, Szedlmayer and Lee 2004). Diet shifts may be due to increasing energetic requirements as fish grow (Mosely 1966), or simply that larger snapper are able to successfully capture and consume a wider variety of prey items at larger sizes.

Besides diet, movement can also affect the observed isotopic values of individuals and may help explain isotopic variability differences between sites. Red snapper movement has been documented at a variety of spatial and temporal scales (Diamond et al. 2007, Patterson, III 2007). Individuals tend to show high site fidelity or move small (<10km) distances, though movements of over 500km have been reported (Patterson, III and Cowan, Jr. 2003, Patterson, III 2007). Size has been shown to be an important factor in both the extent and likelihood of snapper movement, with larger individuals moving further and more often than smaller ones (Patterson, III et al. 2001, Diamond et al. 2007). With regard

to the isotopic composition of an individual, movement has the potential to introduce different isotope sources and food items across the variety of habitats an individual may encounter (Graham et al. 2010). Therefore, movement may explain both the increased isotopic variability with increasing fish size observed across all sites, and the wider isotopic niches observed at Jakkula and McGrail. Because larger snapper are more likely to move, and move further, they may incorporate a wider range of isotopic signatures, leading to more individual variability in larger fish and at sites dominated by larger individuals.

Although the variability of $\delta^{13}C$ and $\delta^{15}N$ increased with increasing size class, there was no indication of the significant linear relationship between size and $\delta^{13}C$ or $\delta^{15}N$, as has reported in some fishes (Davenport and Bax 2002, Reoñes et al. 2002, Melville and Connolly 2003, Hussey et al. 2011, Muto and Soares 2011). The lack of such a relationship is not uncommon (Vander Zanden et al. 2000, Cocheret de la Moriniere et al. 2003, Marie Wilson et al. 2009). Red snapper are opportunistic feeders and will consume prey from various habitats and trophic levels (Gallaway et al. 1981, Szedlmayer and Lee 2004, McCawley and Cowan 2007, Wells et al. 2008a, Schwartzkopf 2014). Such an indiscriminate feeding strategy may contribute to the lack of a significant length- $\delta^{15}N$ relationship that is usually attributed to larger consumers targeting larger, higher trophic level prey (Sweeting et al. 2007b). Additionally, indiscriminant feeding could contribute to the lack of a length-$\delta^{13}C$ relationship that is usually attributed to ontogenetic shifts in feeding location or habitat as the consumer grows (Davenport and Bax 2002).

The high overlap and limited meaningful separation of mean isotope position between seasons suggest that seasonal variation in red snapper isotope composition is minimal. The only site that showed significantly different mean isotope values between

seasons was East Cameron, though these differences were small and may not be biologically significant. The range of average $\delta^{13}C$ and $\delta^{15}N$ values between seasons were nearly the same as the measurement error of the mass spectrometer (±0.2‰ and ±0.3‰), limiting confident interpretation of statistical differences. Even if such differences were valid, such small variations are unlikely to arise from distinctly different carbon or nitrogen source pools.

Isotopic or tissue turnover rate, the amount of time it takes for consumer tissue to integrate prey tissue (Matley et al. 2013), may limit the amount of seasonal variability of isotope values that occurs in red snapper. The measured isotope values of a consumer represent a running average of diet composition over a period of time corresponding to the tissue turnover time. Temporal variations in diet or basal sources won't be accurately expressed through isotopic variation if changes are on a shorter timescale than the tissue turnover time. Adult fish muscle turnover tends to be on the order of several months (Guzzo et al. 2013), with even longer times reported in gag grouper (*Mycteroperca microlepis*) in the northeastern Gulf (6 months, Nelson 2011) and elasmobranch species (12+ months, MacNeil et al. 2006). Therefore, even if source pools of carbon and nitrogen or diet varied seasonally, slow tissue turnover limits the temporal resolution available to detect such changes and likely precluded the detection of any seasonal variation in red snapper in this study.

A pronounced correlation was observed between $\delta^{13}C$ and $\delta^{15}N$ values, overall and within sites. This pattern has been observed across a variety of taxa and environments (Fry 1988, Hobson and Welch 1992, Davenport and Bax 2002, Grey et al. 2004, Polito et al. 2011, Soares et al. 2014), as well as during similar studies of red snapper in the

northwestern Gulf (Simonsen et al. 2014, K. Foss personal comm.[1]). The correlation could be due to the minor fractionation of $\delta^{13}C$ that occurs during trophic transfers (DeNiro and Epstein 1978, Vander Zanden and Rasmussen 2001, Post 2002). If the widely recognized enrichment of $\delta^{15}N$ during trophic transfers is accompanied by a smaller enrichment in $\delta^{13}C$, a steep positive correlation would be produced (Rooker et al. 2006), similar to the relationship observed in this study.

Alternatively, the correlation could be due to variable baselines, with portions of the correlation composed of source signals from different diet items or habitats. For example, low $\delta^{13}C$ and $\delta^{15}N$ may be characteristic of smaller individuals eating low trophic level food items from a system with low basal $\delta^{13}C$, while larger individuals may exhibit high $\delta^{13}C$ and $\delta^{15}N$ due to higher trophic level diets found in a system with higher $\delta^{13}C$. Shifts in prey items and habitat with changing fish size were observed in the diets of the red snapper in this study (Schwartzkopf 2014). At East Cameron, small fish predominantly consumed prey associated with soft sediments, but water column associated prey became more important as size increased. However, different size class individuals did not appear to comprise different segments of the observed correlation so it is unlikely that the relationship is dependent on size-related changes in diet or habitat associations.

