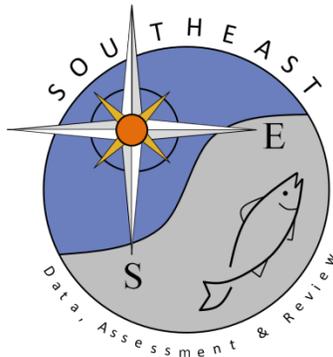


Investigation of the relative habitat value of oil/gas platforms and natural banks in enhancing stock building of reef fish in the western Gulf of Mexico

Gregory W. Stunz, Matthew J. Ajemian, Matthew K. Streich, Rachel Brewton, Charles Downey, and Quentin Hall

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**INVESTIGATION OF THE RELATIVE HABITAT VALUE OF OIL/GAS  
PLATFORMS AND NATURAL BANKS IN ENHANCING STOCK  
BUILDING OF REEF FISH IN THE WESTERN GULF OF MEXICO**

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## II. ABSTRACT

Artificial reef development is a popular management tool used to enhance fish stocks, mitigate degradation or loss of natural habitats, and provide additional recreational opportunities. Despite the popularity and support for artificial reef programs, our understanding of how artificial reefs affect marine fisheries is surprisingly limited. Thus, the goals of this study were to use concurrent comparisons of artificial reefs (standing or reefed oil and gas platforms) and natural habitats to provide key information to evaluate the utility of artificial reefs for reef fishes, in particular Red Snapper (*Lutjanus campechanus*), as well as differences in age, growth, fecundity, and trophic interactions of Red Snapper populations on artificial reefs and natural banks. Remotely operated vehicle (ROV) surveys were used to show how fish communities differed between artificial reefs and natural banks. While Red Snapper density was greater over artificial structures, estimates of total abundance and biomass were much greater on natural banks—approximately 7.6% of the 2012 GOM annual catch limit. In addition, vertical longline surveys determined that Red Snapper size structure, age and growth differed between artificial and natural habitats. Size and age distributions suggested natural banks supported larger and older individuals, and the logistic growth model suggested fish at artificial reefs reached larger sizes-at-age than those from other habitats. Fecundity parameters (sex, total weight, gonad weight, total length) were also measured, and these data indicated that Red Snapper fecundity and spawning behavior were similar among natural, standing, and reefed habitats. These results suggest that artificial reefs are functionally similar to natural reefs in terms of reproductive output. We also compared the diet and stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope signatures of Red Snapper collected from natural reefs to those from artificial structures. Overall, crustaceans of the class Malacostraca dominated the diet (43.20% IRI), followed by fish in the class Osteichthyes (29.69 %IRI). Despite differences in major prey categories, feeding strategy diagrams revealed Red Snapper to be a generalist consumer at all habitats. Stable isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) values differed by habitat and size class with a significant interaction observed (MANOVA  $p < 0.0001$ ). Post-hoc analyses suggest that some size classes of Red Snapper are feeding at a slightly higher trophic level on standing platforms, while natural and reefed habitats were generally similar. These findings broadly suggest that reefed habitats in the GOM are functioning similarly to natural habitats, but there may be subtle trophic differences between habitats and over time based on available prey resources. This study highlights the benefits of artificial reefs to Red Snapper and indicates that these habitats could contribute similarly to overall stock health and productivity.

### III. EXECUTIVE SUMMARY

The western Gulf of Mexico (GOM) is comprised largely of soft-bottom habitat and low-relief natural reefs (Parker et al. 1983). Due to oil and gas production a large number of artificial structures have been installed which function as higher relief reefs surrounded by rich fish communities (Ajemian et al. 2015b). Understanding the environmental function of both standing and reefed oil and gas platforms and especially comparing its natural habitats is essential, because habitat may be limiting to fish populations in the western GOM (Shipp and Bortone 2009). Numerous studies have documented increases in fish (adult, larval and juvenile) abundance and recruitment to oil and gas platforms and other artificial structures. Fisheries catch rates also increase over and around these reefs (Simmons and Szedlmayer 2011; Gallaway et al. 2009). While the amount of increase is still debated in the literature (reviewed in Goodsell and Chapman 2009), most scientists agree that artificial reefs have the potential to positively affect fish populations. However, the actual amount of enhancement and functionality compared to natural reefs remains largely unknown. Therefore, more information about how different reef types (standing and reefed oil and gas platforms, and natural banks) function in terms of age, growth, fecundity, and trophic interactions was needed.

Recent evidence suggests that some artificial structures in the Gulf may serve as long-term residence sites for reef-associated species such as Red Snapper (*Lutjanus campechanus*). There has been extensive debate on how artificial reefs function to enhance Red Snapper productivity, which is critical information with the controversy concerning the management of the species (Cowan et al. 2011). Thus, the goals of this study were to: (1) Investigate the value of offshore habitats for reef fish communities and their potential to enhance stock building efforts in the western Gulf; (2) evaluate biological aspects (e.g., age, growth, fecundity) of Red Snapper among offshore habitats of the western Gulf; and (3) compare trophic differences of Red Snapper across different offshore habitat types.

During fall 2012, remotely operated vehicle (ROV) surveys were used to compare fish communities between artificial reefs (i.e., reefed platforms; n=5) and adjacent natural banks (n=5) in the western GOM. Surveys successfully documented 79 species representing 28 families. Multivariate analyses indicated that fish communities at artificial reefs were distinct from those at natural banks. Post-hoc analyses indicated these differences were driven by high abundances of transient, mid-water pelagics and other gregarious species at artificial reefs. Many fisheries species like Red Snapper were shared between both habitat types, with density estimated to be nearly eight times greater at artificial reefs. Despite lower densities at natural banks, the disproportionately larger areas of these habitats resulted in relatively high total abundance estimates—approximately 7.6% of the 2012 GOM Red Snapper annual catch limit (8.08 million lbs) — a finding that has significant implications for Red Snapper and artificial reef management in the GOM. This study suggests that, although fish community structure may differ between these two habitats, artificial reefs serve as important habitat for species such as Red Snapper and may also divert fishing pressure from for sensitive natural habitats; however, future studies addressing species-specific

life history traits are needed to better understand the function and performance of artificial reefs in supporting fisheries productivity.

From 2012 – 2014, a fishery-independent vertical line survey allowed the assessment of Red Snapper relative abundance, size and age structure, and growth parameters among standing oil and gas platforms, reefed decommissioned platforms, and natural banks in the western GOM. During the study, 1,170 Red Snapper ranging from 275 to 855 mm TL were captured. Vertical line catch per unit effort (CPUE) data showed no differences among these three habitat types. Ages determined for 1,143 individuals ranged from 2 to 30 years; however, most (90%) were younger than age-8. Size and age frequencies revealed natural banks supported more large and relatively old fish compared to standing platforms or artificial reefs, although this difference was heavily influenced by a single bank that had significantly larger and older Red Snapper than other sites. Among a suite of growth models fit to size-at-age data, the logistic model provided the best fit and suggested that fish from artificial reefs reached larger sizes-at-age than fish from either standing platforms or natural banks. Likewise, fish collected from these longline surveys were used to characterize trends in Red Snapper reproduction in the northwestern Gulf at oil and gas platforms relative to natural reefs. Fecundity parameters (sex, total weight, gonad weight, total length) were measured, and these data showed Red Snapper fecundity and spawning behavior were similar among all habitats. These results suggest that artificial reefs are functionally similar to natural reefs in terms of reproductive output.

Identifiable prey was obtained from 533 stomachs collected during 2013-2014 sampling seasons. Overall crustaceans in the Malacostraca class dominated the diet (43.20% IRI), followed by fish in the Osteichthyes class (29.69 %IRI). Despite differences in major prey categories, feeding strategy diagrams revealed Red Snapper to be a generalist consumer at all habitats. Stable isotope analysis of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  was conducted (natural n= 163, standing n=145, and reefed n=139).  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values differed by habitat and size class (100 mm bins) with a significant interaction observed (MANOVA  $p < 0.0001$ ).  $\delta^{13}\text{C}$  varied by size class ( $p < 0.0001$ ), but not by habitats ( $p = 0.06$ ), and there was a significant habitat and size interaction ( $p < 0.01$ ).  $\delta^{15}\text{N}$  varied by size class ( $< 0.0001$ ) and habitat ( $p < 0.0001$ ); the interaction term was also significant ( $p = 0.016$ ). Post hoc multiple comparisons (Tukey HSD) showed that Red Snapper at the 501-600 mm and 601-700 mm size classes on standing platforms were more  $\delta^{13}\text{C}$  depleted than either natural or artificial reef habitats. Similarly,  $\delta^{15}\text{N}$  varied by size class with standing significantly more enriched than natural in 501-600 and 601-700 mm fish but not significantly greater than fish from reefed habitats. This suggests in some size classes, Red Snapper on standing platforms are feeding at a slightly higher trophic level, while natural and reefed habitats were generally similar. This observed isotopic enrichment was supported by a more piscivorous diet at standing platforms, when compared to other habitats. These findings broadly suggest that reefed habitats in the GOM are functioning similarly to natural habitats, but there may be subtle trophic differences between habitats and over time based on available prey resources.

Collectively, our findings suggest artificial reefs can be a valuable tool for enhancing the Red Snapper population. With the rapid decommissioning of oil and gas platforms and subsequent conversion to artificial reefs (via “Rigs-to-Reefs”), our project was developed to assess potential impacts of these artificial habitats on Red Snapper. Generally, we found that individuals from reefed platforms performed similarly (trophic ecology, timing of reproduction) to fish from standing oil and gas platforms and natural banks. As such, continued allocation of decommissioned platform materials to Rigs-to-Reefs should have positive impacts on the Red Snapper stock overall. Given the large area of natural habitats in the GOM, and that the largest and oldest fish were consistently found on these natural banks, artificial reefs may also be an effective management option for diverting fishing effort away from a large portion of the spawning stock. Thus, together, both artificial and natural habitats can play complementary roles in enhancing the Gulf of Mexico Red Snapper stock

## IV. PURPOSE

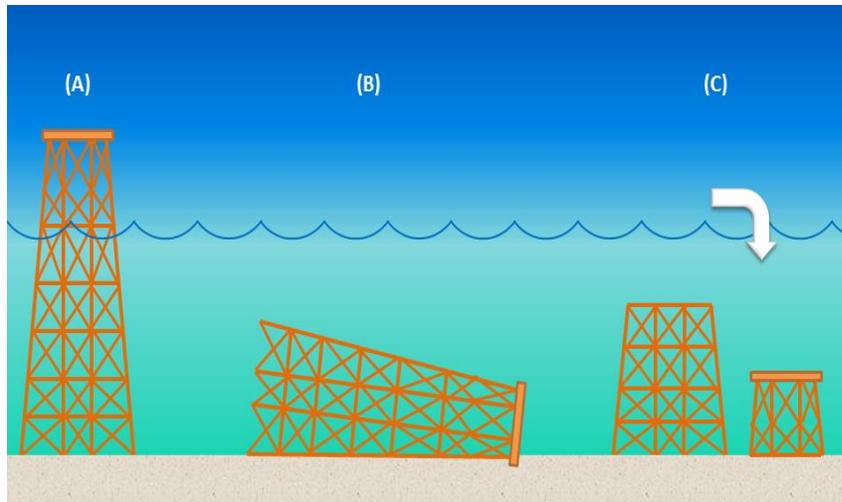
### A. Description of the problem

During the last few decades, artificial reef development has been undertaken to create new habitat for mitigation/restoration, increase fisheries production, and promote recreational use such as diving and fishing (Dupont 2008; Oh et al., 2008; Baine and Side 2003; Baine 2001; Pitcher and Seaman 2000). Numerous studies have documented increases in fish (adult, larval and juvenile) abundance and recruitment to oil and gas platforms and other artificial structures (Simmons and Szedlmayer 2011; Gallaway et al. 2009; Dupont 2008; Lindquist et al. 2005; Szedlmayer and Shipp 1994), and fisheries catch rates also increase over and around these reefs. While the amount (redistribution, aggregation or actual stock enhancement) of increase is still debated in the literature (Gallaway et al. 2009; reviewed in Goodsell and Chapman 2009; Shipp and Bortone 2009; Baine and Side 2003; Pitcher and Seaman 2000; Grossman et al. 1997), most scientists agree that artificial reefs (and restoration projects in general) have the potential to positively affect fish populations and increase opportunities for natural resource use by forming the base of the food web and providing structured habitat for a host of reef fish. However, the actual amount of enhancement and functionality compared to natural reefs remains largely unknown.

The addition of oil and gas production platforms to the northern Gulf has resulted in one of the largest unplanned artificial reef complex, increasing reef habitat by 4.1% (Stanley and Wilson 2003) to an ecosystem composed primarily of mud and sand substrate (Parker et al. 1983). A recent federal policy directive (commonly known as “Idle Iron Policy”) mandated the rapid removal of inactive platforms. The high decommissioning rate has numerous user groups voicing great opposition due to the loss of habitat and marine life that accompany these structures. This controversy has culminated in a flurry of legislation (e.g., “Rigs to Reefs” Habitat Protection Act 2011 and others) to preserve these structures (Figure 1). However, the

decision has been severely handicapped by a lack of data on the value of artificial reefs to exploited fisheries species. For example, while research generally shows positive effects of artificial habitats for Gulf reef fish, the debate over whether these structures enhance stock rebuilding efforts is largely unknown. It has been suggested that the addition of artificial habitat in the Gulf has resulted in an increase in the harvest potential of Red Snapper and any decrease in artificial structure (such as large-scale platform removals) may have negative results on Red Snapper populations (Shipp and Bortone 2009). Yet, others are not convinced that the introduction of artificial structures has been responsible for increased production of Red Snapper (Cowan et al. 2011). Controversy still exists over the exact function and result of artificial reefs in the Gulf – especially in relation to essential fish habitat and the increased fishing pressure exerted at these sites (Powers et al 2003). In the western Gulf, where reef habitat is limiting and platforms are relatively few in number (approximately 156 within 100 nm of Port Aransas), removal of existing platforms may disproportionately affect reef fish populations and could limit settlement of recruits (Lindquist et al., 2005). Previous studies on fish use of platform structures in the western Gulf are limited, and there is a paucity of peer-reviewed literature focusing on comparisons of natural banks and platform structures. Thus, this lack of essential data is greatly hindering management and stock assessment processes, and data on the role of artificial structures will be essential in moving the process forward.

In Texas waters 50% of fishing trips and 100% of dive trips target platforms (Hiatt and Milon, 2002). Recognizing the economic value of these structures, the Texas Legislature created the Texas Artificial Reef Plan that was implemented by the Parks and Wildlife Commission in 1990. This plan created the Artificial Reef Program and outlined its mission. In addition to planning and developing artificial reefs, the program also monitors abundance, stability, and movement of reef associated species. Texas' Artificial Reef Program is directed to pursue three types of reef development: Rigs to Reefs (oil and gas platforms), Ships to Reefs (Liberty ships, etc.), and Nearshore/Shallow Reefs (concrete, bridge/road material). Although Texas has one of the largest rigs-to-reefs programs, clearly much more scientific data and monitoring is needed to assess how fish populations use these habitat types. For example, it is unknown which rig-to-reef option (e.g., toppled versus standing) best supports fisheries production (Fig. 1). Studies have suggested that converting a standing platform to a toppled or partial removal artificial reef results in a significant loss of a portion of the fish community by reducing the vertical relief (Wilson et al. 2003). To better understand the effects of reefing practices on fish communities, there is a need for sound science so that local, state, and federal managers can make informed decisions. Because the number of platforms has been predicted to decline 29% (or more) from 1999-2023 (Pulsipher et al. 2001) as removals exceed installations, additional data which compare the fish community structure of standing and toppled oil and gas platforms and by natural hard-bottom in relation to reef fish is especially important and timely.



**Figure 1. Rigs to Reefs Options:** Upon decommission, rigs may be left standing (a), toppled (b), or partially dismantled or “cutoff” (c).

Recent evidence suggests that some artificial structures in the Gulf may serve as long-term residence sites for reef-associated species such as Red Snapper (Schroepfer and Szedlmayer 2006; Szedlmayer and Schroepfer 2005). However, Peabody and Wilson (2010) found that acoustically tagged Red Snapper exhibit low site fidelity to platforms off the Louisiana coast over time periods of months. In addition, it appears that larger (age 3+) Red Snapper may migrate to deeper, less vertically structured habitat, while artificial structures such as oil and gas platforms are primarily dominated by age-2 and age-3 fish (Nieland and Wilson 2003; Gitschlag et al. 2003). The decrease in individuals older than age-3 on platforms may be caused by emigration, low site fidelity or reduced recruitment of older fish. As Red Snapper continue to mature, larger individuals are less dependent upon structure, including platforms, and can be found on outer shelf-edge reefs (Render 1995; Mitchell et al. 2004). In fact, our lab has acoustically tagged several Red Snapper that moved to and from platforms and natural banks over the course of several years (J. Curtis, dissertation in preparation) suggesting there is at least some connectivity. With such extensive debates on how artificial reefs function to enhance Red Snapper productivity and the controversy concerning the management of the species (Cowan et al. 2011), there is a strong need for a comprehensive assessment of life history characteristics of Red Snapper on natural reefs and banks.

A unique opportunity existed, paring this project with a related, but synergistic, ongoing study we have developed with Texas Parks and Wildlife Department (TPWD) to perform a fishery-independent survey for reef fish on artificial reefs off the Texas coastal-bend. In particular, we are using a remotely operated vehicle (ROV) and SCUBA surveys to examine reef characteristics and fish communities at 15 offshore sites. These sites vary in structure and relief, and include toppled rigs, cut-off rigs, concrete culverts, liberty ships and barges. With limited internal funding we have also been developing the use of vertical longlines as a complementary tool for assessing reef fish abundance, particularly when seasonal fluctuations in turbidity can

severely limit the use of visual-based surveys, and as a means to collect biological samples at these offshore sites. We have collected fish samples over the past several years, however, the analysis, focus, and funding limitation of this synergistic project prevented us from further characterizing these resulting areas. This grant represented a leveraging opportunity for filling data gaps that would otherwise be impossible.