Overall, stable isotope analyses of red snapper indicated that both isotope niche location and extent differed between individual hard substrate sites in the northern Gulf. Niche position differences can likely be attributed to differences in source pools, especially nitrogen. These results agree with previous studies showing enriched source pools of $\delta^{15}N$

[1] Foss, K. 2015. Louisiana State University, M.S. Student, Department of Oceanography and Coastal Sciences.

in areas impacted by terrestrial or fluvial sources (Wissel and Fry 2005, Williams et al. 2007, Dorado et al. 2012, Prouty et al. 2014) and depleted sources where fixation by *Trichodesmium* may be an important source of organic N to the food web (Wells and Rooker 2009, Bisi et al. 2012, Dorado et al. 2012). The observed increase of isotope niche extent as fish size increased agrees with concurrent studies on red snapper diet (Schwartzkopf 2014) and movement data that suggest larger fish move more often and further (Patterson, III and Cowan, Jr. 2003, Patterson, III 2007), allowing for feeding across a wider range of habitats and prey items. Future studies of red snapper isotope ecology would benefit from baseline source sampling to elucidate the relative importance of various sources and determine whether snapper trophic level is consistent between various habitat types or Gulf regions.

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General Summary and Conclusions

This study had three main objectives: 1) define reef fish assemblages at northwestern Gulf shelf-edge banks and determine if assemblages were related to benthic habitat zonation, 2) define large-scale fish distributions at these same features and determine the influence of habitat and environmental factors on distribution, and 3) examine whether trophic ecology differed between reef sites for red snapper, a highly prized reef fish. Baited remote underwater video (BRUV) arrays allowed for fine-scale definition of reef fish assemblages and habitat assessment across the variety of sites and depths examined. However, BRUV survey observations are limited to small spatial scales and vulnerable to the patchy distributions of reef fishes. Therefore, fish distributions were assessed with mobile hydroacoustic surveys at a scale relevant to entire banks. The larger-scale distributions were assessed according to important habitat factors associated with reef fish assemblages, as well as environmental and bathymetric factors that may relate to the distribution patterns. Trophic ecology of red snapper was assessed with stable isotope techniques and a concurrent diet study (Schwartzkopf 2014) to determine differences between the individual shelf-edge banks, where little trophic information exists for red snapper, and an artificial reef. Overall, this project sought to address the lack of comprehensive information about the reef fish assemblages, distributions, and trophic relationships present at natural shelf-edge banks in the northwestern Gulf outside the Flower Gardens Bank National Marine Sanctuary (FGBNMS).

Chapter 1 examined the reef fishes associated with three shelf-edge banks and one artificial reef to determine whether the sites showed variable assemblages, and to determine what factors were most strongly related to any assemblage variability. Baited remote underwater video (BRUV) provided a consistent sampling platform from which reef fish communities could be observed and quantified. Analyses indicated four significant species assemblages that aligned closely with previously defined broad, biological habitat zones (Rezak et al. 1985, Schmahl et al. 2008). As expected, shallow, high complexity coral habitats had the richest reef fish communities, while the deep periphery of bank structures was characterized by fewer species. A stark contrast, especially at coarser taxonomic levels, was observed between fish assemblages at artificial and natural reefs, potentially resulting from the dramatically different type of habitat structure each provides. However, this study only conducted benthic BRUV surveys and results may differ if the full vertical profile of the large artificial reef were examined.

Chapter 2 determined how quantitative habitat complexity characteristics related to previously defined benthic habitat zones at the shelf-edge banks (Rezak et al. 1985, Schmahl et al. 2008), as well as examined the relationship between these habitat characteristics and the variability of associated reef fish assemblages. Complexity characteristics were consistent within, and distinct between, broad habitat zones across the sites sampled. Because species assemblages were strongly related to broad habitat zonation patterns, the complexity characteristics that explained the most species variability also discriminated between broad habitat zones. The complexity characteristics that explained the most fish species variability

were the amount of mud substrate and live cover. Mud substrate dominated at the artificial reef habitat, therefore explained the difference in fish assemblages between the artificial reef and natural banks. Similarly, live cover differed between the natural habitat zones and their associated fish assemblages.

Chapter 3 described the spatial distribution of fishes at three shelf-edge banks and one artificial reef using mobile hydroacoustics, and attempted to generate predictive models of fish presence and density based on spatial and bathymetric factors. Mean volume backscatter (MVBS), an acoustic proxy for biomass, fish presence, and density values were similar to those observed during the limited previous work in the northwestern Gulf and were highly variable with respect to seasonal, site, and habitat zone effects. When predictive models were generated for fish presence and density at the natural banks based on a suite of spatial and bathymetric factors, water column position factors were most important, while design-associated factors (season, site, habitat) were generally less important. Fish were most likely to be present near the seafloor and at depths that corresponded with average bank depths. Predictive models performed well when predicting the presence of fish, but struggled with density values. Future work may benefit from modeling different sized or classes of fish separately, as distributions and responses to various factors are likely not universal.

Chapter 4 examined the trophic ecology of a common and valuable reef fish, red snapper, to describe differences that may exist between reef types (natural vs. artificial) or between sites with differing habitat availability. Isotope techniques provided a complimentary analysis to the concurrent diet study conducted by

Schwartzkopf (2014). Contrary to diet analyses, isotope techniques provided information about longer-term dietary trends and baseline energy sources. Results of this chapter indicated that trophic relationships at the mid-shelf artificial reef may be influenced by anthropogenic nutrient loading, while the isolated shelf-edge bank relationships may be based on the pelagic nitrogen fixer *Trichodesmium*. Larger fish tended to exhibit a wider trophic niche, leading to the observation of higher overall variability at sites that were dominated by larger fishes. The large trophic niche of larger individuals likely stems from their increased movement potential and ability to consume a wider range of prey items. Future work defining isotopic composition of baseline resources at various reefs and structures would help illuminate whether the site-specific differences observed during this study are a result of baseline or consumer isotope variability.

The results of this study describe productive, diverse fish assemblages associated with reef structure that vary predictably according to benthic habitat characteristics. Assemblages showed consistency both within sites surveyed during this study and with previous descriptions at reef habitats in the northwestern Gulf. The majority of the fish at these structures were found closely associated with the reef structure itself, the seafloor at natural banks and vertical structure at the artificial reef. The strong apparent relationship between habitat and fish assemblages, which include many commercially and recreationally important species, suggests that the habitat provided by these features is crucial to the persistence of a variety of reef fishes throughout the northwestern Gulf.

In an era of declining reef health and increasing anthropogenic impact, it is important that these habitat and fisheries resource be recognized, monitored, and maintained. The FGBNMS, which consists of three banks within the network of banks in the northwest Gulf, is regarded as "one of the least impacted, thriving coral reef ecosystems in the western Atlantic and Caribbean region" (Clark et al. 2014). Results of this study have shown that additional, currently unprotected banks harbor similar species assemblages at similar densities to the highly regarded FGBNMS. An updated management plan for the FGBNMS published in 2012 proposed the addition of up to 9 new banks, including McGrail and Bright, to the sanctuary to both preserve the resources associated with additional banks, as well as maintain the integrity of the biological and ecological connectivity of the northwest Gulf bank network (USDOC et al. 2012). This study supports the proposed expansion by demonstrating that additional banks do provide critical habitat for abundant, diverse reef fish communities.

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APPENDIX A

Supplementary information for Chapter 1

PERMANOVA details

The PERMANOVA routine is a permutational multivariate analog to Fisher's *F*-ratio and is calculated from a dissimilarity matrix, a matrix of pairwise dissimilarities between surveys. Dissimilarity, sometimes called distance, between surveys was estimated with the Bray-Curtis dissimilarity. The dissimilarity between the *j*th and *k*th surveys was defined as:

$$D_{jk} = 100 - S_{jk}$$

where S_{jk} is the Bray-Curtis similarity, the complement of dissimilarity, and the value initially calculated by PRIMER. Bray-Curtis similarity is defined as:

$$S_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p}|y_{ij}-y_{ik}|}{\sum_{i=1}^{p}(y_{ij}-y_{ik})}\right\},$$

where y_{ij} and y_{ik} represent the abundance of species *i* in the *j*th and *k*th surveys, respectively. The sums in the numerator and denominator are both over all species (p). The computation of the Bray-Curtis coefficient inherently weights the contributions to (dis)similarity based on species abundance, so rare species were not removed, a practice which would lead to a loss of information (Clarke and Warwick 2001).

The PERMANOVA routine used these dissimilarities to partition the total sum of squares (SS_T), the sum of squared distances from the samples to the overall centroid, into two parts needed for testing H_0:

1) Residual sum of squares (SS_{Res}): sum of squared distances from the

samples to their own group centroid, and

2) Among-Group sum of squares (SS_A): sum of squared distances from the group centroids to the overall centroid

such that $SS_T = SS_{Res} + SS_A$. The test statistic, a pseudo-*F*, was calculated as:

$$F_{pseudo} = \frac{SS_A/(a-1)}{SS_{Res}/(N-a)}$$

where *a* was the number of groups of the factor and *N* was the number of surveys. The true F_{pseudo} was tested against a distribution of simulated F_{pseudo} values (F^*_{pseudo}) generated by permuting the labels of both bank and habitat zone. The probability that F_{pseudo} was generated under a true null hypothesis was calculated as:

$$P = \frac{\left(\text{No. of } F^*_{pseudo} \geq F_{pseudo}\right) + 1}{\left(\text{Total no. of } F^*_{pseudo}\right) + 1}$$

MDS Details

MDS is as an ordination technique used to create a configuration of the surveys in two and three dimensions that attempts to satisfy the relationships present in the similarity matrix, such that more similar surveys were located nearer to one another than to less similar surveys. The algorithm used to create the MDS iteratively regressed the interpoint distances from the plot on the corresponding Bray-Curtis coefficients, measured the goodness-of-fit (stress), and perturbed the configuration in such a way that stress was reduced, until convergence (Clarke and Warwick 2001). Stress was calculated as:

$$Stress = \sqrt{\frac{\sum_j \sum_k \left(d_{jk} - \hat{d}_{jk}\right)^2}{\sum_j \sum_k {d_{jk}}^2}}$$

with d_{jk} denoting the distance between the *j*th and *k*th survey points, and $\hat{d}_{jk}$ as the distance predicted from the fitted regression line corresponding to dissimilarity δ_{jk}, the actual dissimilarity in the original matrix.

SIMPER details

SIMPER analysis breaks down overall intergroup dissimilarity and intragroup similarity into contributions from individual species. The contribution of species *i* to the Bray-Curtis dissimilarity δ_{jk} between samples *j* and *k* was defined as:

$$\delta_{jk}(i) = \frac{100\left|y_{ij} - y_{ik}\right|}{\sum_{i=1}^{p}\left(y_{ij} + y_{ik}\right)}$$

Values of $\delta_{jk}(i)$ were averaged over all pairs of surveys between the two groups being compared to estimate the average contribution of species *i* ($\overline{\delta_i}$), to the overall dissimilarity ($\bar{\delta}$) between the groups. The standard deviation of $\delta_{jk}(i)$ was used to measure the consistency of contribution to the dissimilarity and define the ratio $\overline{\delta_i}/SD(\delta_i)$.