Specifically, funding from this project allowed us to expand these assessments and comprehensively quantify other potentially important metrics to the structure and function of artificial reefs such as age, growth rates, diet, trophic level, and fecundity of economically important species. These life history data are crucial to understanding the relative habitat value of platforms and natural banks and will also include key parameters that are much needed for ongoing data assessments for these species. Additionally, we added three natural bank sites to our survey design to quantify the relative habitat value differences between artificial reefs and natural habitats in the western Gulf. In anticipation of federal management needs, we opportunistically began collecting otoliths, tissue samples, stomachs, and gonads from reef fish collected during these studies on three natural bank sites, three standing platforms and three toppled platforms in 2013. This grant allowed us to further analyze the samples already acquired, as well as collect an additional two years of life history data. This study improved our understanding of how structure type influences various biological processes in reef fish at various habitats. Thus, this project represents an unprecedented opportunity to couple biological information with estimated abundance data from our fishery-independent surveys, which were specifically identified as data needs in the latest Red Snapper South East Data, Assessment, and Review (SEDAR 2012). These data were used to estimate the relative habitat value of artificial reefs and natural habitats for Red Snapper, which is routinely assessed under the SEDAR.

## **B. Objectives of the project**

The specific objectives of this study were to:

- (1) Investigate the value of offshore habitats for reef fish communities and their potential to enhance stock building efforts in the western Gulf.
- (2) Evaluate biological aspects (e.g., age, growth, fecundity) of Red Snapper among offshore habitats of the western Gulf.
- (3) Compare trophic differences of Red Snapper across different offshore habitat types.

## V. APPROACH

### A. Description of the work performed

#### *Fish Community Comparison - Artificial Reefs and Natural Banks (Obj. 1)*

**Introduction** - Artificial reefs are constructed from a diverse assortment of materials and serve a wide variety of purposes, but they are widely regarded as habitat for fishes (Bohnsack and Sutherland 1985; Seaman 2000; Baine 2001; Baine and Side 2003; Broughton 2012). In the northwestern Gulf of Mexico (GOM), oil and gas infrastructure represents the largest artificial reef complex in the world (Dauterive 2000). Currently, about 2,300 oil and gas platforms (hereafter “platforms”) are installed across the northern GOM shelf (BSEE 2016), providing additional hard substrate on an otherwise unstructured bottom that becomes suitable ‘reef’ habitat for a variety of marine life (Gallaway and Lewbel 1982; Dauterive 2000; Stanley and Wilson 2000; Kaiser and Pulsipher 2005). Prior to the introduction of platforms, hard substrate was relatively scarce as the northwestern GOM shelf is dominated by soft sediments consisting of clay, silt, and sand (Parker et al. 1983; Rezak et al. 1985). Consequently, artificial reefs including platforms and the high abundance of fish that occur on these structures have become an integral component of regional fisheries.

Many of the platforms in the northwestern GOM are nearing the end of their production lifespans and will soon be decommissioned (Macreadie et al. 2011; Fowler et al. 2014). Typically, this process entails severing the platform below the seafloor and towing it to shore (i.e., complete removal); however, platforms may also be accepted into a state-run reefing program known as Rigs-to-Reefs (RTR) in which structures can be retained as permitted artificial reefs. Accepted structures can be towed to permitted reefing areas, toppled in place (i.e., laid on seafloor), or partially removed (i.e., only top portion of the steel jacket removed), and thus continue to serve as habitat for fish and other reef species (Dauterive 2000; Kaiser and Pulsipher 2005). While a portion of these platforms will be accepted into RTR programs, much of this habitat will be permanently removed from the northern GOM ecosystem. As such, it is critical to determine what effects these changes in habitat may have on marine fish populations.

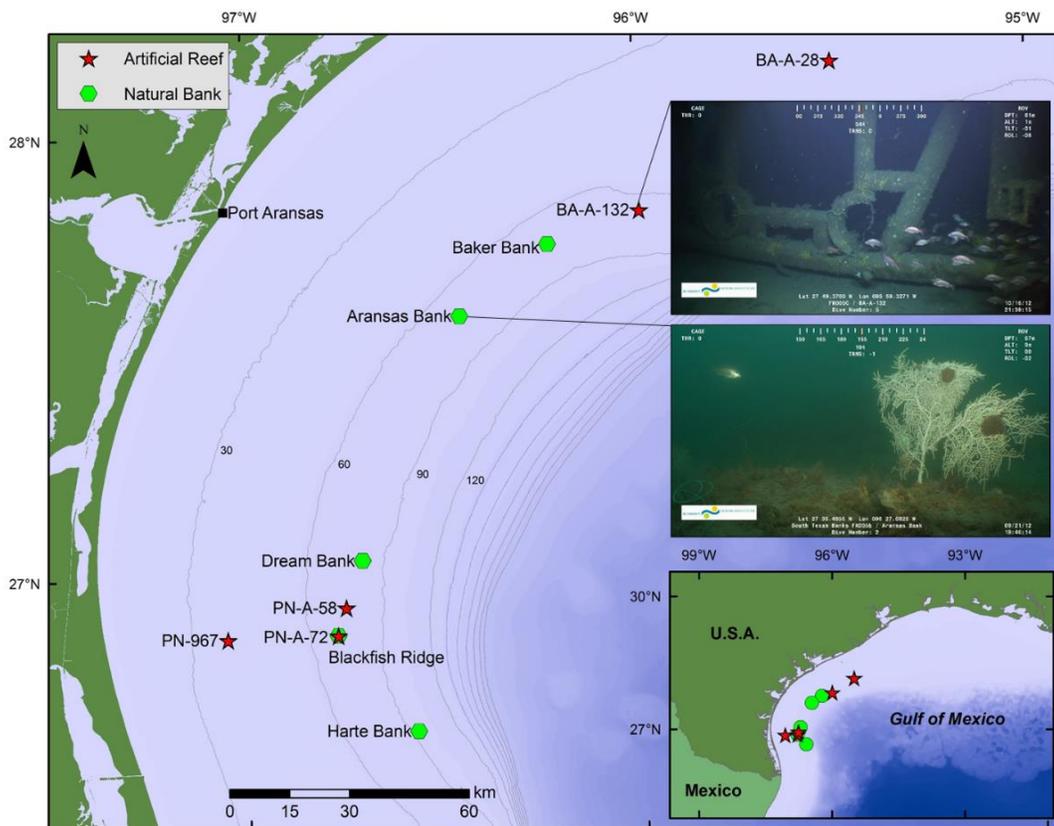
Several studies assessing fish communities at artificial reefs have shown that densities of many important fisheries species are higher on artificial reefs than nearby natural habitats (Stanley and Wilson 1996, 1997, Love and York 2005; Love et al. 2005, 2006). Whether these observed increases in fish densities represent increased production (i.e., stock enhancement) or simply redistribution (i.e., aggregation) of existing biomass has been and is currently vigorously debated (Bohnsack 1989; Carr and Hixon 1997; Grossman et al. 1997; Lindberg 1997; Shipp and Bortone 2009; Cowan et al. 2011; Claisse et al. 2014). Generally, this uncertainty is driven by a lack of fishery-independent studies comparing artificial reefs to their natural counterparts, leaving significant knowledge gaps regarding the relative value and function of artificial reefs towards supporting fisheries productivity.

Determining the effects of artificial reefs on marine fish populations necessitates information on species composition and abundances from both natural and artificial habitats (Carr and Hixon 1997). In the northern GOM, previous investigations of community composition have primarily focused on assessing the fish populations inhabiting standing platforms. Although less common, natural banks providing hard substrate and substantial vertical relief are scattered across the mid- to outer-shelf (Rezak et al. 1985). In fact, these prominent bathymetric features are thought to be the historical centers of abundance for diverse reef species and also economically important Red Snapper (*Lutjanus campechanus*) and Vermilion Snapper (*Rhomboplites aurorubens*; Camber 1955; Dennis and Bright 1988; Gledhill 2001). Despite the likely importance of these habitats, limited studies comparing artificial reef fish communities to those of nearby natural habitats in the northern GOM have been conducted (e.g., Rooker et al. 1997; Wilson et al. 2003, 2006; Patterson et al. 2014; Langland 2015). With the exception of Patterson et al. (2014) who compared fish community structure at smaller scale artificial reefs (i.e., reef pyramids) and natural reef habitat in the northeastern GOM, these studies have focused on comparisons between diapiric shelf-edge banks (e.g., the intensively studied Flower Garden Banks), standing platforms, and a limited number of artificial reefs in the northwestern GOM. Certainly, more research is needed to better understand these dynamics.

Farther south off the coast of Texas, natural bank habitats have different geological and physical characteristics than the shelf-edge banks of the northern GOM (i.e., drowned corallgal banks rather than diapiric banks with extensive vertical relief; Berryhill 1987). In fact, relatively little is known about fish community structure at natural banks or artificial reefs in the western GOM region given the difficulties in sampling these deep offshore habitats (Dennis and Bright 1988; Ajemian et al. 2015a). Dennis and Bright (1988) presented the first quantitative study of fish communities at natural banks off the coast of Texas using data from submersible transects. Using ROV surveys, Ajemian et al. (2015b) performed the first comprehensive assessment of fish community structure among artificial reefs (standing platforms, RTR artificial reefs, and liberty ship reefs) in the region. In their assessment, bottom depth alone best explained patterns in fish community structure that were observed, and they speculated that variation was driven by the ambient communities present among the various depth strata.

In this section, we present the first comparative study of reef fish community structure among RTR artificial reefs and drowned corallgal banks in the western GOM region. Despite the importance of these two habitats to fish and fisheries in the GOM, such comparative investigations have not been conducted. The primary goal of this study was to assess fish community structure of mesophotic natural banks and RTR artificial reefs in the western GOM using ROV surveys.

**Study area** - Our study area encompassed five artificial reef sites and five natural banks interspersed along the Texas shelf in the western GOM (Figure 2). The region is characterized by a gently sloping shelf, substrates dominated by terrigenous sediments consisting of silt and clay muds, and a generally low availability of natural hard substrates with vertical relief  $\geq 1$  m (Parker et al. 1983; Rezak et al. 1985).



**Figure 2. Map of artificial reefs (red stars) and natural banks (green circles) surveyed using the Global Explorer ROV in September and October 2012. Bathymetric contours (gray lines) are displayed in 30 m intervals. Inset map (bottom right) shows study location**

Artificial reefs surveyed in this study are part of Texas Parks and Wildlife Department's Artificial Reef Program and consisted of multiple RTR structures at each reef site (i.e., within a permitted reef site, 2-4 structures were present). Ambient bottom depths of these reefs ranged from 36 to 75 m (mean = 58 m), while vertical relief ranged from 16 to 40 m (mean = 25 m; Table 1). The natural habitats surveyed in this study are part of a group of bathymetric features collectively known as the South Texas Banks (Rezak et al. 1985; Nash et al. 2013). Unlike the natural banks in the northern GOM, which formed atop diapiric salt intrusions, the South Texas Banks have been classified as drowned remnant corallgal reefs that flourished during the Pleistocene (Rezak et al. 1985; Belopolsky and Droxler 1999). Natural banks surveyed in this study were characterized by ambient bottom depths ranging from 70 to 96 m (mean = 79 m) and vertical relief ranging from 12 to 16 m (mean = 13 m; Table 1). All sites surveyed in this study are influenced by a persistent but variable nepheloid layer which can be up to 35 m thick (Shideler 1981; Rezak et al. 1985). The nepheloid layer is formed from re-suspended sediments and undoubtedly affects the ecology of biota inhabiting the reefs (Dennis and Bright 1988; Rezak et al. 1990; Tunnell et al. 2009).

**Table 1. Physical characteristics of natural banks and artificial reefs surveyed with ROV along the Texas Shelf in fall 2012. Structure depth is the shallowest depth of structure at the site while relief is the vertical extent from the seafloor to the top of structure.**

Habitat	Site	Survey date	Bottom depth (m)	Structure depth (m)	Relief (m)	Survey temp (°C)	Area (km <sup>2</sup> )
Natural	Baker Bank	09/19/12	74	58	16	24.0	1.33
	Aransas Bank	09/21/12	70	58	12	24.0	0.50
	Dream Bank	09/23/12	82	68	14	24.6	2.29
	Blackfish Ridge	09/26/12	72	60	12	25.5	1.12
	Harte Bank	09/27/12	96	83	13	22.9	0.31
Artificial	BA-A-28	10/09/12	46	27	19	27.1	3.90E-03
	PN-A-58	10/15/12	75	52	23	27.1	1.65E-03
	PN-A-72	10/15/12	72	32	40	27.1	1.08E-03
	PN-967	10/15/12	36	20	16	27.3	1.60E-03
	BA-A-132	10/16/12	61	32	29	27.0	6.73E-03

**ROV Community Surveys** — Surveys of fish communities were conducted using the Global Explorer MK3 ROV (Deep Sea Systems International, Inc.) during two cruises aboard the R/V *Falkor* spanning September 17-29, 2012 (natural banks), and October 8-20, 2012 (artificial reefs). The Global Explorer is a large, working-class ROV (3,200 lbs; 3,000-m depth rating) equipped with Ocean ProHD<sup>®</sup> cameras (160° tilt and 105° viewing angle), digital photo with laser scaler, multibeam imaging and scanning sonar, real-time CTD, LED lights, and a manipulator arm. During ROV deployments, the R/V *Falkor* maintained a fixed distance away from the artificial reef or natural bank under investigation using a dynamic positioning system. The position of the Global Explorer was logged using a Sonardyne Ranger 2 Ultra-Short BaseLine (USBL) acoustic positioning system allowing estimates of distance surveyed. The ROV lights remained on during all ROV deployments. Real-time observations were made possible via live-feed video in the ROV control room, and all video was recorded and saved for further viewing and processing.

We surveyed the fish communities of both artificial reefs and natural banks using continuous transects that began as soon as the ROV entered the water and terminated when the ROV surfaced (i.e., one continuous transect per site; artificial n = 5; natural n = 5). However, the distinct differences in the physical constraints of the structure of the two habitats (e.g., artificial – complex, high relief; natural – lower relief spread over a large area; Table 1) necessitated some slight modifications to our survey methods. Continuous roving transects (CRT) were used to survey reef fish communities at artificial reefs (Ajemian et al. 2015a). Generally, CRTs entailed a horizontal rove around the top of the artificial reef, then 10 m depth intervals for 1 min periods

until the bottom was reached or the nepheloid layer prevented further observations. When this depth was reached, the ROV performed another rove around the outer surface of the down-current side of the reef. This method was recently demonstrated to be effective in documenting the reef fish community over the large vertical expanse of RTR structures (Ajemian et al. 2015a, 2015b). Because artificial reef sites had multiple RTR structures, we attempted to survey at least two structures when currents and other conditions allowed. During CRTs, the ROV maintained a distance of approximately 1-2 m from the artificial reef structures to minimize the possibility of entanglement.

Transect placement on natural banks was guided by geo-referenced multibeam maps of bank bathymetry. Transects typically started at the base of the bank, ascended over the terraces, across the reef crest, and continued down to the base on the opposite side. Accordingly, ROV transects spanned the entire range of habitat zones present at each natural bank surveyed. We used direct observations from these ROV transects to document the fish communities inhabiting the five natural banks surveyed. The ROV maintained a consistent camera tilt, viewing angle ( $105^\circ$ ), and height above the seafloor ( $\sim 1$  m). Visual field width was estimated using the laser scale to measure the field of view at approximately fixed intervals along transects. Measurements were then averaged to provide a visual field width for each transect. Visual field width ( $\sim 3.5$  m) and ROV speed (0.1 m/s) were the same as CRT surveys on the artificial reefs except when the ROV occasionally paused to photograph species with uncertain identification or make collections of rock, coral, or other invertebrate fauna.

Recorded video was examined in the lab by two independent viewers. Viewing began as soon as the ROV entered the water and ended when the ROV surfaced. Fish were identified to the lowest possible taxon, enumerated, and recorded each time they entered the field of view. If directionality of large schools was apparent, enumeration was completed by viewing paused frames in succession and then summing the counts. Time of day, depth, salinity, temperature, and ROV heading were also recorded with each count. Species-specific counts of the two viewers were compared and jointly reviewed only if the counts differed by  $>5\%$ . For each survey, we generated a MinCount for each species that was observed (i.e., at minimum, that many individuals were present during the survey). The MinCount, also commonly referred to as MaxN, is a conservative metric that minimizes the probability of double counting. It represents the maximum number of individuals on the screen at any one time during the survey, and its use as an index of relative abundance is widespread throughout the literature (Ellis and DeMartini 1995; Cappo et al. 2004; Wells and Cowan 2007; Ajemian et al. 2015a, 2015b; Campbell et al. 2015).

**Community Analyses** — We began our comparison of fish communities on artificial reefs and natural banks by assessing species frequency of occurrence and identification and enumeration of species unique to either habitat. Patterns of diversity were investigated using traditional diversity measures including species richness, Shannon diversity ( $H'$ ), and Pielou's evenness ( $J'$ ). Diversity metrics were calculated using the DIVERSE routine (Primer v7; Clarke

and Warwick 2001). Potential differences in richness, diversity, and evenness between artificial reefs and natural banks were tested using Welch's *t*-test. MinCounts were examined by species for each ROV survey.