Similarly, the average contribution of species *i* to the similarity within a group ($\overline{S_i}$) was calculated as the average, over all sample pairs within a group, of the contribution of *i* to each intra-group pair similarity:

$$S_{jk}(i) = \frac{\sum_{i=1}^{p} 2\min\left(y_{ij}, y_{ik}\right)}{\sum_{i=1}^{p}\left(y_{ij} + y_{ik}\right)}$$

The standard deviation of $S_{jk}(i)$ was used to measure the consistency of contribution to the dissimilarity and define the ratio $\overline{S_i}/SD(S_i)$.

Table A.1. List of species observed during video surveys. Indicated for each species are: the number observed over all deployments (N), percentage of total number of fishes seen, number of deployments within which the species was seen, and the percentage of all deployments during which each species was observed.

Family	Species	N	Percent Total	Deployments	Percent Deployments
Acanthuridae	*Acanthurus bahianus*	6	0.10	1	3.85
	Acanthurus chirurgus	2	0.03	1	3.85
	Acanthurus coeruleus	5	0.08	2	7.69
Balistidae	*Balistes capriscus*	6	0.10	6	23.08
	Balistes vetula	8	0.13	6	23.08
	Canthidermis sufflamen	27	0.43	2	7.69
	Melichthys niger	9	0.14	1	3.85
	Xanthichthys ringens	8	0.13	3	11.54
Carangidae	*Caranx crysos*	13	0.21	2	7.69
	Caranx latus	43	0.69	3	11.54
	Caranx lugubris	8	0.13	5	19.23
	Caranx ruber	5	0.08	1	3.85
	Elagatis bipinnulata	16	0.26	1	3.85
	Selene vomer	1	0.02	1	3.85
	Seriola dumerili	85	1.36	18	69.23
	Seriola rivoliana	26	0.42	10	38.46
	Trachinotus falcatus	1	0.02	1	3.85
Carcharhinidae	*Carcharhinus falciformis*	2	0.03	2	7.69
	Carcharhinus leucas	1	0.02	1	3.85
	Carcharhinus obscurus	2	0.03	2	7.69
	Carcharhinus perezi	2	0.03	2	7.69
	Carcharhinus plumbeus	6	0.10	5	19.23
	Rhizoprionodon terraenovae	1	0.02	1	3.85
Chaetodontidae	*Chaetodon ocellatus*	2	0.03	1	3.85
	Chaetodon sedentarius	25	0.40	11	42.31
	Prognathodes aculatus	12	0.19	8	30.77
	Prognathodes aya	1	0.02	1	3.85
Diodontidae	*Diodon hystrix*	1	0.02	1	3.85
Holocentridae	*Holocentrus adscensionis*	18	0.29	6	23.08
Kyphosidae	*Kyphosus sectatrix*	3	0.05	1	3.85
Labridae	*Bodianus pulchellus*	13	0.21	6	23.08
	Bodianus rufus	4	0.06	2	7.69
	Clepticus parrae	1	0.02	1	3.85
	Halichoeres bathyphilus	9	0.14	1	3.85
	Halichoeres bivittatus	7	0.11	3	11.54
	Halichoeres garnoti	1	0.02	1	3.85

	Halichoeres maculipinna	1	0.02	1	3.85
	Thalassoma bifasciatum	6	0.10	1	3.85
Lutjanidae	*Apsilus dentatus*	1	0.02	1	3.85
	Lutjanus buccanella	14	0.22	2	7.69
	Lutjanus campechanus	106	1.70	18	69.23
	Lutjanus griseus	12	0.19	3	11.54
	Lutjanus synagris	1	0.02	1	3.85
	Ocyurus chrysurus	16	0.26	1	3.85
	Rhomboplites aurorubens	7	0.11	2	7.69
Malacanthidae	*Caulolatilus chrysops*	2	0.03	1	3.85
	Caulolatilus microps	5	0.08	1	3.85
	Malacanthus plumieri	20	0.32	9	34.62
	Cantherhines macro	2	0.03	1	3.85
Mullidae	*Pseudupeneus maculatus*	4	0.06	3	11.54
Muraenidae	*Gymnothorax moringa*	2	0.03	2	7.69
	Muraena retifera	1	0.02	1	3.85
Opistognathidae	*Opistognathus aurifrons*	48	0.77	4	15.38
Pomacanthidae	*Centropyge argi*	33	0.53	8	30.77
	Holacanthus ciliaris	1	0.02	1	3.85
	Holacanthus tricolor	6	0.10	4	15.38
	Pomacanthus arcuatus	3	0.05	2	7.69
	Pomacanthus paru	2	0.03	1	3.85
	Chromis cyanea	5	0.08	1	3.85
	Chromis enchrysurus	404	6.48	11	42.31
	Chromis insolata	100	1.60	5	19.23
	Chromis multilineata	1247	20.01	2	7.69
	Stegastes partitus	8	0.13	3	11.54
Rachycentridae	*Rachycentron canadum*	2	0.03	2	7.69
Scaridae	*Sparisoma atomarium*	9	0.14	4	15.38
	Sparisoma aurofrenatum	6	0.10	3	11.54
Sciaenidae	*Equetus lanceolatus*	1	0.02	1	3.85
Scorpaenidae	*Pterois volitans*	7	0.11	4	15.38
Serranidae	*Anthias tenuis*	1588	25.49	3	11.54
	Dermatolepis inermis	1	0.02	1	3.85
	Epinephelus adscensionis	3	0.05	2	7.69
	Epinephelus fulvus	2	0.03	1	3.85
	Epinephelus guttatus	1	0.02	1	3.85
	Epinephelus nigritus	1	0.02	1	3.85
	Hyporthodus flavolimbatus	3	0.05	2	7.69
	Liopropoma eukrines	1	0.02	1	3.85
	Mycteroperca bonaci	1	0.02	1	3.85
	Mycteroperca interstitialis	6	0.10	3	11.54
	Mycteroperca microlepis	2	0.03	2	7.69

	Mycteroperca phenax	31	0.50	10	38.46
	Mycteroperca venenosa	3	0.05	2	7.69
	Paranthias furcifer	1808	29.02	7	26.92
	Pronotogrammus martinicensis	190	3.05	4	15.38
	Serranus annularis	19	0.30	9	34.62
	Serranus phoebe	15	0.24	11	42.31
Sparidae	*Calamus calamus*	7	0.11	3	11.54
	Calamus nodosus	3	0.05	3	11.54
	Pagrus pagrus	14	0.22	5	19.23
Sphyraenidae	*Sphyraena barracuda*	57	0.91	10	38.46
Sphyrnidae	*Sphyrna lewini*	1	0.02	1	3.85
	Sphyrna mokarran	2	0.03	2	7.69
Synodontidae	*Synodus synodus*	1	0.02	1	3.85
Tetraodontidae	*Canthigaster rostrata*	9	0.14	5	19.23

Table A.2 Species contributing the most to survey dissimilarity between significant clusters, ranked by percent contribution (Contrib%). Also included are the average abundance of the species within the groups being compared, average dissimilarity contribution relative to its standard deviation (Diss/SD), and the cumulative percent contribution of species to the average dissimilarity (Cum.%, species up to 60% included).

Groups	Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
A vs B		Group a	Group b				
Average dissimilarity = 96.80	*Paranthias furcifer*	21.59	0.09	19.62	1.74	20.27	20.27
	Anthias tenuis	13.27	0	12.78	0.7	13.2	33.46
	Chromis multilineata	12.49	0	8.43	0.82	8.71	42.18
	Chromis enchrysurus	7.56	0	5.37	1.12	5.54	47.72
	Chromis insolata	4.34	0	3.5	2.65	3.62	51.33
	Caranx latus	3.24	0	3.39	1.23	3.5	54.83
	Canthidermis sufflamen	2.34	0	2.36	1	2.44	57.27
	Sphyraena barracuda	2.77	0.09	2.33	2.11	2.4	59.67
	Lutjanus campechanus	0.47	2.34	1.8	1.21	1.86	61.54
A vs C		Group a	Group c				
Average dissimilarity = 95.85	*Paranthias furcifer*	21.59	0	19.94	1.67	20.8	20.8
	Anthias tenuis	13.27	0	12.93	0.67	13.48	34.28
	Chromis multilineata	12.49	0	8.5	0.79	8.87	43.16
	Chromis enchrysurus	7.56	0.47	5.35	1.12	5.58	48.74
	Chromis insolata	4.34	0	3.54	2.55	3.69	52.43
	Caranx latus	3.24	0	3.43	1.18	3.58	56.01
	Canthidermis sufflamen	2.34	0	2.39	0.96	2.49	58.5
	Holocentrus adscensionis	1.96	0	1.94	2.41	2.02	60.52
A vs D		Group a	Group d				
Average	*Paranthias furcifer*	21.59	1.24	15.37	1.68	18.42	18.42

dissimilarity = 83.42	*Anthias tenuis*	13.27	0.3	10.69	0.71	12.82	31.24
	Chromis multilineata	12.49	0	7.35	0.81	8.81	40.05
	Chromis enchrysurus	7.56	2.09	4.36	1.25	5.23	45.28
	Caranx latus	3.24	0	2.76	1.27	3.3	48.58
	Chromis insolata	4.34	0.8	2.67	2.04	3.21	51.79
	Canthidermis sufflamen	2.34	0	1.93	1.03	2.31	54.1
	Pronotogrammus martinicensis	0	2.43	1.86	0.6	2.23	56.33
	Sphyraena barracuda	2.77	0.57	1.64	1.75	1.97	58.3
	Holocentrus adscensionis	1.96	0.27	1.37	1.99	1.65	59.95
	Ocyurus chrysurus	1.33	0	1.28	0.69	1.53	61.48
B vs C		Group b	Group c				
Average dissimilarity = 87.97	*Lutjanus campechanus*	2.34	0	18.23	1.58	20.72	20.72
	Sphyraena barracuda	0.09	1.89	12.26	1.14	13.94	34.66
	Seriola dumerili	1.05	1.58	10.43	1.54	11.86	46.52
	Caulolatilus microps	0	0.75	6.78	0.66	7.71	54.23
	Serranus phoebe	0.31	0.67	5.24	1.11	5.95	60.18
B vs D		Group b	Group c				
Average dissimilarity = 85.92	*Pronotogrammus martinicensis*	0	2.43	6.59	0.65	7.67	7.67
	Chromis enchrysurus	0	2.09	6.08	1.43	7.08	14.75
	Lutjanus campechanus	2.34	1.24	4.71	1.06	5.49	20.23
	Seriola dumerili	1.05	1.76	4.38	1.39	5.1	25.33
	Centropyge argi	0	1.37	3.94	1.31	4.59	29.92
	Opistognathus aurifrons	0	1.36	3.68	0.76	4.28	34.2
	Paranthias furcifer	0.09	1.24	3.64	0.58	4.23	38.43
	Serranus annularis	0	1.08	3.05	1.28	3.55	41.98
	Mycteroperca phenax	0.27	0.98	2.93	1.19	3.41	45.39
	Malacanthus plumieri	0.29	0.97	2.69	1.22	3.13	48.52
	Chaetodon sedentarius	0.22	0.9	2.52	1.16	2.93	51.45
	Seriola rivoliana	0.4	0.86	2.32	1.09	2.71	54.16
	Serranus phoebe	0.31	0.8	2.02	1.21	2.35	56.51
	Chromis insolata	0	0.8	1.79	0.53	2.08	58.6
	Prognathodes aculatus	0	0.65	1.64	1.09	1.9	60.5
C vs D		Group c	Group d				
Average dissimilarity = 83.25	*Pronotogrammus martinicensis*	0	2.43	6.8	0.64	8.17	8.17
	Chromis enchrysurus	0.47	2.09	5.5	1.26	6.61	14.77
	Sphyraena barracuda	1.89	0.57	4.87	1.06	5.85	20.62
	Centropyge argi	0	1.37	4.08	1.3	4.9	25.52
	Opistognathus aurifrons	0	1.36	3.8	0.75	4.57	30.09
	Paranthias furcifer	0	1.24	3.67	0.55	4.41	34.5
	Lutjanus campechanus	0	1.24	3.36	1.2	4.04	38.54
	Serranus annularis	0.33	1.08	2.86	1.26	3.44	41.98
	Chaetodon sedentarius	0	0.9	2.83	1.23	3.4	45.38
	Mycteroperca phenax	0	0.98	2.77	1.15	3.33	48.71
	Malacanthus plumieri	0.33	0.97	2.48	1.18	2.98	51.69
	Caulolatilus microps	0.75	0	2.37	0.66	2.85	54.54
	Seriola rivoliana	0	0.86	2.35	0.94	2.83	57.37