Patterns in the observed fish community data were investigated with multivariate methods in the PRIMER v7 statistical package (Clarke et al. 2014a). Species-specific MinCounts were first square-root transformed to down-weight the contribution of dominant species to subsequent analyses. These data were then converted into a resemblance matrix using Bray-Curtis similarities. Non-metric multidimensional scaling (nMDS) was run on the resemblance matrix to visually assess group structure among our samples. Overall effects of habitat type on the observed reef fish communities were tested with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). We used a one-way design to test the null hypothesis that there was no difference in fish community structure between artificial and natural habitats. Species-specific contributions to the observed similarity within or dissimilarity between habitats were investigated with similarity percentages (SIMPER; Clark 1993). We followed this analysis with hierarchical agglomerative clustering (via CLUSTER) and similarity profile (SIMPROF) testing to determine whether it was appropriate to interpret the resulting nMDS groupings. We used SIMPER to determine which species were responsible for the variation among resulting groups. Because species do not arrive independently in samples (Clarke et al. 2006), we also performed an inverse analysis (e.g., Field et al. 1982) to determine if species were positively associated in our samples (i.e., MinCounts fluctuate in proportion across samples). Prior to beginning this analysis, we used Type 2 SIMPROF to test the null hypothesis that species were not associated with each other (Sommerfield and Clark 2013). The species-specific count data set was reduced to include only those species whose MinCount accounted for >5% in any one sample. A species similarity matrix was then created using standardized species counts and Whittaker's Index of Association (1952). Hierarchical agglomerative clustering in combination with Type 3 SIMPROF were used to test the null hypothesis that species were coherently associated (Sommerfield and Clarke 2013). MinCounts of identified species groups were visualized in a shade plot to qualitatively describe species associations with habitat and habitat characteristics (Clarke et al. 2014b).

Considering that our surveys spanned two distinct habitats with varying physical characteristics, we performed additional analyses to determine whether abiotic factors including structure depth [i.e., depth to top of reef or bank], bottom depth, relief, reef area, and survey water temperature [i.e., taken as the temperature at the median depth of all fish observations]; Table 1) potentially influenced the fish communities we observed. Abiotic data were normalized and converted to a resemblance matrix based on Euclidean distance measures. We ran a RELATE test to assess the agreement between the biotic and abiotic resemblance matrices. Given a significant RELATE test, we then performed a BEST analysis (i.e., Bio-env) to determine which combination of abiotic factor(s) best explained the variation in observed reef fish communities (i.e., highest Spearman's rank correlation coefficient; Clarke 1993; Clark and Ainsworth 1993). All tests of significance were conducted using  $\alpha = 0.05$ .

**Red Snapper Density Estimates** — We estimated Red Snapper density on artificial reefs and natural banks within the study area using standardized transects from the previously described ROV community surveys. We were able to standardize abundance estimates by estimating the area surveyed (e.g., area surveyed = mean visual field width x transect length). Visual field width was estimated as described for community transects, and transect length was estimated using the USBL position data. On artificial reefs, 40 m transects (the approximate length of a toppled RTR structure), representing subsets of the entire CRT used for analysis of community structure, were selected if the ROV was 1) traveling forward at a constant speed (0.1 m/s) and 2) along an approximately straight path. Only Red Snapper that were within 1 m of the outer plane of the reef were counted to control visual field width (i.e., fish were not counted if they were more than 1 m inside the reef). We chose these criteria to help minimize double counting fish and allow better estimates of surface area surveyed – thus providing more accurate density estimates. Generally, transects at artificial reefs were located along piles (toppled RTR structures) or crossbeams (partially removed RTR structures) close to the benthos because the ROV often traveled along these features as it moved from one side of the structure to the next. One transect was analyzed for each structure that was surveyed at an artificial reef site (i.e., two transects were possible at the artificial reefs where two structures were surveyed and the ROV path during the CRT met the two criteria described above). On the natural banks, transects included the entire distance surveyed from the base of the structure, across the bank crest, and down to the opposite base. Red Snapper counts from the community data set were summed if they fell within transect start and end times to generate a total Red Snapper count for each transect. This total count was then divided by the surface area each transect surveyed to estimate Red Snapper density (no. of individuals/m<sup>2</sup>). Because we had a limited number of transects (artificial, n = 8; natural, n = 5), non-parametric bootstrapping with replacement (n = 1000) was used to generate 95% bias-adjusted confidence intervals for Red Snapper density without making assumptions about the population distribution (Efron 1987; Efron and Tibshirani 1993). We used the non-parametric bootstrap test for equality (n = 1000) to determine if there was statistical evidence that mean Red Snapper density differed between artificial reef and natural bank habitats (Bowman and Azzalini 1997). Differences were considered significant at  $\alpha = 0.05$ . All analyses of Red Snapper density were carried out in R 3.2.3 (R Core Team 2015) using functions from the ‘boot’ (Canty and Ripley 2015) and ‘sm’ (Bowman and Azzalini 2014) packages. Total Red Snapper abundance at each site was calculated by multiplying the known area of each bank or reef site (i.e., footprint) by the mean density estimated for the respective habitat type [e.g., known area of BA-A-132 (m<sup>2</sup>) times the mean density on artificial reefs (# of fish/m<sup>2</sup>)].

**Red Snapper Size Structure, Age, and Growth - Artificial Reefs and Natural Banks (Obj. 2)**

**Introduction** - The Red Snapper is an early-maturing, long-lived, demersal reef fish distributed over the western Atlantic continental shelf from North Carolina to the Yucatan Peninsula including the Gulf of Mexico (GOM; Hoese and Moore 1998). They are commonly associated with natural habitats including shell ridges, reefs, and banks, and also a wide assortment of artificial structures such as designated artificial reefs (e.g., reef pyramids, ships, decommissioned oil and gas platforms) and existing oil and gas infrastructure including production platforms and pipelines (Moseley 1966; Wells and Cowan 2007; Gallaway et al. 2009; Topping and Szedlmayer 2011; Piraino and Szedlmayer 2014). In fact, Red Snapper may account for a significant proportion of the total fish abundance at both natural and artificial habitats (Stanley and Wilson 1997, 2000; Gledhill 2001). Consequently, directed recreational and commercial fisheries commonly target Red Snapper at these habitats (e.g., Garner and Patterson 2015).

In the U.S. GOM, the Red Snapper stock has been exploited since the mid-19<sup>th</sup> century and has been classified as overfished since the first stock assessment was conducted in 1988 (Goodyear 1988; Hood et al. 2007; SEDAR 2013). Despite this status, Red Snapper continue to support economically valuable fisheries. For example, from 2010-2014 the recreational fishery averaged > 370,000 targeted trips generating at least \$45 million in economic impact, while commercial dockside revenues from Red Snapper landings during this period averaged \$13.4 million (GMFMC 2015). Nevertheless, due to the continued overfished status of GOM Red Snapper and consequent rebuilding mandates, the fishery is subject to severe regulatory measures (Hood et al. 2007; Strelcheck and Hood 2007).

Given that GOM Red Snapper occur across a variety of natural and artificial habitats, consideration of potential differences in stock demographics among habitats is critical for accurate assessments of stock status and subsequent management recommendations. In addition, the distribution of Red Snapper among these habitat types and potential changes in the availability of different habitats undoubtedly influence stock dynamics (Pulliam and Danielson 1991). Studies identifying demographic differences among habitats are especially timely as changes in the relative amount and types of artificial habitats in the northwestern GOM are occurring. For example, the number of oil and gas platforms (hereafter “standing platforms”) has decreased over the past decade as removals through the decommissioning process have and will likely continue to exceed new installations (Pulsipher et al. 2001; BSEE 2016). A portion of these structures will be converted to artificial reefs via state reefing programs such as Rigs-to-Reefs (RTR), where they are partially removed or toppled (Macreadie et al. 2011). However, the majority of these structures will be returned to shore and scrapped, ceasing their role as fish habitat (BSEE 2016). Thus, an understanding of habitat-specific demographics is imperative to predict what effects these changes in habitat may have on GOM Red Snapper as well as informing the industry and fisheries managers regarding the utility of these structures as artificial reefs.

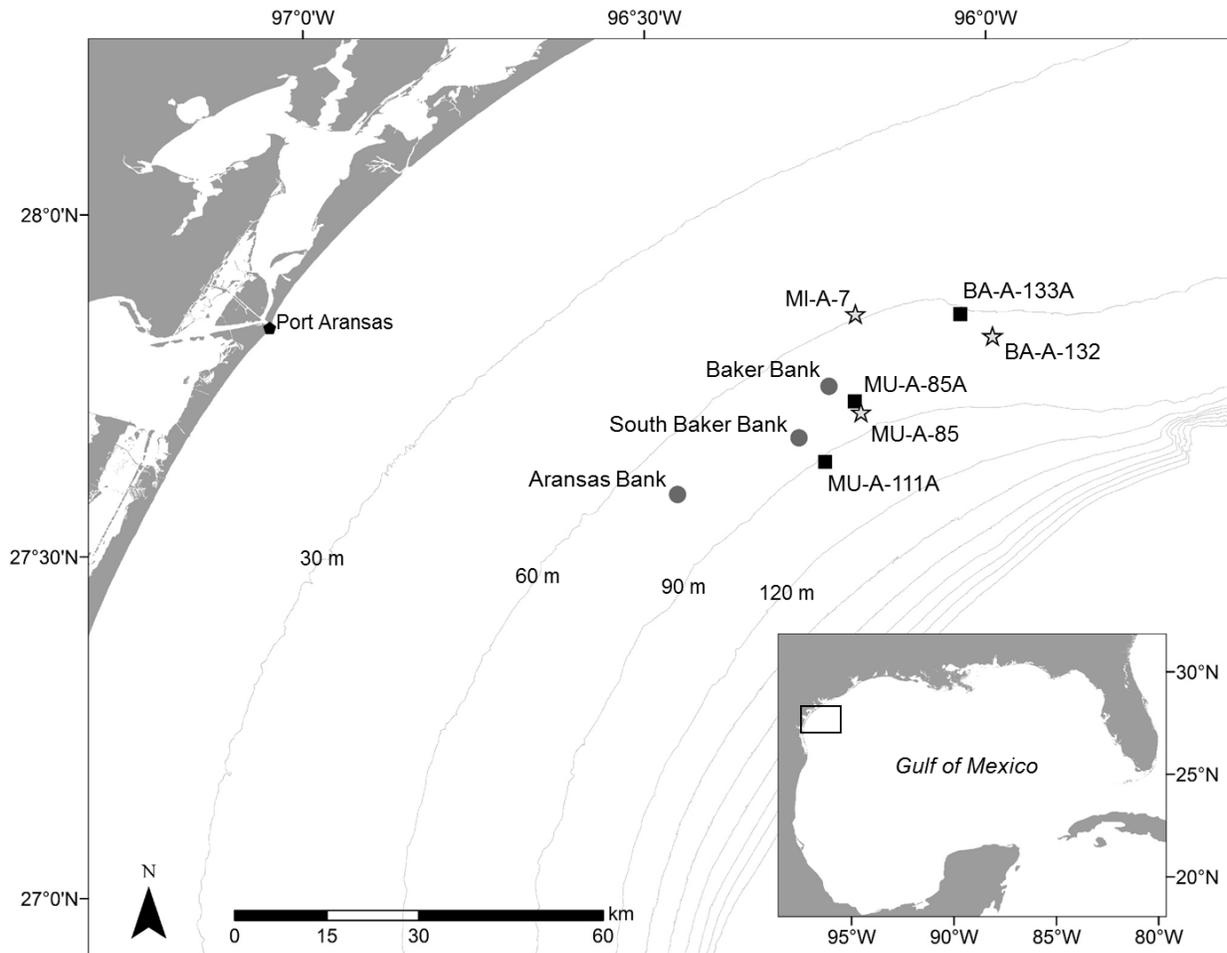
The vast majority of information on Red Snapper life history has been amassed from artificial habitats due to a heavy reliance on fishery-dependent data sources (SEDAR 2013); however, data regarding Red Snapper life history among various habitat types are limited. Specifically, few studies have simultaneously compared Red Snapper demographics from artificial reefs and nearby natural habitats, leaving significant uncertainty in the role artificial reefs play in maintaining the GOM stock. Saari (2011) and Kulaw (2012) provided the first fishery-independent comparisons of Red Snapper demographics among standing platforms, artificial reefs, and shelf-edge natural banks off the coast of Louisiana in the northern GOM, and they demonstrated differences in the age structure, size-at-age, and age-at-maturity among habitats. Further studies of this nature from different regions have been recommended in recent stock assessments (SEDAR 2013) and are warranted, as such Gulf-wide comparisons with fish from natural habitats are essential to understanding how artificial reefs function to support marine fish populations (Carr and Hixon 1997; Love et al. 2006).

The overall goal of this study was to provide new information necessary to evaluate the relative importance of artificial and natural habitats in supporting the GOM Red Snapper stock. To accomplish this goal, we used a fishery-independent assessment of Red Snapper sampled from standing platforms, RTR artificial reefs, and natural banks off the Texas coast in the western GOM. Using vertical line surveys, Red Snapper relative abundance was estimated at each habitat type. In addition, we compared the size structure and age and growth of Red Snapper among the three habitat types to identify potentially important sub-regional differences in these demographic parameters.

**Study area** — The continental shelf of the northwestern GOM is dominated by open expanses of mud, silt, and sand substrates offering little to no vertical relief (i.e., < 1 m; Parker et al. 1983; Rezak et al. 1985). Hard reef habitat is generally limited to natural banks located on the mid- to outer-shelf although there are exceptions (see Rooker et al. 2004; VERSAR 2009; Nash et al. 2013). The prevalence of these features increases as one moves north along the Texas shelf and continues east along the outer Louisiana shelf-edge (Rezak et al. 1985). In addition, artificial structures including standing platforms and artificial reefs also provide reef habitat to a variety of marine life in the region (Gallaway and Lewbel 1982; Ajemian et al. 2015a).

In this study, sampling occurred at three standing platforms (BA-A-133A, MU-A-85A, and MU-A-111A), three artificial reefs (BA-A-132, MI-A-7, and MU-A-85), and three natural banks (Baker Bank, South Baker Bank, and Aransas Bank) in the western GOM (Figure 3). The artificial reefs in this study were developed as part the Texas Parks and Wildlife Department's Artificial Reef Program and consist of multiple decommissioned RTR structures at each reef site. Natural banks in this study were part of a group of bathymetric features known as the South Texas Banks, which have a different geological origin and ecology when compared with the shelf-edge banks off of Louisiana (Rezak et al. 1985; Nash et al. 2013). Sites were interspersed within the 60 – 90 m isobaths and were located approximately 65 – 80 km offshore to limit spatial variability in prevailing hydrographic conditions. A nepheloid layer with varying

thickness persisted at all sites, likely affecting the ecology of these habitats (Shideler 1981; Rezak et al. 1985; Tunnell et al. 2009).



**Figure 3.** Map of the study area depicting locations of artificial reefs (stars), natural banks (circles), and standing platforms (black squares) that were sampled with fishery-independent vertical line surveys from 2012-2014. Gray contour lines represent relevant bathymetry within the study area (30-m isobaths), while the inset map shows the location of the study area relative to the Gulf of Mexico.

**Sampling procedure** — Red Snapper were sampled at the three habitat types with standardized vertical line gear from October 2012 through October 2014. When sampling occurred, all sites were visited within a similar timeframe (i.e., 2-3 weeks) to minimize potential effects of seasonality. Vertical line gear followed specifications of the Southeast Area Monitoring and Assessment Program (SEAMAP) and consisted of commercial grade “bandit” reels spooled with 136-kg-test (300 lb) monofilament mainline, which terminated in a 7.3-m backbone (i.e., leader) constructed with 181-kg-test (400 lb) monofilament. The backbone contained 10 equally-spaced 45-kg-test (100 lb) monofilament gangions, each terminating with

identical circle hooks (Mustad® 39960D; 8/0, 11/0, or 15/0 sizes; same-sized hooks fished on a backbone) baited with cut Atlantic Mackerel (*Scomber scombrus*). A 4.5-kg sash weight was attached to the end of the backbone to allow the gear to fish vertically.

A vertical line “set” consisted of one deployment of each hook size. Therefore, upon arrival at the sampling location, a randomly selected hook size was deployed over either the port or starboard bow of the vessel and allowed to soak for 5 minutes. The gear was then retrieved, and a second randomly chosen hook size (of the two remaining) was immediately deployed off the opposite side of the vessel. Following retrieval of this second backbone, the backbone containing the third (unused) hook size was fished. Hook sizes were then rotated such that each hook size was fished on the first, second, and third drop at a site on a given sampling day. We conducted three replicate sets (i.e., 3 drops of each hook size in each set; 9 drops total) at each site visited on a given sampling day. At standing platforms and RTR artificial reefs, each set was conducted around the artificial structure. Because natural banks were considerably larger than artificial structures (~ 0.006 km<sup>2</sup> compared to ~ 1 km<sup>2</sup>, respectively), sampling area at natural banks was constrained to an area approximately equivalent to the extent of artificial habitats. To do this, a grid with cells the size of the sampling area at artificial sites was overlain onto multibeam imagery of the natural bank in ArcMap 10.3.1 (ESRI 2015). Grid cells were sequentially numbered, and a single cell was randomly selected for sampling before each sampling trip using a random number generator. Locations for the three vertical line sets were then randomly allocated within the selected grid cell using the ‘Create Random Points’ tool in ArcMap. Water quality data including temperature (°C), dissolved oxygen (DO; mg·L<sup>-1</sup>), and salinity (‰) were measured at each site with a vertical cast from surface to depth using a Hydrolab® DS5 data sonde.

**Fish Processing** — Upon retrieval of the gear, captured fishes were identified to species and assigned a unique call number. Species of interest such as Red Snapper were given a temporary tag labeled with that individual’s call number and retained on ice for later processing. In the laboratory, fish were measured (SL, FL, TL; mm), weighed (TW; kg), and sexed. Other tissues and hard parts including stomachs, gonads, and sagittal otoliths were also extracted and stored for future study.

Red Snapper otoliths were weighed (g) and then processed following the guidelines of VanderKooy (2009). The left otolith of each fish was embedded in epoxy and then thin sectioned (0.5 mm) in the transverse plane using an IsoMet® 1000 Precision Sectioning Saw. If the left otolith was unavailable, the right otolith was used. Thin sections containing the core were mounted to slides using thermoplastic cement and then viewed under a dissecting microscope with reflected light. For each section, two independent readers made blind counts of opaque annuli along the dorsal edge of the sulcus acousticus, and the edge condition was coded following VanderKooy (2009). When counts of opaque annuli differed, the two readers read the sections a second time. If counts still differed following the second read, the section was jointly examined, and if a consensus could not be reached, the section was discarded from further

analyses. Precision between readers was assessed using the average coefficient of variation ( $SD / \text{mean} \times 100$ ; ACV; Chang 1982) and average percent error (APE; Beamish and Fournier 1981).