Seriola dumerili	1.58	1.76	2.17	1.17	2.61	59.98
Chromis insolata	0	0.8	1.84	0.52	2.21	62.19

APPENDIX B

Supplementary information for Chapter 2

PERMANOVA details

The non-parametric PERMANOVA routine used is a permutational multivariate analog to Fisher's *F*-ratio and is calculated from a dissimilarity matrix, a matrix of pairwise dissimilarities between surveys (Anderson 2001, McArdle and Anderson 2001). For environmental data the dissimilarity between surveys, also known as distance, was calculated as the conventional Euclidian distance (Clarke and Gorley 2006). A matrix of distances between surveys based on normalized environmental data, defining the distance between the *j*th and *k*th surveys as:

$$d_{jk} = \sqrt{\sum_{i=1}^{v} \left(x_{ij} - x_{ik}\right)^2}$$

where x_{ij} and x_{ik} represent the normalized estimates for environmental variable *i* in the *j*th and *k*th surveys, respectively. The PERMANOVA routine used these distances to partition the total sum of squares (SS_T), the sum of squared distances from the samples to the overall centroid, into two parts needed for testing H_0:

1) Residual sum of squares (SS_{Res}): sum of squared distances from the samples to their own group centroid, and

2) Among-Group sum of squares (SS_A): sum of squared distances from the group centroids to the overall centroid

such that $SS_T = SS_{Res} + SS_A$. The test statistic, a pseudo-*F*, was calculated as:

$$F_{pseudo} = \frac{SS_A/(a-1)}{SS_{Res}/(N-a)}$$

where a was the number of groups of the factor and N was the number of surveys. The true F_{pseudo} was tested against a distribution of simulated F_{pseudo} values (F^*_{pseudo}) generated by permuting the labels of both bank and habitat zone. The probability that F_{pseudo} was generated under a true null hypothesis was calculated as:

$$P = \frac{\left(\text{No. of } F^*_{pseudo}\right) \geq F_{pseudo}) + 1}{\left(\text{Total no. of } F^*_{pseudo}\right) + 1}$$

PCA Detail

The PCs were fitted as linear combinations of optimally weighted original environmental variables (Clarke and Warwick 2001). The first PC accounted for the maximal amount of the total variation in the original data possible, after which the second PC accounted for the maximal amount of the variance in the data not accounted for by the first PC, a procedure repeated until all requested PCs had been fit.

DISTLM Detail

DISTLM modeled the relationship between the standardized matrix of environmental and habitat variables versus the Bray-Curtis resemblance matrix of square-root transformed species abundance with a distance-based redundancy analysis approach. DISTLM partitioned the multivariate variation in the species data cloud described by the Bray-Curtis resemblance matrix according to a multiple regression model. Further specifics of how the partitioning is accomplished can be found in Legendre and Anderson (1999), McArdle and Anderson (2001), and Anderson et al. (2008). From this partitioning, the simple ratio of explained sum of

squares for the regression ($SS_{Regression}$) versus the total sum of squares (SS_{Total}) described the proportion of the variation in the multivariate data cloud that was explained by the model:

$$R^2 = \frac{SS_{Regression}}{SS_{Total}}$$

To test the null hypothesis of no relationship between environmental variables and multivariate species observations, a pseudo-F statistic was calculated as:

$$F_{pseudo} = \frac{SS_{Regression}/q}{SS_{Residual}/(N - q - 1)}$$

where q is the number of explanatory variables and N is the number of samples in the species resemblance matrix. The null hypothesis was tested by comparing F_{pseudo} against a distribution of 999 simulated pseudo-F values (F^*_{pseudo}), calculated in the same manner, but using a species resemblance matrix in which the sample labels had been randomly permuted.

APPENDIX C

Supplementary information for Chapter 3.