Ages were assigned based on the count of opaque annuli and the degree of marginal edge completion (Allman et al. 2005). Because Red Snapper in the northern GOM are expected to complete annulus formation by July, fish captured on or before June 30<sup>th</sup> had their age advanced one year if the section displayed a large translucent edge. For fish captured after June 30<sup>th</sup>, age was equal to the opaque annulus count. Thus, annual age cohorts were based on calendar year rather than time since spawning (Jearld 1983; Allman et al. 2005; VanderKooy 2009). Biological ages, which account for the time since spawning, were also determined and used for subsequent analyses of growth (VanderKooy 2009). Following Wilson and Nieland (2001), biological ages were estimated using the equation:

$$\text{Biological age (yrs)} = (-182 + (\text{annulus count} \times 365) + ((m-1) \times 30) + d) / 365$$

where  $m$  is the ordinal month of capture and  $d$  is the ordinal day of the month of capture.

*Data Analyses* — Analysis of variance was used to test for potential differences in Red Snapper catch per unit effort (CPUE; fish·set<sup>-1</sup>), TL, TW, and age among the three habitats. To account for variation among sites, site was nested within habitat and treated as a random factor in the model. Data were assessed for homogeneity of variance and normality of residuals and log transformed if necessary. Tukey contrasts were used for post-hoc comparisons when ANOVA detected differences among habitats. As an ancillary analysis, we also examined differences in mean TL, TW, and age among sites with ANOVA and visually assessed the distributions of these variables with boxplots. Length, weight, age frequency distributions among habitats were evaluated with pairwise G-tests (Sokal and Rohlf 1995). If differences in frequency distributions were detected, standardized residuals were evaluated to determine which categories (i.e., length, weight classes, or age groups) most contributed to the observed difference (Agresti 2007). All testing was carried out in R 3.3.1 (R Core Team 2016) using  $\alpha = 0.05$ .

Red Snapper length-weight relationships were evaluated among habitats using nonlinear least squares fit to the traditional power function:

$$TW = aTL^b,$$

where  $a$  is a constant, and  $b$  is an exponent describing the curve of the relationship and indicating isometric growth when equal to 3 (Beverton and Holt 1996). Non-parametric bootstrapping with replacement ( $n = 10,000$ ) was used to estimate 95% confidence intervals for the model parameters  $a$  and  $b$  for each habitat (Efron and Tibshirani 1993). If confidence intervals overlapped, model parameters were considered similar between habitats.

Four types of non-linear growth models were fit to Red Snapper length-at-age and weight-at-age data. To minimize potential bias due to few fish in the older age groups, size-at-

age data were constrained to age-2 to age-10 individuals only. The original von Bertalanffy growth model (VBGM; von Bertalanffy 1938) was fit to TL-at-age and TW-at-age data using the equations:

$$L_t = L_\infty [1 - e^{-k(t-t_0)}];$$

$$W_t = W_\infty [1 - e^{-k(t-t_0)}]^b;$$

where  $L_t$  is the predicted TL at time  $t$ ;  $L_\infty$  is the mean asymptotic TL;  $k$  is the Brody growth coefficient;  $t_0$  is the theoretical age when TL is zero. For the weight-at-age model,  $W_t$  is the predicted TW at time  $t$ ;  $W_\infty$  is the mean asymptotic TW;  $t_0$  is the theoretical age when TW is zero; and  $b$  is the exponent derived from the TW-TL regression. A two parameter modification of the VBGM, which is commonly implemented when younger fish are lacking in the sample (e.g. Fischer et al. 2004), was specified in the forms:

$$L_t = L_\infty [1 - e^{-kt}];$$

$$W_t = W_\infty [1 - e^{-kt}]^b;$$

with parameters as defined above. The logistic growth function (Ricker 1979) was specified as:

$$L_t = \frac{L_\infty}{1 + e^{g(t-t_0)}};$$

$$W_t = \frac{W_\infty}{1 + e^{g(t-t_0)}};$$

where  $g$  is the instantaneous rate of growth when  $L$  or  $W \rightarrow 0$ , respectively,  $t_0$  is the time when the absolute rate of increase begins to decrease (i.e., inflection point of curve), and the remaining parameters are as previously defined. The Gompertz growth function (Ricker 1979) was also fit to the data as:

$$L_t = L_\infty [e^{-ke^{(-gt)}}];$$

$$W_t = W_\infty [e^{-ke^{(-gt)}}];$$

where  $g$  is the instantaneous rate of growth when  $t = t_0$ ,  $k$  is a dimensionless rate parameter such that  $kg$  is the instantaneous growth rate when  $t = t_0$  and  $L$  or  $W = L_0$  or  $W_0$ , respectively. All other parameters are as previously defined.

Each of the four candidate growth models was fit to length-at-age and weight-at-age data separately for each habitat and 95% confidence intervals were estimated for all model parameters with non-parametric bootstrapping as described above. An information-theoretic approach (Burnham and Anderson 2002) was used to assess the likelihood of the candidate models among

habitats. Akaike's Information Criteria (AIC; Akaike 1973) with the small-sample bias adjustment ( $AIC_c$ ; Hurvich and Tsai 1989) was used to assess goodness-of-fit of each model. The model with the lowest  $AIC_c$  is considered the best fitting model, and models with an  $AIC_c$  difference  $\leq 2$  (i.e.,  $\Delta_i \leq 2$ ) are considered to be strongly supported (Burnham and Anderson 2002). Akaike weights ( $w_i$ ), ranging from 0 to 1, were also calculated to assess the likelihood of each model given the data, with the greatest Akaike weight corresponding to the most plausible model of the candidate set (Burnham and Anderson 2002). We selected the best fitting growth model to compare growth among habitats.

Overall differences in growth curves among habitats were evaluated using likelihood ratio tests (Kimura 1980). Pairwise comparisons were conducted to assess differences because three habitats were included in the dataset. The first hypothesis tested was that growth could be modeled for equally well for both datasets using a single curve (i.e., coincident curves). If a significant difference was detected ( $\alpha = 0.05$ ), nested models were constructed and null hypotheses assuming one parameter (e.g., equal  $L_\infty$  between habitats) or two parameters (e.g., equal  $L_\infty$  and  $k$  between habitats) were similar between habitats were sequentially tested.

### **Red Snapper Fecundity - Artificial Reefs and Natural Banks (Obj. 2)**

**Introduction** - Red Snapper is an economically and ecologically important reef fish that has been pursued commercially and recreationally in the Gulf of Mexico (Gulf) since the 1840s (Hood et al. 2007). They are associated with hard substrate throughout their range, often occupying natural banks, ridges, and reefs (Patterson et al. 2001; Walter and Ingram 2009; Ajemian et al. 2015; Streich et al. in press). However, the Gulf is largely bare, mud-bottom with relatively few areas of natural hard-bottom reef, which may be a limiting factor for Red Snapper populations (Shipp and Bortone 2009).

Energy exploration in the western Gulf has created additional hard structure through the installation of oil and gas platforms (platforms) that also serve as artificial reef habitat, where Red Snapper is often the dominant species observed (Stanley and Wilson 2003; Ajemian et al. 2015). There is evidence that Red Snapper associate with artificial structures over long periods of time (Szedlmayer and Schroepfer 2005), while in other areas low site fidelity to artificial structure is exhibited (Peabody and Wilson 2006).

The relative value of these artificial reefs in comparison to natural habitat is still widely debated. Several studies argue that artificial reefs do not provide suitable habitat and also increase fishing pressure, which act together to create a sink in the population (Jackson et al. 2007; Cowan et al. 2011). However, others have argued that artificial reefs do provide suitable habitat and have significantly contributed to the recovery of Red Snapper in the Gulf (Szedlmayer 2007; Gallway et al. 2009; Shipp and Bortone 2009; Streich et al. in press). As many platforms are mandated for removal due to federal regulations such as "Idle Iron" (United States Department of the Interior 2010), it is important to understand how artificial structures

function in comparison to natural reefs to provide key data to determine if these structure and enhancing the population.

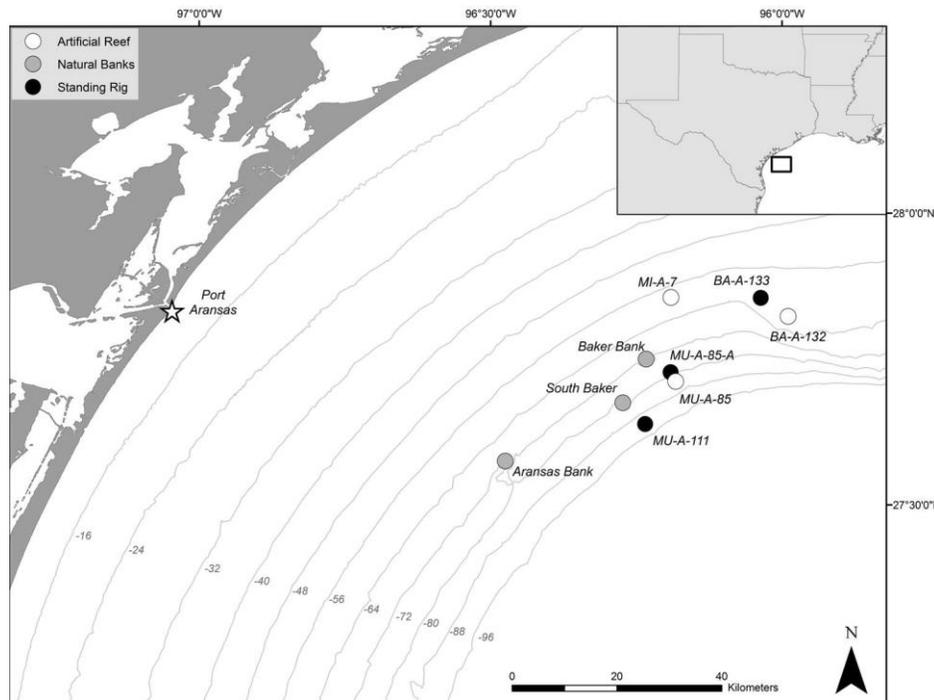
Generally, reproductive characteristics of Red Snapper have been well-studied in the Gulf. Red Snapper have been shown to be sexually mature by age 2 and are asynchronous batch spawners that develop oocytes continuously, but at different rates within a single individual (Porch et al. 2007; Lowerre-Barbieri et al. 2011). Fecundity has been shown to increase with age, and individuals spawn multiple times throughout the season with diel periodicity (Winemiller and Rose 1992, 1993; Collins et al. 2001; Jackson et al. 2006). Red Snapper are long-lived, capable of reaching 50 years in age, and potentially producing 55.5 million eggs over their lifespan (Szedlmayer and Shipp 1994; Wilson and Nieland 2001; SEDAR 2005). Generally, spawning in the Gulf is thought to occur from April through September (Gallaway et al. 2009), with peak spawning occurring along the Texas coast during June, July and August (Collins et al. 2001).

Previous studies of Red Snapper reproduction in the Gulf of Mexico have focused on the northern Gulf near Louisiana and Alabama (Collins et al. 2001; Woods et al. 2003; Jackson et al. 2006, 2007; Kulaw 2012), Florida (Brown-Peterson et al. 2008), and the southern Gulf (Brulé et al. 2010). Offshore of Louisiana, differences in GSI, maturity, and spawning frequency were found among natural shelf-edge banks, standing platform sites, and toppled platform sites (Kulaw 2012). Additionally, differences in reproduction, including GSI, spawning frequency, and batch fecundity were found among six sites including differences among Red Snapper collected offshore of Galveston and South Padre Island, TX (Kulaw 2012). Variation in size at maturity has been found between fish collected offshore of Louisiana and Alabama, with Alabama Red Snapper reaching maturity at smaller sizes but similar ages (Woods et al. 2003). In Florida, east and west coast Red Snapper appear to exhibit reproductive differences in spawning seasonality, batch fecundity, and spawning frequency (Brown-Peterson et al. 2008). Red Snapper from Florida (Brown-Peterson et al. 2008) and the northern Gulf (Woods et al. 2003) show differences in spawning seasonality from the southern Gulf near the Yucatan Peninsula, with Red Snapper in the southern Gulf exhibiting protracted spawning seasons, possibly due to the warmer waters (Brulé et al. 2010). These studies suggest there may be regional differences in reproduction throughout the Gulf; specifically that there could be differences in the western Gulf compared to previously studied regions as well as localized differences among habitat types.

Thus, these differences in region and habitat type warrant further research. Few studies have investigated differences in Red Snapper reproduction among habitat types, particularly in the western Gulf. To date, the focus has been on large spatial and regional differences, on the order of 1000s of km (Brown-Peterson et al. 2008; Kulaw 2012). Population-level effects of artificial structures on Red Snapper reproduction are sparse; yet, there is the potential for enhancement of fish production by providing additional habitat (Powers et al. 2003). In addition, there is growing evidence that subpopulations of Red Snapper exist throughout the Gulf that could drive important differences in life history parameters such as reproduction (Gold and Saillant 2007). To address this debate, it is essential to understand if Red

Snapper are using these habitats similarly by identifying reproductive parameters at different habitat types. Given the lack of information on life history differences between natural reefs and artificial habitat in the Gulf of Mexico, the purpose of this study is to further characterize regional trends in Red Snapper reproduction in the western Gulf of Mexico with particular interest in the influence of oil and gas platforms on Red Snapper reproductive parameters relative to natural reefs.

**Study Area** - The study area was located in the western Gulf of Mexico approximately 45-60 nautical miles east of Port Aransas, Texas (Figure 4). Three habitat types with three replicate sites each were sampled (n=9 total sites): natural banks (natural: Aransas Bank, Baker Bank, and South Baker), standing oil and gas platforms (standing: MU-A-111-A, MU-A-85-A, and BA-133-A), and “reefed” oil and gas platforms (reefed: MU-A-85, MI-A-7, and BA-A-132) that were decommissioned oil and gas platforms converted to artificial reefs. The sites were selected within a 30 nautical mile area, and were restricted to 60-90 m to control depth.



**Figure 4.** The study area was comprised of nine sites located in the northwestern Gulf of Mexico offshore of Port Aransas, Texas. Each habitat type was represented by three sites. Natural bank sites are: Baker, South Baker, and Aransas Bank. Standing rig sites are: BA-A-133, MU-A-85A, and MU-A-111. Artificial reef sites are: MI-A-7, BA-A-132, and MU-A-85.

**Collection and Sample Processing** - Red Snapper were collected from 2013-2015 during April through October, in an effort to capture the extend of the primary spawning season, (Woods 2003; Fitzhugh et al. 2004; Jackson et al. 2007) using Gulf-wide standardized vertical longline sampling following the Southeast Area Monitoring and Assessment Program (SEAMAP) protocol

(Gregalis et al. 2012). Individuals were tagged with an identifying label in the field and kept on ice and brought to the laboratory processing. Total weight (TW, kg) and total length (TL, mm) were recorded. Fish were dissected to collect biological samples, including gonad weight (g) and otoliths. Sex was determined by macroscopic examination of gonads. Using the TL (in) to weight (lbs) conversion formula for Red Snapper from SEDAR 31 ( $0.00047 * TL \text{ in} ^{2.994}$ , SEDAR 2013), a condition index, relative weight ( $Wr = \text{actual weight (lbs)}/\text{predicted weight (lbs)} * 100$ ; Anderson and Neumann 1996), was calculated for female fish.  $Wr$  is interpreted with a baseline value of 100 indicating a healthy individual and should be used as a benchmark for comparison among samples or populations (Murphy et al. 1990). A value well below 100 means the individual is in worse condition relative to the population while a value above 100 means the individual is in better condition, to a point, relative to the population (Murphy et al. 1990). Red Snapper otoliths were weighed and processed following VanderKooy (2009). Thin sections containing the core of the left otolith were mounted to slides and viewed under a dissecting microscope. Two independent readers made blind counts of opaque annuli and assigned an edge code according to VanderKooy (2009). When counts of annuli differed, the section was jointly examined and a consensus was reached. Age was determined based on the annuli count and edge code assigned (Allman et al. 2005).

Reproduction status was determined by using well-established methods (Fitzhugh et al. 2004; Kulaw 2012). Briefly, Ovaries were fixed in 10% formalin for a minimum of two weeks. Following a random number generator, 2mm subsamples were removed from the ovaries post-fixation and secured in labeled histology cassettes. The subsamples were encased in paraffin wax, cut into 4  $\mu\text{m}$  sections and stained using hematoxylin and eosin. Red Snapper oocytes develop continuously and asynchronously throughout the spawning season, and progresses through stages starting with primary growth (PG) followed by cortical alveoli (CA), vitellogenic (V), and hydrated (H; Wallace and Selman 1981; Glenn 2014). Thus, a reproductive stage was assigned and maturity was determined through microscopic examination (Olympus BX51, 40-100x) based on the most advanced oocyte stage present. An individual was considered spawning capable if the ovary exhibited vitellogenic stage oocytes (Hunter and Goldberg 1980; Jackson et al. 2007; Brown-Peterson et al. 2011). Two other oocyte spawning markers were also considered: atresia (ATR), the breakdown and resorption of oocytes into the body, and post ovulatory follicles (POF), the remains of hydrated cells after spawning which indicate recent spawning activity.

**Reproductive Biology Analysis** - Male to female ratios were calculated per habitat type for all fish collected. To reduce the influence of season on reproductive characteristics, the remaining analyses were restricted to individuals collected during May-August, which captures the peak spawning period for Red Snapper. A gonadosomatic index (GSI) was calculated for each fish using total weight and gonad weight:

$$GSI = \frac{\text{Gonad weight (g)}}{\text{Total weight (g)}} \times 100$$

Percent maturity, batch fecundity (BFE), spawning frequency (SFE), and annual fecundity (AFE) were calculated for female fish collected from each habitat type. Based on microscopic evaluation, ovaries containing hydrated oocytes were used to calculate BFE. Three random subsamples weighing between 0.03 – 0.05 g were taken from ovaries containing hydrated oocytes. The subsamples were spread on a gridded petri dish with a few drops of 10% glycerin and the hydrated cells were counted under a dissecting microscope (Olympus SZ61, 6.7-10x). The BFE was calculated for each subsample according to the method by (Hunter et al. 1983), and the subsamples were averaged to obtain the average BFE for the fish:

$$BFE = \frac{\text{Number hydrated oocytes}}{\text{subsample weight}(g)} \times \text{gonad weight}(g)$$

Spawning frequency estimates were calculated using the time-calibrated method as described by Wilson and Nieland (1994) using the formula:

$$SFE = \frac{\# \text{ Mature Females}}{\# \text{ with POFs} + \# \text{ with H}}$$

Woods (2003) and Fitzhugh et al. (2004) estimated a spawning season duration of 150 days for Red Snapper, which was used for AFE calculations. Individual annual fecundity was calculated using the formula following Nieland and Wilson (1993) and averaged to obtain the mean AFE per habitat type:

$$AFE = \frac{\text{Spawning Season (days)}}{SFE (days)} \times BFE$$

**Statistical Analyses** - Differences in TL, age,  $W_r$ , GSI, BFE, and AFE among habitat types and season were assessed using nested ANOVA (Site within Habitat) using R Statistical Software v3.3.1. GSI values were arcsine square root transformed to correct for ratio data (Gotelli and Ellison 2004). ANCOVA was used to test for differences in BFE and AFE at age among habitat types. Chi-square tests were performed to examine differences in male:female ratios, spawning frequency, and number of spawning capable individuals. Multivariate statistical analyses were conducted in PRIMER-E. Oocyte stages were grouped by sample site and date, square root transformed, and then a Bray-Curtis index similarity was calculated on the resulting oocyte composition. A multidimensional scaling (MDS) plot of reproductive stage by habitat was created to visualize differences in oocyte composition. A permutational analysis of variance (PERMANOVA) was conducted to examine the statistical differences among habitat and month, with site nested in habitat, for oocyte stage (Clarke et al. 2014). Results were considered significant at  $\alpha \leq 0.05$ .

### **Red Snapper Trophic Ecology - Artificial Reefs and Natural Banks (Obj. 3)**

**Introduction** - The western Gulf of Mexico (GOM) is comprised largely of soft-bottom habitat and low-relief natural reefs (Parker et al. 1983). Due to oil and gas production a large number of artificial structures have been installed which function as higher relief reefs surrounded by rich fish communities (Ajemian et al. 2015). There has been much debate about the function of these structures and whether they simply attract or actually produce fish (Powers et al 2003; Shipp and Bortone 2009; Cowan et al. 2011; Cresson et al. 2014). Understanding the function of oil and gas platforms is essential because habitat may be limiting to fish populations in the western GOM (Shipp and Bortone 2009) and due to idle iron policies many are slated for removal (BSEE 2010). Some platforms enter artificial reef programs which preserve a portion of the structure with the intent of creating more fish habitat, diving opportunities, and fishing areas for constituents. Many aspects of artificial reef ecology relating to fishery species have been examined. For example, artificial reefs may be subject to more boat traffic than natural reefs (Simard et al. 2016), which could have population level effects if fishing pressure increases with increased boat traffic (Cowan et al. 2011). Therefore more information about how different reef types function can help these programs make scientifically informed decisions regarding their reefing practices.

On artificial reefs in the western GOM, Red Snapper are the dominant species (Stanley and Wilson 2003; Ajemian et al. 2015), thus they are a good indicator species to gauge the functionality of the habitat. Red Snapper is a contentious fishery in the GOM with great ecological, social, and economic importance (SEDAR 2013). How Red Snapper use artificial habitat can be informative as to how it functions in the local environment. Additionally, it is not clearly understood how the residence time of fish on these reefs relates to the functionality. Confounding the question of residency, past research has found that Red Snapper are long-term residents on artificial reefs (Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011), while others have found them to make more wide-scale movements (Patterson et al. 2001).

Red Snapper are opportunistic predators known to consume a wide range of benthic organisms (McCawley et al. 2007; Wells et al. 2008), as well as reef related prey (Outz and Szedlmayer 2003; Szedlmayer and Lee 2004). Ontogenetic shifts have been observed in Red Snapper diets from small crustaceans and zooplankton to larger crustaceans and fish (Szedlmayer and Lee 2004; McCawley et al. 2007; Wells et al. 2008). In the northern GOM, offshore of Louisiana, a subtle difference in diet has been observed between habitat types (natural reefs, standing oil and gas platforms, and reefed platforms), with Red Snapper collected from natural reefs consuming the most diverse diet (Simonsen et al. 2015).

Stable isotopes ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) in fish tissues vary in relation to consumed prey and have been used to better understand energy flow on a longer time scale than diet analysis (Fry 2007).  $\delta^{13}\text{C}$  varies little per trophic level (<1%) making it a good indicator of basal carbon sources, while  $\delta^{15}\text{N}$  varies about 3.4% per trophic level, making it a good proxy for trophic level (Peterson and Fry 1987; Post et al. 2002; Layman et al. 2007). Stable isotope

analysis (SIA) can be used to determine the trophic niche of a population (Jackson et al. 2011), thus allowing for comparison of the niche space of communities. Basal carbon values have been found to not vary significantly for offshore habitats in the GOM (Daigle et al. 2013), so variations in  $\delta^{15}\text{N}$  can be used to examine subtle differences in diet (Zapp-Sluis et al. 2013; Simonsen et al. 2015). In the Mediterranean, isotope ratios of fish tissues do not vary between natural and artificial reefs (Cresson et al. 2014); however more variability between habitat types has been observed in the GOM (Zapp-Sluis et al. 2013; Simonsen et al. 2015; Foss 2016). Additionally in the GOM, Red Snapper from platform habitats have been found to be enriched in  $\delta^{15}\text{N}$  compared to non-platform habitats (Zapp-Sluis et al. 2013; Simonsen et al. 2015). Despite this enrichment, the trophic niche of Red Snapper has shown that a similar prey base exists between habitats (Simonsen et al. 2015).

The purpose of this study was to compare the diet and relative  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of Red Snapper from natural reef sites to standing and reefed oil and gas platforms in an effort to better understand the trophic ecology of these habitats. This information will be important to fishery managers and will enable a better understanding of how artificial reefs are functioning in the western GOM.

**Study area** - Red Snapper were collected using a standardized long-line fishing gear from nine sites in the GOM, offshore of Texas (Figure 4). These sites were selected because they represented three habitat types (natural reefs, standing oil and gas platforms, and reefed platforms) in similar depth strata (60-90m). Natural reef sites (natural) included Aransas Banks, South Baker, and Baker Bank; standing oil and gas platform sites (standing) included MU-A-111, MU-A-85, and MU-A-111; reefed platform sites (reefed) included MU-A-85, BA-A-132, and MI-A-7.

**Sampling procedure** - Fishing was conducted in three randomly selected locations at each site per sampling day. Following Southeast Area Monitoring and Assessment Program (SEAMAP) vertical line protocols, in each location nine drops were conducted using three sets of long-line gangions in a randomly selected order over three hook sizes (8/0, 11/0, and 15/0) baited with chunked Atlantic mackerel *Scomber scombrus* (Gregalis et al. 2012). Each site was visited multiple times over a three year period (2013-2015). After capture, fish were stored on ice until processing (less than 24 h). Fish were weighed (g), measured (mm), sexed, and dissected to collect otoliths, gonads, stomachs, and epaxial muscle samples. Stomachs collected from 2013-2014 were initially placed whole into 10% formalin for at least a month of preservation after which the contents were removed and transferred to 70% ethanol.

**Diet Analysis** - Following fixation, stomach contents were enumerated and identified to the lowest possible taxon (LPT) and individual prey items were weighed (g). Frequency of occurrence (FO), percent frequency of occurrence (%FO), percent by number (%N), and percent composition by weight (%W) were calculated for each prey type. Using these parameters, the

Index of Relative Importance ( $IRI = (\%N + \%W) \times FO$ ; Liao et al. 2001) and percent IRI (%IRI) was calculated. Prey weight was converted to standardized prey weight by dividing each taxon by individual body weight of the fish to control for fish size in all multivariate analyses (Ajemian and Powers 2012). Additionally, feeding strategy diagrams were created, using frequency of occurrence and prey specific abundance of prey items grouped by family or the next highest taxon identifiable, to further investigate dietary patterns of Red Snapper among the three habitat types. Prey specific abundance, using prey weight, was determined by dividing the total weight of prey items by the total content weight of stomachs containing that prey item (Amundsen et al. 1996; Ajemian and Powers 2011).

**Stable Isotope Analysis (SIA)** - Due to low sample sizes for other months, only fish collected from May through October in 2013 and 2014 were used in SIA. Muscle samples were frozen until processing (n=647). Red Snapper were selected for SIA by size class. For selection, a list was made of all tissue samples available by site and organized in 100 mm size bins by total length (TL); approximately 120 samples per habitat were selected with an attempt to select equally from each bin. If no samples were available in a size class for a certain site, an attempt was made to fill these slots with fish from another site within the same habitat type. The TL distribution of Red Snapper used for SIA was visualized with a histogram by size class using 100 mm bins. Selected isotope samples were defrosted on ice, rinsed with DI water, trimmed to remove discoloration or connective tissue, placed in sterilized aluminum weigh boats, and dried in an oven at 60°C for approximately 48 h. After drying samples were homogenized using a sterile mortar and pestle, then approximately 1 mg of sample was loaded into tin capsules for isotope analysis. Previous studies on Red Snapper trophic ecology have demonstrated that there is no need for lipid extractions before analysis (Zapp-Sluis et al. 2012).

Elemental and isotopic compositions of carbon and nitrogen were determined by the Texas A&M University-Corpus Christi Isotope Core Lab using a Costech ECS4010 elemental analyzer connected to a continuous flow Thermo Delta V Plus isotope ratio mass spectrometer via a Thermo ConFlo IV interface. A multi-point calibration (Costech methionine standard: N = 9.39%; C = 40.25%) was used to determine carbon and nitrogen content of samples. Preliminary isotopic values were measured relative to reference gases. Replicate analyses of isotopic standard reference materials USGS 40 ( $\delta^{15}\text{N} = -4.52 \text{‰ AIR}$ ;  $\delta^{13}\text{C} = -26.39 \text{‰ VPDB}$ ) and USGS 41 ( $\delta^{15}\text{N} = 47.57 \text{‰ AIR}$ ;  $\delta^{13}\text{C} = 37.63 \text{‰ VPDB}$ ) were used to normalize preliminary isotopic values to the AIR and VPDB scales (Paul et al. 2007). Individual tissue samples were analyzed in duplicate and averaged for statistical analysis.

**Diet Statistical Analysis** - To facilitate the relatability of diet data to isotope data, only fish collected in 2013 and 2014 were considered for analyses. The distribution of analyzed stomachs was visualized with a histogram by size class (100 cm bins). Univariate statistical analyses were conducted in R Statistical Software v3.3.1. Prey items identified to LPT were

grouped according to family or the next highest taxon when family could not be identified for all analyses.

Multivariate analyses were conducted in PRIMER-E. A Bray Curtis similarity index was created using square-root transformed standardized weight and permutational multivariate analysis of variance (PERMANOVA) was conducted to identify differences among habitat and size class (Clarke et al. 2014a). Dispersion of prey within each habitat was assessed with permutational dispersion (PERMDISP) analysis. Differences between factors for both habitat and size class were assessed using a similarity percentages (SIMPER) analysis. Results were considered significant at  $\alpha \leq 0.05$ .

***Stable Isotope Statistical Analysis*** - Exploratory data analysis was conducted in SigmaPlot 11.0. Potential linear relationships between fish TL and isotope values were determined using simple linear regressions on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values with TL. A simple linear regression was also conducted for  $\delta^{15}\text{N}$  by  $\delta^{13}\text{C}$  to assess the linear relationship of these factors. Mean isotopic ratios were visualized using a biplot of  $\delta^{15}\text{N}$  to  $\delta^{13}\text{C}$ . Additional analyses were performed in R version 3.3.1. The non-linear relationship and ontogenetic variations in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  by habitat type were visualized using a scatterplot with a locally weighted smoothing (LOESS) curve (R v.3.3.2, package ggplot2).

To better understand differences between habitats, variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between habitat and size class was compared in JMP® v.13, SAS Institute Inc., (Cary, NC) using multivariate analysis of variance (MANOVA) followed by separate univariate ANOVAs for each factor. The MANOVA design was Type III, full factorial with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  as dependent variables, and habitat and size class as explanatory variables. Significance was considered at  $\alpha = 0.05$ . Individual dependent variable responses of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were compared with analysis of variance (ANOVA). Post-hoc multiple comparisons with a Tukey honest significant difference were used to compare significant differences between treatment groups.

## **B. Project management**

Gregory W. Stunz, Ph.D., - Endowed Chair Fisheries and Ocean Health, and Professor of Marine Biology, was Principal Investigator of the project. Dr. Stunz was in charge of overall project oversight, training students, analysis of results, dissemination of findings, and coordination between TAMU-CC and cooperative partners on this project. He co-authored all progress reports and the final report.

Matthew J. Ajemian, Ph.D., - Assistant Research Scientist, was a Co-Principal Investigator of the project. Dr. Ajemian was in charge of scientific operations and helped design the field sampling program and oversaw statistical analyses and manuscript development by research technicians and graduate students. He co-authored all progress reports and the final report.

Judson M. Curtis, Ph.D., – Assistant Research Scientist, has expertise in fisheries biology, community ecology, and behavior of marine fishes. He also has extensive experience conducting research in both inshore and offshore environments using fisheries sampling techniques and advanced analytical methods. Curtis assisted with day-to-day aspects of the research project, including the execution of field studies, collection of biological samples, and project management.

Matthew K. Streich, M.S., - Ph.D. student, was responsible for analysis of results and writing the community structure and Red Snapper age and growth portions of the final report.

Rachel A. Brewton, M.S., - Research Specialist II, was responsible for coordination of laboratory analyses and training students in laboratory protocols. She led the analysis of trophic ecology data, assisted in the analysis of reproductive data, and participated in the dissemination of findings. She also assisted in sample collection and fish processing. She co-authored all progress reports and the final report.

Charles H. Downey, B.S., – M.S. student, was responsible for all aspects of the fecundity portion of this study. He was also heavily involved in collecting and analyzing the Red Snapper diet and isotope data.

Jennifer J. Wetz, M.S., - Fisheries Project Manager, was in charge of all field logistics and sampling plans.

Quentin A. Hall, M.S. – Research Specialist, assisted with field research, data acquisition, and final report assembly.

## VI. FINDINGS

### A. Actual accomplishments and findings

#### **Fish Community Comparison - Artificial Reefs and Natural Banks (Obj. 1)**

*Community Analyses* - Video-based surveys from the ROV deployments resulted in 22.2 hours of footage. Survey times at artificial reef sites (mean = 118.0 min) and natural banks (mean = 148.8 min) were similar (Welch's  $t$ -test:  $t = 2.78$ ,  $df = 4$ ,  $P = 0.324$ ), and these surveys were successful in documenting 79 species representing 28 families (48 at artificial reefs and 51 at natural; Table 2). We observed the highest species richness at Baker Bank with 33 species. Among artificial sites, BA-A-132 had the highest richness with 30 species observed. The lowest species richness was observed at the southernmost natural sites, Blackfish Ridge (15) and Harte Bank (16). Water temperatures among survey sites ranged from 20.1°C to 29.2°C at the natural

banks and from 23.1°C to 28.2°C at artificial reefs. Survey water temperatures ranged from 27.0°C to 27.3°C at artificial reefs and from 22.9°C to 25.5°C at natural banks (Table 1). Salinity was similar at both habitats and averaged 36.5 psu.