Table C1. Physical characteristics and habitat zonation of the sites sampled. Bright, Jakkula, and McGrail are natural banks, while East Cameron is an artificial reef. Habitat location is a depth range at natural banks and distance from the structure at East Cameron. East Cameron depths were based on acoustics surveys.

Site	Dimensions (km)	Deepest/crest depth (m)	Habitats present	Habitat location (m)
Bright	4.8 × 6.2[a]	130/33[a]	Coral Community	33-37[c]
			Coralline Algal Reef	37-74[c]
			Deep Coral	74-110[c]
			Soft Bottom	110+[c]
Jakkula	1.7 × 1.7[a]	160/64[a]	Coralline Algal Reef	64-90[c]
			Deep Coral	90-120[c]
			Soft Bottom	120+[c]
McGrail	3.0 × 4.4[a]	110/45[a]	Coral Community	45-47[c]
			Coralline Algal Reef	47-82[c]
			Deep Coral	82-110[c]
			Soft Bottom	110+[c]
East Cameron	0.065 × 0.065[b]	55/29	Artificial Reef	<250
			Mud	>250

[a] Gardner and Beaudoin (2005)
[b] Louisiana Department of Wildlife and Fisheries, Multibeam Artificial Reef Survey Imagery (2012)
[c] Rezak et al. (1990)

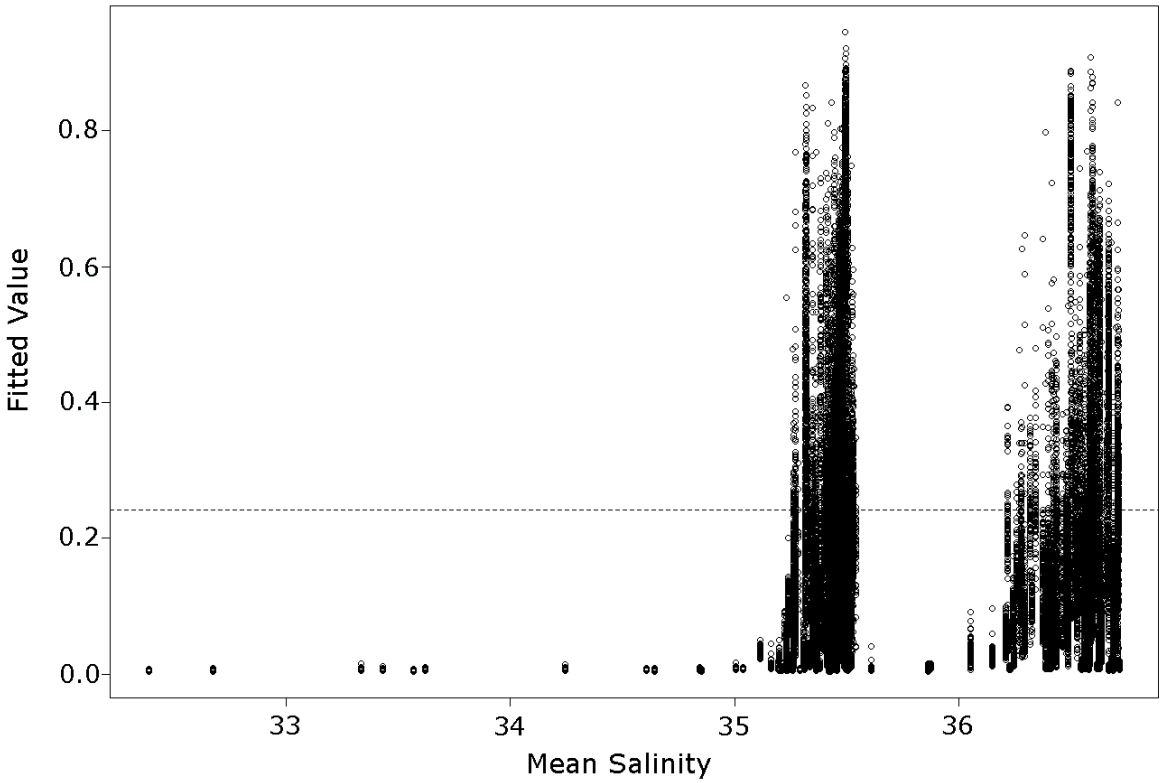

Figure C.1. Fitted values from the Presence BRT model across the range of salinities sampled. The marginal effect of salinity may be overly influenced by the few low salinity values with zero probability of presence.