**Table 2. Record of various taxa observed during ROV surveys at five natural banks and five artificial reef sites along the Texas Shelf in fall 2012.**

Family	Species	Scientific name	Natural banks					Artificial reefs				
			Baker	Aransas	Dream	Blackfish	Harte	BA-A-28	BA-A-132	PN-A-58	PN-A-72	PN-967
Acanthuridae	Blue Tang	<i>Acanthurus coeruleus</i>									X	
	Doctorfish	<i>Acanthurus chirurgus</i>									X	
Apogonidae	Twospot Cardinalfish	<i>Apogon pseudomaculatus</i>			X	X	X					
Balistidae	Gray Triggerfish	<i>Balistes capriscus</i>		X		X		X				X
Carangidae	African Pompano	<i>Alectis ciliaris</i>										X
	Bar Jack	<i>Caranx ruber</i>						X				
	Black Jack	<i>Caranx lugubris</i>							X			
	Blue Runner	<i>Caranx crysos</i>						X				
	Crevalle Jack	<i>Caranx hippos</i>									X	X
	Horse-eye Jack	<i>Caranx latus</i>						X	X	X	X	X
	Yellow Jack	<i>Caranx bartholomaei</i>						X	X			X
	Rainbow Runner	<i>Elagatis bipinnulata</i>						X		X	X	
	Lookdown	<i>Selene vomer</i>		X						X	X	X
	Almaco Jack	<i>Seriola rivoliana</i>		X	X	X	X	X	X	X		X
	Greater Amberjack	<i>Seriola dumerili</i>		X	X	X	X	X	X	X	X	
Carcharhinidae	Sandbar Shark	<i>Carcharhinus plumbeus</i>		X								
Chaetodontidae	Banded Butterflyfish	<i>Chaetodon striatus</i>	X									
	Reef Butterflyfish	<i>Chaetodon sedentarius</i>	X	X	X	X	X		X	X		X
	Spotfin Butterflyfish	<i>Chaetodon ocellatus</i>		X				X	X	X		X
	Bank Butterflyfish	<i>Prognathodes aya</i>			X							
Ephippidae	Atlantic Spadefish	<i>Chaetodipterus faber</i>						X		X	X	X
Epinephelidae	Atlantic Goliath Grouper	<i>Epinephelus itajara</i>										X
	Rock Hind	<i>Epinephelus adscensionis</i>	X					X	X	X	X	X
	Black Grouper	<i>Mycteroperca bonaci</i>	X									
	Grouper sp.	<i>Mycteroperca</i> sp.	X						X	X	X	
	Scamp	<i>Mycteroperca phenax</i>		X					X	X		
	Yellowmouth Grouper	<i>Mycteroperca interstitialis</i>							X			
Gobiidae	Atlantic Creolefish	<i>Paranthias furcifer</i>						X	X	X	X	X
	White-eye Goby	<i>Bolmannia boqueronensis</i>			X							
Haemulidae	Neon Goby	<i>Elacatinus oceanops</i>	X									
	Porkfish	<i>Anisotremus virginicus</i>										X
Holocentridae	Tomtate	<i>Haemulon aurolineatum</i>						X	X			X
	Squirrelfish	<i>Holocentrus adscensionis</i>	X		X	X	X	X				
	Deepwater Squirrelfish	<i>Sargocentron bullisi</i>	X	X	X							
Kyphosidae	Bermuda Chub	<i>Kyphosus saltatrix</i>						X				
Labridae	Spanish Hogfish	<i>Bodianus rufus</i>						X	X	X	X	X
	Spotfin Hogfish	<i>Bodianus pulchellus</i>	X	X	X	X		X	X	X	X	X
	Creole Wrasse	<i>Clepticus parrae</i>							X			
	Greenband Wrasse	<i>Halichoeres bathyphilus</i>	X	X	X							
	Parrotfish sp.	<i>Sparisoma</i> sp.							X			
	Bluehead	<i>Thalassoma bifasciatum</i>							X			
Lutjanidae	Gray Snapper	<i>Lutjanus griseus</i>						X	X		X	X
	Lane Snapper	<i>Lutjanus synagris</i>		X								
	Red Snapper	<i>Lutjanus campechanus</i>	X	X	X		X	X	X	X	X	X
	Yellowtail Snapper	<i>Ocyurus chrysurus</i>										X
	Vermilion Snapper	<i>Rhomboplites aurorubens</i>	X	X	X			X	X		X	
Muraenidae	Spotted Moray	<i>Gymnothorax moringa</i>	X									
Ostraciidae	Scrawled Cowfish	<i>Acanthostracion quadricornis</i>		X								
Pomacanthidae	Cherubfish	<i>Centropyge argi</i>	X			X						
	Blue Angelfish	<i>Holacanthus bermudensis</i>	X	X				X	X		X	X
	Queen Angelfish	<i>Holacanthus ciliaris</i>	X					X				
	Townsend Angelfish	<i>Holacanthus</i> sp.						X				
	French Angelfish	<i>Pomacanthus paru</i>	X	X				X	X			
Pomacentridae	Brown Chromis	<i>Chromis multilineata</i>							X			
	Purple Reeffish	<i>Chromis scotti</i>	X	X	X	X						
	Sunshinefish	<i>Chromis insolata</i>	X	X	X	X						
	Yellowtail Reeffish	<i>Chromis enchrysurus</i>	X	X	X	X						
	Bicolor Damselfish	<i>Stegastes partitus</i>								X		
	Damselfish sp.	<i>Stegastes</i> sp.	X	X	X				X	X	X	X

Priacanthidae	Bigeye	Priacanthus arenatus	X	X	X	X	X					
	Short Bigeye	Pristigenys alta	X	X	X							
Ptereleotridae	Blue Dartfish	Ptereleotris calliura	X	X	X							
Rachycentridae	Cobia	Rachycentron canadum						X		X		
Sciaenidae	Jackknife-fish	Equetus lanceolatus			X							
	Cubby	Pareques umbrosus	X	X								
Scorpaenidae	Red Lionfish	Pterois volitans	X					X				
Serranidae	Threadnose Bass	Choranthias tenuis	X		X					X		
	Candy Basslet	Liopropoma carmabi	X									
	Wrasse Basslet	Liopropoma eukrines	X	X	X	X	X					
	Roughtongue Bass	Pronotogrammus martinicensis	X	X	X	X	X					
	Freckled Soapfish	Rypticus bistrispinus		X						X		
	Orangeback Bass	Serranus annularis	X									
	Snow Bass	Serranus chionaraia				X						
	Tattler	Serranus phoebe	X	X	X					X		
Sparidae	Sheepshead	Archosargus probatocephalus						X		X		
	Porgy sp.	Calamus sp.		X		X			X			
Sphyraenidae	Great Barracuda	Sphyraena barracuda						X	X	X		
Synodontidae	Inshore Lizardfish	Synodus foetens			X					X		
Tetraodontidae	Pufferfish sp.	Canthigaster sp.	X	X	X	X						
Richness	79		33	32	26	15	16	26	30	20	18	24
Diversity (H')			2.589	2.354	2.146	2.366	2.106	1.892	2.518	1.73	1.96	1.79
Evenness (J')			0.7406	0.6792	0.6586	0.8738	0.7596	0.5807	0.7403	0.5774	0.678	0.5633

Interestingly, no single species was observed at all 10 sites; however, five species were observed at  $\geq 8$  sites including economically important species like Red Snapper (9 sites), Greater Amberjack (*Seriola dumerili*; 8 sites), and Almaco Jack (*Seriola rivoliana*; 8 sites; Table 2). Many of the documented species were only observed at one of the habitat types we surveyed. For example, there were 28 species, including 7 species of carangids, observed at artificial reef sites that were not observed on natural banks. Conversely, 31 species were documented on natural banks but not on artificial reefs. These included 8 species of small serranids such as Wrasse Basslet (*Liopropoma eukrines*), Roughtongue Bass (*Pronotogrammus martinicensis*), several *Serranus* spp., and 3 species of pomacentrid damselfishes including Purple Reefish (*Chromis scotti*), Sunshinefish (*C. insolata*), and Yellowtail Reefish (*C. enchrysur*). Twenty species of fish occurred on both artificial and natural habitats. Included in this group was the invasive Red Lionfish (*Pterois volitans*), which was observed at one artificial reef (BA-A-132) and one natural bank (Baker Bank). Species richness was not significantly different between habitats ( $t = 2.78$ ,  $df = 8$ ,  $P = 0.860$ ). Diversity was generally higher at natural banks (mean = 2.31; SE = 0.09) than artificial reefs (mean = 1.98; SE = 0.14; Table 2). We observed the highest diversity at Baker Bank ( $H' = 2.59$ ) and the lowest diversity at PN-A-58, an artificial reef ( $H' = 1.73$ ); however, the effect of habitat type on Shannon diversity was not significant ( $t = 2.31$ ,  $df = 8$ ,  $P = 0.078$ ). Similarly, Pielou's evenness index was also higher on natural banks (mean = 0.74; SE = 0.04) than artificial reefs (mean = 0.62; SE = 0.03), but statistical evidence for an effect of habitat type on evenness was marginal ( $t = 2.31$ ,  $df = 8$ ,  $P = 0.056$ ).

Species-specific MinCounts were highly variable between and within habitats. At artificial reefs, proportional counts were dominated by pelagic, schooling species such as Horse-eye Jack (*Caranx latus*), Blue Runner (*C. crysos*), Bar Jack (*C. ruber*), Rainbow Runner (*Elagatis bipinnulata*), and Lookdown (*Selene vomer*). On average, this group accounted for 47% of the total counts at artificial reefs, but among surveys, this group represented as little as 3% (BA-A-132) and as much as 77% (PN-A-72) of the total counts. At natural bank sites, these

carangids accounted for < 1% of the total counts. As a group, federally managed lutjanids, including Red Snapper, Gray Snapper (*Lutjanus griseus*), and Vermilion Snapper (*Rhomboplites aurorubens*), accounted for similar proportions of the total fish counts at artificial and natural sites (20% and 21%, respectively), despite the fact that Gray Snapper were not observed during any of the natural bank surveys. MinCounts of federally managed species were highly variable among sites and habitats (Table 3). Vermilion Snapper MinCounts ranged widely among artificial sites from a high of 255 at BA-A-28 to a low of zero at two different sites. The highest Vermilion MinCount at natural habitats was observed at Aransas Bank (76). Red Snapper were observed at all five artificial reefs, with MinCounts ranging from 4 at PN-A-72 to as many as 65 at BA-A-132. Red Snapper were observed at 4 of 5 natural sites, with the highest MinCounts occurring at Aransas (31) and Baker (22) banks. Although no Gray Snapper were observed on the natural banks we surveyed, as many as 95 were observed on artificial reefs (PN-967). Gray Triggerfish (*Balistes capriscus*) occurred sporadically in our surveys, and MinCounts never exceeded 2 individuals at either habitat. Greater Amberjack were consistently found in low numbers across both habitat types with the highest MinCount (8) recorded at Harte Bank—the deepest site surveyed in this study.

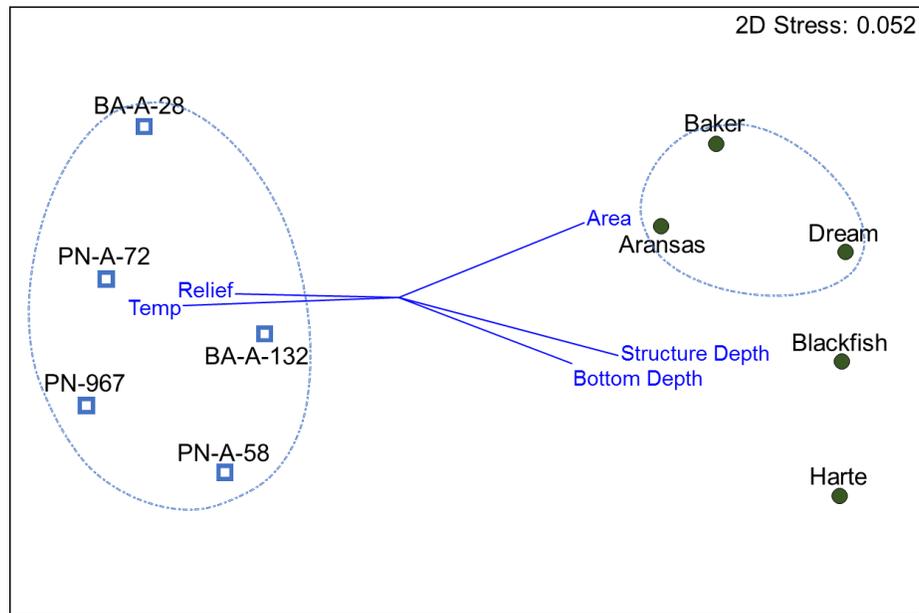
**Table 3. Relative abundance (i.e., MinCounts) of five federally managed species from ROV surveys of artificial reefs and natural banks in the western Gulf of Mexico in fall 2012.**

Common name	Site									
	BA-A-28	BA-A-132	PN-A-58	PN-A-72	PN-967	Baker	Aransas	Dream	Blackfish	Harte
Gray Snapper	15	37	0	9	95	0	0	0	0	0
Gray Triggerfish	2	0	0	0	2	0	1	0	1	0
Greater Amberjack	3	5	1	1	0	0	1	2	2	8
Red Snapper	7	65	10	4	32	22	31	1	0	3
Vermilion Snapper	255	3	0	21	0	39	76	5	0	0

Ordination using nMDS revealed clear grouping of reef fish communities by habitat type (Figure 5). When tested using PERMANOVA, the effect of habitat type on reef fish community structure was significant ( $F_{1,8} = 6.54$ ,  $P = 0.007$ ). Similarity percentages (i.e., SIMPER) revealed that this divergence was driven by gregarious or schooling species such as Horse-eye Jack, Atlantic Spadefish (*Chaetodipterus faber*), Lookdown, and Vermilion Snapper, all of which were more abundant on artificial reefs (Table 4). A subsequent cluster analysis of the samples with SIMPROF testing ( $P < 0.005$ ) revealed four groups with distinct community structure: an artificial reef group containing all artificial reef sites (37% similarity), a group containing the three northernmost natural banks (i.e., Baker, Aransas, and Dream banks; 57% similarity), and two groups containing only one site (i.e., Blackfish Ridge and Harte Bank; Figure 5).

Investigation of these groups with SIMPER suggested that differences in community structure between the artificial group and each of the three natural bank groups were driven by higher contributions of pelagic, schooling species. Higher MinCounts of Vermilion Snapper, Purple Reefish, and Red Snapper at the three northernmost natural banks differentiated that

group from Blackfish Ridge. A prevalence of Threadnose Bass (*Choranthias tenuis*) and a lack of pomacentrid damselfishes at Harte Bank distinguished this group from Blackfish Ridge and the other natural bank group (i.e., three northernmost banks).



**Figure 5.** Non-metric multidimensional scaling (nMDS) ordination using square-root transformed MinCounts and Bray-Curtis similarities from ROV surveys of artificial reefs (blue squares) and natural banks (green circles). Significant groups determined with SIMPROF ( $P < 0.005$ ) are denoted by the dashed circles. The relationship of the five habitat variables tested with Bio-Env are displayed in the blue vector plot.

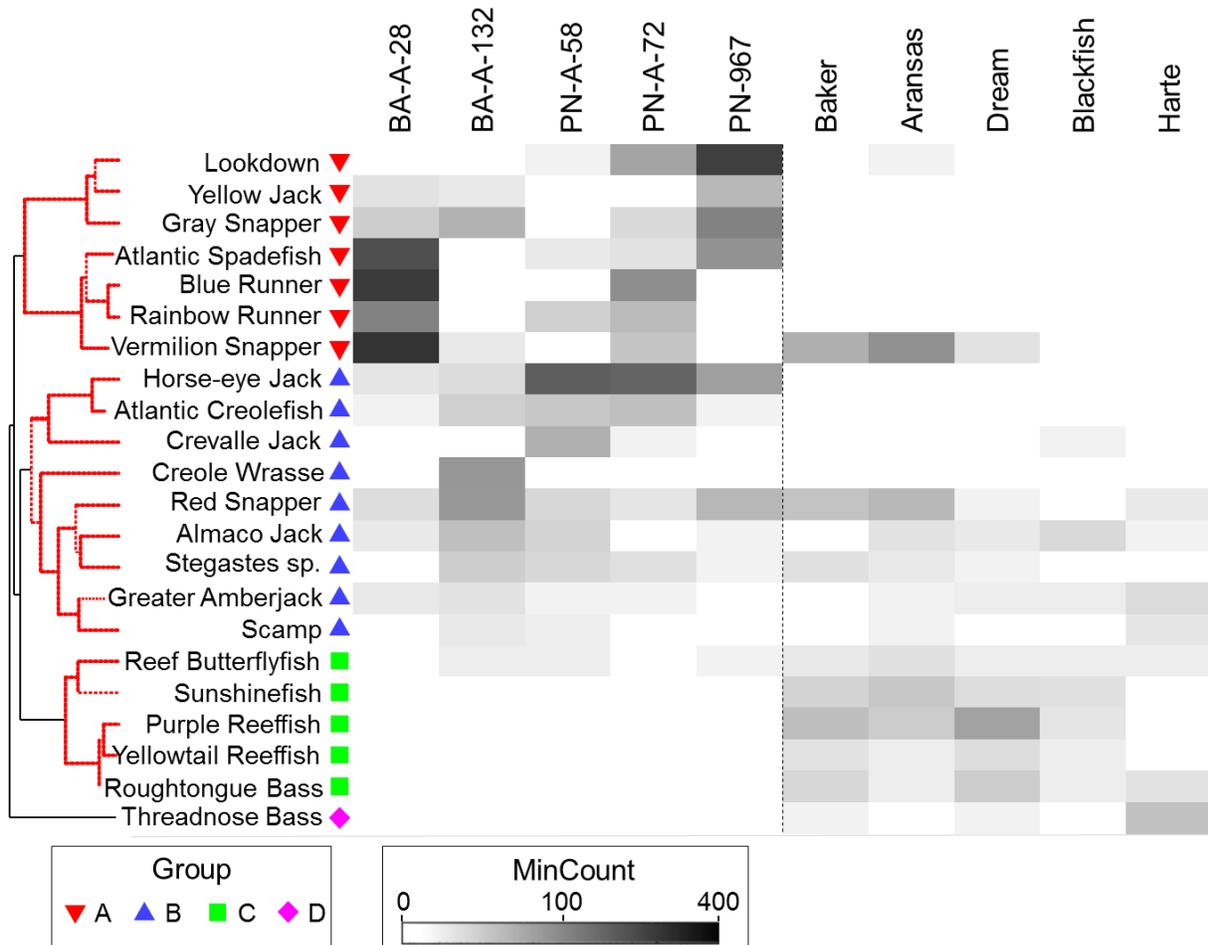
**Table 4.** Species most contributing to between-habitat dissimilarity for artificial reefs and natural banks surveyed in fall 2012. Mean abundance of most contributing species in each habitat, contribution to mean dissimilarity (DIS), dissimilarity/standard deviation ratio (DIS/SD), and percent contribution of species derived via SIMPER using a 50% cut-off for cumulative % contribution of species.

Species	Mean <sub>Artificial</sub>	Mean <sub>Natural</sub>	Avg. Diss.	DIS/SD	% Contribution	% Cum. contribution
Horse-eye Jack	7.42	0.00	7.15	1.40	8.57	8.57
Atlantic Spadefish	5.24	0.00	4.28	1.10	5.13	13.69
Lookdown	4.62	0.20	4.21	0.79	5.04	18.73
Vermilion Snapper	4.46	3.43	4.18	1.14	5.01	23.74
Gray Snapper	4.54	0.00	3.93	1.29	4.71	28.45
Blue Runner	4.83	0.00	3.90	0.78	4.68	33.12
Rainbow Runner	3.78	0.00	3.24	1.10	3.88	37.01
Purple Reefish	0.00	3.67	3.10	1.41	3.71	40.72
Atlantic Creolefish	3.04	0.00	2.90	1.51	3.47	44.19
Red Snapper	4.31	2.59	2.68	1.29	3.21	47.40
Sunshinefish	0.00	2.58	2.19	1.82	2.62	50.02

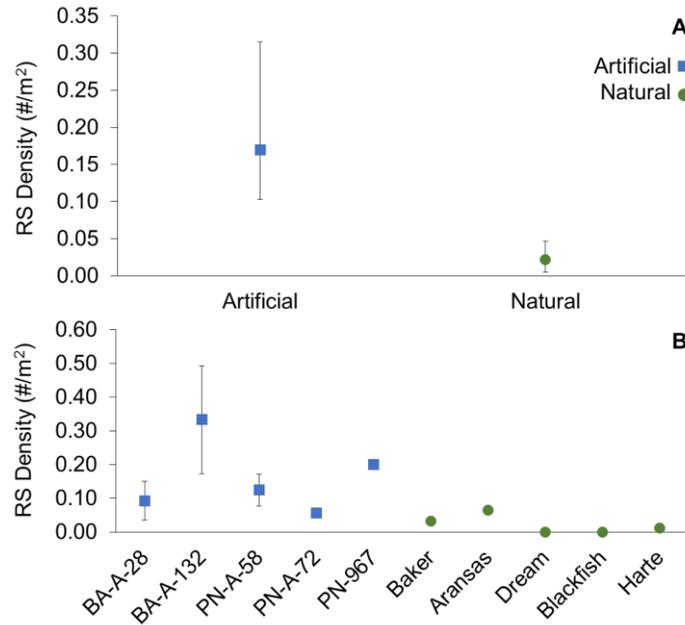
Our inverse analysis indicated that there was strong evidence of association among species observed in our surveys, thus warranting further investigation (Type 2 SIMPROF:  $\pi = 2.19$ ,  $P < 0.001$ ). After removing rare species (i.e., those that contributed  $< 5\%$  in any one sample), 22 species were retained for further analysis. Clustering based on the resulting species similarity matrix and Type 3 SIMPROF testing ( $P < 0.001$ ) identified four species groups whose member species co-occurred a similar fashion throughout our surveys (Figure 6). The first group (e.g., A in Figure 6) contained many of the gregarious or schooling species that could potentially be found in extremely high abundances at artificial reefs, and with the exception of Vermilion Snapper, were not observed at natural banks. The second group (e.g., B in Figure 6) included Red Snapper and several other fisheries species that were generally detected at both habitats but were usually found in higher abundances at artificial reefs (with exceptions). A third group of species (e.g., C in Figure 6), typifying natural bank habitats, was comprised of Reef Butterflyfish (*Chaetodon sedentarius*), three species of pomacentrid damselfishes, and Roughtongue Bass. Generally, these species were consistently observed across all natural bank sites and were not observed on artificial reefs with the exception of Reef Butterflyfish. The final species group identified (e.g., D in Figure 6) contained only the Threadnose Bass, which was observed only on natural banks and only in high abundances on Harte Bank.

There was significant agreement between biotic and abiotic similarity matrices (RELATE:  $\rho = 0.76$ ,  $P = 0.001$ ). Among the five abiotic variables tested, the BEST analysis (i.e., Bio-env) suggested that structure depth and survey temperature best matched the observed patterns in reef fish communities ( $\rho = 0.78$ ,  $P < 0.001$ ). The Spearman rank correlation for individual variables was greater for structure depth ( $\rho = 0.78$ ) than survey temperature ( $\rho = 0.68$ ).

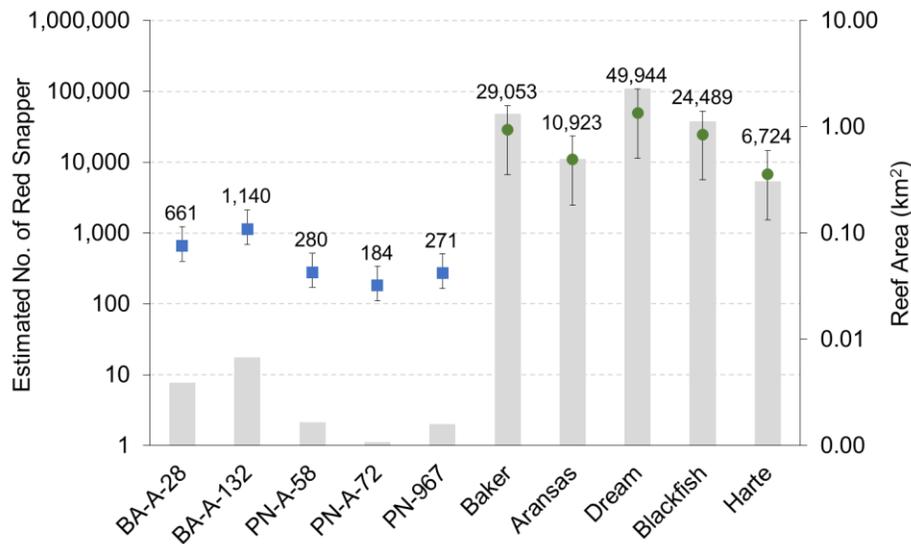
**Red Snapper Density Estimates** - Red Snapper density was estimated from 8 transects on artificial reefs and 5 transects on natural banks. The bootstrap test of equality suggested that mean density at artificial reefs and natural banks was significantly different ( $P = 0.011$ ). In fact, estimated Red Snapper density at artificial reefs (mean = 0.169 fish/m<sup>2</sup>; 95% CI [0.103 – 0.315]) was nearly 7.8 times greater than density at natural banks (mean = 0.022 fish/m<sup>2</sup>; 95% CI [0.005 – 0.047]; Figure 7A). Density estimates from artificial reefs were nearly 5 times more variable than those from natural banks (SD = 0.14 and SD = 0.03, respectively; Figure 7). Estimated densities from individual transects at artificial reefs ranged from a low of 0.03 fish/m<sup>2</sup> at BA-A-28 to as high as 0.49 fish/m<sup>2</sup> at BA-A-132. Among natural banks, Blackfish Ridge had the lowest density (0 fish/m<sup>2</sup>), while Aransas Bank had the highest estimated density (0.06 fish/m<sup>2</sup>; Figure 7B). Total abundance estimates at artificial sites ranged from 184 (95% CI [112 – 341]) Red Snapper at PN-A-72 to 1,140 (95% CI [694 – 2,120]) at BA-A-132 (Figure 8). Estimates at natural banks ranged from 6,724 (95% CI [1,540 – 14,468]) at Harte Bank to 49,944 (95% CI [11,432 – 107,459]) at Dream Bank.



**Figure 6.** Shade plot of square-root transformed species counts (only species accounting for > 5% of the total counts in any one sample are shown) by sample site. The linear gray scale shows back-transformed MinCounts. The dendrogram on the left displays the hierarchical clustering of species groups based on Whittaker's (1952) index of association resemblances computed on species-standardized MinCounts. Species groups identified using Type 3 SIMPROF ( $P < 0.001$ ) are indicated by connected red lines in the dendrogram and a range of symbols displayed next to species names (e.g., Group A = red, inverted triangles).



**Figure 7. Red Snapper (RS) density estimates (# of individuals/m<sup>2</sup>) from ROV transects on artificial reefs (squares) and natural banks (circles) in the western GOM in fall 2012. Density is displayed by (A) habitat (error bars represent bootstrapped 95% confidence intervals) and by (B) site to display variation in individual estimates (error bars representing standard error are displayed for sites that had two transects).**



**Figure 8. Estimated total abundance of Red Snapper (based on habitat density estimate multiplied by reef area; error bars represent bootstrapped 95% confidence interval) at artificial reefs (squares) and natural banks (circles). Reef area (gray bars) is plotted on the secondary y-axis. Note that both number of Red Snapper and reef area are plotted on log scales. For ease of interpretation, estimated number of Red Snapper is printed above each data point.**

**Discussion** - Concurrent surveys of artificial and natural habitats that provide basic information on species composition and abundance are essential to better understanding the role of artificial reefs as habitat for marine fish populations (Carr and Hixon 1997). Our study represents the first attempt to quantify the differences in fish communities at RTR artificial reefs and coralgal banks, two disparate but understudied habitats in the western GOM. Despite the vast physical differences in these two habitats, video-based ROV methods documented 79 species of fish ranging from small, reef-dependent species to large, highly mobile, apex predators. Our analyses suggest that fish communities at artificial reefs were different than fish communities at natural habitats, a finding that is supported by several studies of community structure in the northern GOM (Rooker et al. 1997; Wilson et al. 2003, 2006; Langland 2015). While many species were shared between natural and artificial habitats, there were several reef-dependent species only observed on natural banks suggesting that artificial reefs may not be suitable for all species. Nevertheless, many economically important species including Red Snapper, Vermilion Snapper, Greater Amberjack, Almaco Jack, and Scamp were observed at both natural and artificial habitats. Furthermore, our data suggest that Red Snapper occur in higher densities on RTR artificial reefs than natural banks, consistent with Wilson et al. (2003) who reported higher densities of Red Snapper at two RTR artificial reefs than at the West Flower Garden Bank where no Red Snapper were observed. The observation of Red Lionfish at both natural and artificial habitats is notable given their negative impacts on native fish recruitment (Albins and Hixon 2008). Furthermore, subsequent ROV-based surveys of artificial reefs in our region indicate that lionfish have become more common (Ajemian et al. 2015b); therefore, we recommend continued monitoring of these habitats to determine potential impacts this invader may have on fish community structure.

Differences in fish community composition at RTR artificial reefs and coralgal banks were observed for several taxa—many of which were undetected or absent in surveys of one habitat or the other. For example, 31 species were only observed on natural banks and 28 species were only observed on artificial reefs. Several species that we did not observe at the south Texas banks but have been recorded in the literature included Gray Snapper (Tunnell et al. 2009), Great Barracuda (*Sphyraena barracuda*; Dennis and Bright 1988), and Blue Runner (Dennis and Bright 1988). While the majority of these presence-absence observations are likely real (e.g., obligate natural reef species; Roughtongue Bass), some may be attributable to our ability to detect species that are rare, cryptic, or have secretive behaviors, varying environmental conditions, or from sampling effort (Gu and Swihart 2004). For example, the nepheloid layer was present on all sites except for BA-A-132, which generally prohibited observations from the bottom 2-6 m (artificial reef mean nepheloid depth = 2 m; natural mean = 3 m) of structured habitat. Thus, MinCounts for more benthic species were likely underestimated. In addition, the large ROV and its lights may have caused some species to avoid the ROV (e.g., burrowing or hiding in crevices; gobies). In contrast, other species like Greater Amberjack appeared to be less disturbed by the presence of the ROV and sometimes swam along with the ROV for brief periods. These behaviors seemed to hold for both natural and artificial habitats; however,

differences in species behavior and detectability at each habitat must be considered as such differences could bias resulting MinCounts and subsequent analyses.

Our community indices suggest that species richness and Shannon diversity were similar at natural banks and RTR artificial reefs, supporting several previous studies (Clark and Edwards 1999; Fowler and Booth 2012). In contrast to this finding, other investigations have suggested that natural habitats support higher species richness and diversity than artificial habitats (Carr and Hixon 1997; Rooker et al. 1997; Patterson et al. 2014; Langland 2015). In a comparative study of fish communities in the northern GOM, Rooker et al. (1997) reported higher species richness at the Flower Garden Banks than HI-389, a standing oil and gas platform, and cited the increased complexity of habitats available over a larger area at the Flower Garden Banks as a possible driver of this difference. The Flower Garden Banks are well-developed coral reefs providing significant amounts of reef habitat with high diversity (e.g., 280 fish species reported; Schmahl et al 2008). However, unlike the Flower Garden Banks and other diapiric shelf-edge banks in the northern GOM, the South Texas Banks surveyed in this study are relatively less complex, providing relatively little true ‘reef’ habitat in comparison due to the lack of contemporary reef-building activity (Dennis and Bright 1988). These banks also have fewer benthic habitat zones than the Flower Garden Banks, a difference driven largely by their comparatively low relief (e.g., Flower Garden Banks exhibit over 50 m of relief while the banks in this survey averaged 13 m of relief), and consequently, more prevalent interaction with the nepheloid layer (Rezak et al. 1985, 1990; Dennis and Bright 1988). Accordingly, lower species richness and diversity at the South Texas Banks—comparable to that of the RTR artificial reefs we surveyed—may be driven by more frequent interactions with the nepheloid layer (and its associated high turbidity). Although potential differences in species detectability could also play a role, these conditions likely prevent diverse epibenthic communities from developing which in turn may limit reef fish food and habitat availability (Dennis and Bright 1988).

Our multivariate analyses indicated that differences in reef fish communities inhabiting RTR artificial reefs and natural banks largely resulted from high counts of schooling species such as Atlantic Spadefish, Vermilion Snapper, and carangids including Horse-eye Jack and Lookdown at artificial reefs. This finding is supported by previous work in the northern GOM, which also demonstrated high abundances of transient, midwater carangids (Rooker et al. 1997; Ajemian et al. 2015b), spadefish (Gallaway et al. 1979; Stanley and Wilson 2000), and Vermilion Snapper (Ajemian et al. 2015b) at artificial habitats. Several of these species including Atlantic Spadefish, Blue Runner, and Lookdown are generally less dependent on food resources living directly on oil and gas platform reefs, but they commonly can account for most of the fish biomass (Gallaway et al. 1979; Gallaway and Lewbel 1982; Stanley and Wilson 1997; Stanley and Wilson 2000). Local changes in hydrographic conditions associated with the high vertical relief of oil and gas platform reefs have been attributed to increased concentrations of planktonic prey near these structures—a finding that may explain the high abundances of these more planktivorous, reef-associated species at these habitats (Hernandez et al. 2003; Keenan et al. 2003; Lindquist et al. 2005). In contrast, natural banks in this study were typified by more reef-

dependent taxa including Purple Reef fish, Yellowtail Reef fish, Sunshinefish, Reef Butterflyfish, and small serranids such as Roughtongue Bass and Wrasse Basslet. Species of this reef-dependent assemblage were also identified as characteristic of the south Texas banks by several previous studies (Dennis and Bright 1988; Tunnell et al. 2009; Hicks et al. 2014). Certainly, foodweb-based examination to better understand these ecological linkages is warranted.

Although artificial reef communities in this study were generally similar, our analyses suggested these relatively rare natural banks could be further divided into three groups with differing community composition—one consisting of the three northernmost banks (i.e., Baker, Aransas, and Dream banks) and two single groups including Blackfish Ridge and Harte Bank. Nash et al. (2014) used geomorphic variables including regional depth, shallowest depth, rugosity, number of terraces, distance to nearest neighbor, and bank area and derived similar bank groupings. In this study, Harte Bank and Blackfish Ridge generally had lower species richness, possibly because of unique physical characteristics of each site. Harte Bank differed from the other banks we surveyed because it was located in deeper water (e.g., base depth at Harte = 96 m; remaining banks mean depth = 75 m). Blackfish Ridge was unique because PN-A-72, an artificial reef surveyed in this study, was located in extremely close proximity to the main bank feature (~300 m). Interestingly, both of these sites represented the lowest species richness from each of their respective habitat types. Previous work has reported that Blackfish Ridge experiences persistent high turbidity which often covers the entire bank, a condition that limits epibenthic primary production and is generally attributed to lower observed species richness (Rezak et al. 1985, 1990; Dennis and Bright 1988; Tunnell et al. 2009); however, when we surveyed this bank, its terrace did extend out of the nepheloid layer. Nevertheless, we did notice lower MinCounts of several pomacentrid damselfishes at Blackfish Ridge, possibly an indication of nepheloid effects on benthic primary productivity. The proximity of the artificial reef to Blackfish Ridge provides another possible explanation of lower species richness and diversity—namely that the artificial reef may have concentrated high abundances of large piscivores, which in turn could negatively influence community structure by increasing predation rates (Hixon and Beets 1993; Cowan et al. 2011) or by decreasing post-settlement survival of fish that would normally recruit to the natural habitat (Carr and Hixon 1997). Despite this possibility, we documented low abundances of potential predators like Red Snapper at both of these sites. While effects of the nepheloid layer probably influenced the communities we observed, further investigation of proximity effects of artificial reefs on fish communities is warranted as new artificial reefs may fail to meet management objectives depending on their proximity to existing reef habitat (e.g., Mudrak and Szedlmayer 2012).

Environmental factors including bottom depth and vertical relief have often been identified as important drivers of fish community structure at natural and artificial habitats (Gallaway et al. 1981; Stanley and Wilson 2000; Wilson et al. 2003; Zintzen et al. 2012; Bryan et al. 2013; Patterson et al. 2014). Seminal work by Gallaway et al. (1981) classified standing platform communities across the Texas-Louisiana shelf into three groups including a coastal group (<30 m), an offshore group (30-60 m), and a bluewater group (>60 m). In a more recent

study of artificial reefs across the shelf in our study region, Ajemian et al. (2015b) noticed a similar transition in fish communities around the 60 m isobath. Our analyses identified structure depth (i.e., shallowest depth of structure at a site) and survey temperature as the most important factors influencing the fish communities we observed—a difference possibly related to the bottom depths of the sites in our survey. For example, with the exception of BA-A-28, PN-967, and Harte Bank, the sites we surveyed were located in bottom depths of 61-82 m rather than a wide range of depths across the shelf. While our analyses also suggested survey temperature was important in explaining the patterns in fish community structure, it is difficult to assess the relative importance of structure depth and survey temperature because they were highly correlated.