APPENDIX D

Supplementary information for Chapter 4

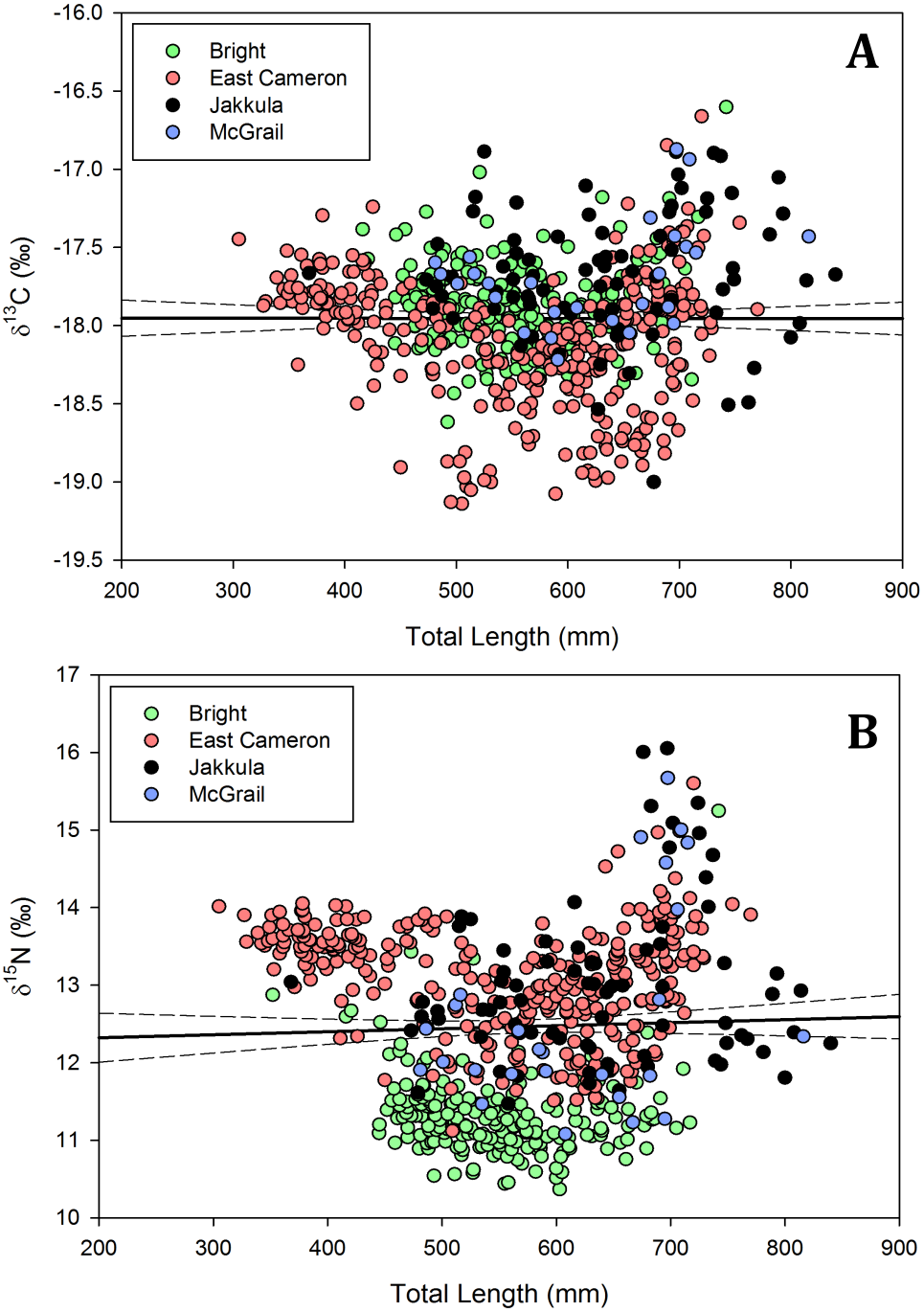

Figure D.1. Plots of red snapper (A) $\delta^{13}C$ (‰) and (B) $\delta^{15}N$ (‰) versus total length (mm). Solid line indicates linear regression of points and dotted lines denotes the 95% confidence interval. Note that the slope of this line is not significantly different from zero, indicating no linear relationship between red snapper length and either $\delta^{13}C$ or $\delta^{15}N$.

Table D.1. LSmean $\delta^{13}C$, $\delta^{15}N$ and their associated standard errors derived from the significant MANOVA site-by-season interaction. Significant differences between site-by-season combinations are indicated by unique letters, based on Tukey post-hoc comparisons.

Season	Site	LS Mean $\delta^{13}C$ (‰)	Standard Error	Group	LS Mean $\delta^{15}N$ (‰)	Standard Error	Group
Spring	Bright	-17.937	0.06103	A	11.2676	0.12243	A
	East	-18.317	0.03506		12.7535	0.07033	B
	Cameron			B			
	Jakkula	-17.639	0.06013	C	13.1512	0.12061	B
	McGrail	-17.973	0.24792	ABC	12.1493	0.49731	AB
Summer	Bright	-17.899	0.03455	AB	11.2956	0.0693	A
	East	-17.949	0.03149		13.321	0.06316	B
	Cameron			A			
	Jakkula	-17.648	0.06511	AB	12.7201	0.1306	C
	McGrail	-17.778	0.08765	B	12.3465	0.17582	C
Fall	Bright	-17.866	0.0541	AB	11.3885	0.10852	A
	East	-17.963	0.05764		13.2399	0.11562	B
	Cameron			A			
	Jakkula	-17.62	0.13252	AB	13.5951	0.26582	B
	McGrail	-17.461	0.12396	B	13.3597	0.24865	B
Winter	Bright	-17.701	0.06297	A	11.3086	0.12632	A
	East	-18.122	0.04489		12.9908	0.09005	B
	Cameron			B			
	Jakkula	-17.955	0.11687	AB	12.6368	0.23443	B

VITA

Todd Langland was born in November 1988 in Monterey, California. He grew up in Carmel Valley, California where he enjoyed a childhood spent in the outdoors throughout the greater Monterey Bay area. He graduated from Carmel High School in 2006, after which he attended the University of California, San Diego in La Jolla, California. It was here, inspired by both the exceptional courses and his work with the Ohman lab down the hill at Scripps Institutions of Oceanography, that Todd realized his true passion for marine research. He graduated with a Bachelor of Science in Ecology, Behavior, and Evolution in 2010 from UCSD, followed by a trip across the country to participate in an aquarist internship with Mote Marine Laboratory in Sarasota, Florida. He entered the masters program in the Department of Oceanography and Coastal Sciences at Louisiana State University in 2011 under the supervision of Dr. James H. Cowan, Jr. In October 2013, Todd switched to the Department of Oceanography and Coastal Sciences doctoral program, and will receive his PhD in August 2015.