Specifically, survey temperature was generally warmer on artificial reefs because the CRTs spanned the greater vertical relief of the artificial reefs and thus spent more time higher in the water column. Structure depth however, was nearly twice as shallow at artificial reefs (mean artificial = 33 m; mean natural = 65 m). Previous studies have shown that many species responsible for the dissimilarity between the two habitats we surveyed (e.g., Atlantic Spadefish, Blue Runner, Horse-eye Jack, Lookdown, Vermilion Snapper) are commonly found in high but variable abundances in the middle to upper portions of the water column around reefs with high vertical relief (Rooker et al. 1997; Stanley and Wilson 1997, 2000; Wilson et al. 2006; Ajemian et al. 2015a, 2015b). Similarly, we observed many of these species in highest abundances at BA-A-28 and PN-967, two artificial reefs with the shallowest structure depths. While we recognize that bottom depth and vertical relief of a site influence structure depth, our data supports previous studies that suggest that the presence of structure high in the water column influences the occurrence and possibly abundances of these pelagic, schooling species (Wilson et al. 2003). Thus, as standing platforms are removed throughout the northern GOM, RTR artificial reefs may become increasingly valuable habitat for these types of fish. For these reasons, we recommend that future video-based surveys designed for assessing fish community structure at these habitats apply more appropriate survey designs and dedicate the effort necessary to assess these species that are more transient and typically occur higher in the water column.

Species-specific habitat requirements likely influenced the occurrence of several species in our samples. Several species groups were identified that occurred in similar fashion throughout our samples. For example, species in the reef-dependent group (i.e., group C in Figure 6; excluding Reef Butterflyfish), only occurred at the natural banks. Bright and Rezak (1976) regarded one of these species, the planktivorous Roughtongue Bass, as the most characteristic species of the south Texas banks. This species is reported as a common member of the deep reef fish community and an important forage base for larger fish like grouper and snapper (Weaver et al. 2006). Among artificial habitats, Sheepshead (*Archosargus probatocephalus*) were only observed at the two shallowest sites (i.e., BA-A-28 and PN-967), aligning well with the species life history and dependency on bio-fouling communities at shallower reefs (Gallaway and Lewbel 1982; Parker et al. 1994; Stanley and Wilson 1997). Collectively, the consistency that these species arrived in our samples suggests that their

association is not by chance (Sommerfield and Clarke 2013). Indeed, different habitats are characterized by differing food resources, shelter, and abiotic conditions—all of which affect growth, survival, and successful recruitment—resulting in consistent and distinct fish assemblages (Dennis and Bright 1988; Rezak et al. 1985, 1990; Beck et al. 2001; Sommerfield and Clark 2013).

Our analysis of Red Snapper density at oil and gas platform reefs compared to natural bottom south Texas banks suggests that densities were nearly 7.8 times greater at artificial reefs, and these densities were more variable than estimates from natural structure. These results are supported by other studies that also found high but variable abundances of Red Snapper at standing platforms and is likely due to the patchy nature of their populations over large expanses of structured habitat. For example, Stanley and Wilson (1997) noted Red Snapper abundance varied up to a factor of four between months, a finding they attributed to movement away from the platform. Inferences regarding our density estimates must be made with the following considerations. First, our ability to estimate Red Snapper density was hindered by visibility constraints imposed by the nepheloid layer (Shideler 1981; Ajemian et al. 2015a). Because Red Snapper are a demersal species deriving a portion of their food resources from soft sediments surrounding reefs (McCawley and Cowan 2007; Gallaway et al. 2009), our estimates are likely a conservative underestimate of true density. For example, we routinely observed Red Snapper moving in and out of the nepheloid layer, but observations within this feature were not possible due to the near-zero visibility. An exception was BA-A-132 where no nepheloid layer was present; however, even when we excluded density estimates from this site, the resulting mean Red Snapper density at artificial reefs ( $0.115 \text{ fish/m}^2$ ) was still 5.2 times greater than the density estimated at natural banks ( $0.022 \text{ fish/m}^2$ ). Second, our density estimates were based on relatively few transects given the nature of offshore research logistics, ship time costs, and the self-imposed sample criteria to minimize double counting. Despite these issues, our results are similar to previous investigations documenting higher densities of Red Snapper at artificial reefs than natural habitats (Wilson et al. 2003, 2006; Patterson et al. 2014). Furthermore, in a comparative study of reef fish community structure at artificial and natural reefs in the northern GOM, Patterson et al. (2014) reported Red Snapper densities approximately 6 times greater at artificial reefs than natural reefs—remarkably similar to our estimate of 7.8 fold. Our estimates of total Red Snapper abundance at artificial reefs are also similar to the range reported by hydroacoustic surveys at standing platforms and RTR artificial reefs in the northern GOM (Stanley and Wilson 1997, 2000; Wilson et al. 2003, 2006) and estimates of Red Snapper abundance based on explosive platform removals (Gitschlag et al. 2003). However, our estimates appear low, and this may be attributable to a characteristic of our sites that included the presence of nearby RTR structures at some of our reef sites (i.e., previous estimates of Stanley and Wilson [1997, 2000] and Wilson et al. [2003, 2006] were based on single structures). This could simply be attributed to underestimated densities because of visibility constraints, but it may also be a function of artificial reef density (i.e., number of structures in close proximity). For example, Strelcheck et al. (2005) observed decreasing Red Snapper abundance and size with increasing

artificial reef abundance and density. Our estimates of Red Snapper density and subsequently total abundance at the five natural banks in our study suggest that at least 121,100 (likely more) Red Snapper inhabited these sites at the time of our survey. Assuming the average weight of Red Snapper from natural banks in our area (2.3 kg; estimated from fishery-independent vertical line surveys; Streich, unpublished data) and multiplying it by the estimated number of individuals implies these five natural banks held approximately 278,530 kg (614,053 lbs) of Red Snapper or approximately 7.6% of the GOM annual catch limit (ACL) set by NOAA Fisheries in 2012 (8.08 million pounds; NOAA 2012). Thus, despite higher densities at artificial reefs, natural banks likely support much higher total abundances of Red Snapper because of their comparatively much larger habitat area (i.e., footprint). Given the stock has recovered substantially since this time (SEDAR 2015), these estimates also likely underestimate the true current abundance based on visibility constraints, sampling design, and because our survey was performed in 2012.

Our estimate of Red Snapper total abundance on the five banks surveyed suggests that these five relatively small areas, which account for < 0.4% of the estimated natural reef habitat in the northern GOM (i.e., area of the five banks in this survey = 5.55 km<sup>2</sup> [Table 1] divided by the estimated natural reef habitat in northern GOM = 1578 km<sup>2</sup> [Gallaway et al. 2009]), show natural banks in this region likely hold a large Red Snapper biomass. Thus, these areas warrant further investigation, particularly given the Red Snapper management uncertainties in the GOM. Moreover, there are hundreds of known bathymetric features scattered across the northern GOM shelf (Ludwick and Walton 1957; Rezak et al. 1985; Shroeder et al. 1988, 1995; Weaver et al. 2001; Rooker et al. 2004; Dufrene 2005; VERSAR 2009). While the vast majority of these have yet to be characterized, many are well-known from anecdotal fishing reports to harbor large concentrations of Red Snapper. Moreover, many features have yet to be discovered. For example, during this cruise a prominent unknown bank, now formally known as Harte Bank, was described and mapped. Although Harte Bank was the smallest natural bank surveyed in this study (0.31 km<sup>2</sup>), it represents a significant bathymetric feature and highlights the likelihood of additional unmapped natural reef habitat for Red Snapper in the GOM.

The dynamics between natural and artificial reefs may also have important implications for reef fish management. Other work has shown fishing mortality and fish density are not equally distributed between artificial and natural habitats, with natural banks often a refuge from at least some fishing mortality. The refuge from fishing mortality provided by known and unknown natural banks may to some extent explain the lack of a clear spawner-recruit relationship observed in this population (Cowan et al. 2011; SEDAR 2015). For example, Garner and Patterson (2015) observed that for-hire captains fishing during the open Red Snapper season targeted artificial reef sites. Consequently, fishing mortality may often be concentrated at artificial reef sites (Polovina 1991; Grossman et al. 1997; Garner and Patterson 2015). Although fishing mortality can be quite high at these habitats (e.g., Addis et al. 2016), artificial reefs have the potential to divert fishing effort away from more sensitive natural habitats, and based on findings here, away from a large portion of the Red Snapper population in the western GOM.

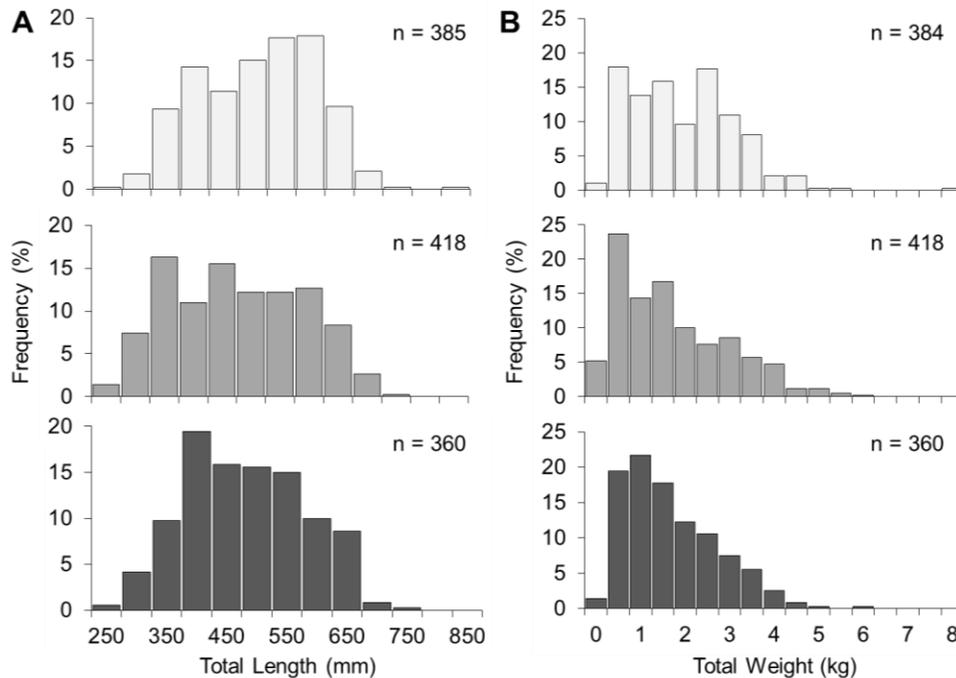
This inference is supported by a recent survey of recreational anglers in Texas which suggested that over 70% of the anglers used artificial reefs, with nearly 40% of these anglers targeting standing platforms (Schuett et al. 2015). Moreover, in a Gulf-wide study, Porch et al. (2015) observed the highest Red Snapper spawning frequencies at natural habitats in our region—further highlighting the potential benefits of RTR and diversion of fishing pressure from natural habitats. While more detailed study of fishing effort among habitat types is needed, these findings certainly reveal several management implications for RTR vs natural banks. For example, as the number of standing platforms in the GOM continues to decline (Pulsipher et al. 2001), RTR artificial reefs will likely become increasingly important in supporting the Red Snapper fishery in the northwestern GOM which has relied on the abundance of standing platforms and the habitat they provide in recent decades. Subsequently, future levels of fishing effort at natural habitats may increase if the amount of RTR or other artificial habitat available to fishermen does not replace the current abundance of standing platforms. Nonetheless, we caution strict interpretation of our estimates for direct management advice due to a relatively small sample size and restricted geography; however, they clearly point toward the beneficial aspects of both natural and artificial reef effects on fisheries species such as Red Snapper in the GOM.

We recommend that future surveys increase replication and geographic coverage of both natural and artificial reefs to gain better estimates across the northern Gulf of Mexico. While our study provides new information necessary for evaluating the effects of RTR artificial reefs in the western GOM compared to natural bank habitats, we stress the need for additional comparisons of species-specific life history traits (e.g., reproductive potential, age distribution, growth, mortality, site fidelity) at both artificial and natural habitats as well. Only with more characterization of these habitat types and comparative performance metrics will it be possible to fully understand the value and function of natural and artificial reefs as fish habitat.

### **Red Snapper Size Structure, Age, and Growth - Artificial Reefs and Natural Banks (Obj. 2)**

**Overview** - During the sampling period, fishery-independent vertical line surveys captured 1,170 Red Snapper. After discarding vertical line sets that were unsuitable for abundance estimation (e.g., snagged on structure; fished longer than five minutes), 42 sets at artificial reefs captured 410 Red Snapper, 42 sets at natural banks captured 387 Red Snapper, and 37 sets at standing platforms captured 356 Red Snapper (1,153 total individuals). No differences among male : female ratios were observed at artificial reefs (1:0.86;  $\chi^2 = 2.12$ ,  $P = 0.146$ ), natural banks (1:0.85;  $\chi^2 = 2.66$ ,  $P = 0.103$ ), or standing platforms (1:0.92;  $\chi^2 = 0.63$ ,  $P = 0.429$ ). Vertical line CPUE was similar among habitats ( $F_{2,6} = 0.04$ ,  $P = 0.960$ ), averaging 9.76 fish/set (SE = 0.76) at artificial reefs, 9.62 fish/set (SE = 0.88) at standing platforms, and 9.21 fish/set (SE = 1.05) at natural banks.

**Size Structure** - Red Snapper ranged in size from 275 mm to 855 mm TL and from 0.26 kg to 8.26 kg TW. Among habitats, mean length was similar ( $F_{2,6} = 0.64$ ,  $P = 0.558$ ), averaging 548.5 mm TL (SE = 10.91) at natural banks, 517.2 mm TL (SE = 12.09) at artificial reefs, and 510.3 mm TL (SE = 10.65) at standing platforms. Red Snapper TW averaged 2.38 kg (SE = 0.12) at natural banks, 2.17 kg (SE = 0.13) at artificial reefs, and 1.98 kg (SE = 0.11) at standing platforms, and was not significantly different among habitats ( $F_{2,6} = 0.47$ ,  $P = 0.645$ ). Length frequency distributions were different among all habitats (artificial vs. natural:  $G = 97.93$ ,  $df = 12$ ,  $P < 0.001$ ; artificial vs. standing:  $G = 64.48$ ,  $df = 10$ ,  $P < 0.001$ ; natural vs. standing:  $G = 42.48$ ,  $df = 12$ ,  $P < 0.001$ ). An evaluation of standardized residuals suggested that artificial reefs had over two times more fish under 400 mm TL than expected when compared with natural banks (25.1% compared to 11.4%, respectively; Figure 9A). Similarly, standing platforms had more small fish than natural banks, especially those under 500 mm TL. Natural banks generally had greater proportions of larger fish than either standing platforms or artificial reefs. For example, 45.2% of fish from natural banks were 550 mm to 700 mm TL compared with 33.3% at artificial reefs and 33.6% at standing platforms. Standing platforms had a greater proportion of fish from 400 mm to 600 mm TL than artificial reefs; however, nearly twice as many fish less than 400 mm TL were sampled at artificial reefs (25.1%) than standing platforms (14.4%; Figure 9A). Weight frequency distributions also differed among the three habitats (artificial vs. natural:  $G = 81.16$ ,  $df = 16$ ,  $P < 0.001$ ; artificial vs. standing:  $G = 47.03$ ,  $df = 12$ ,  $P < 0.001$ ; natural vs. standing:  $G = 42.52$ ,  $df = 16$ ,  $P < 0.001$ ). A greater proportion of larger fish (> 2.5 kg TW) were sampled from the natural banks (41.7%) than either artificial reefs (29.9%) or standing platforms (27.5%; Figure 9B). Weight frequency distributions were more similar between artificial reefs and standing platforms as both were dominated by smaller individuals. Standardized residuals suggested that the main differences stemmed from a greater proportion of fish less than 1 kg at artificial reefs and more 1 to 1.5 kg fish at standing platforms (Figure 9B). No differences were observed in TW-TL regressions among habitats as 95% confidence intervals (CI) overlapped for both the  $a$  and  $b$  parameters. Length-weight data were then pooled, and the overall TW-TL regression parameters estimated were  $a = 2.19 \times 10^{-8}$  (95% CI [ $1.80 \times 10^{-8}$ ,  $2.64 \times 10^{-8}$ ]) and  $b = 2.92$  (95% CI [2.89, 2.95]).

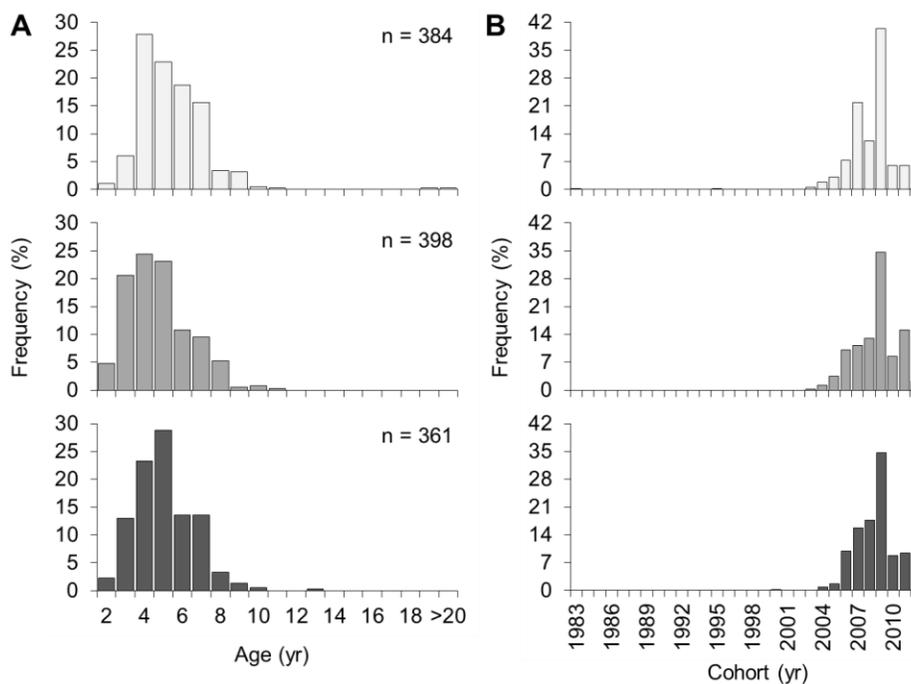


**Figure 9. Length (A) and weight (B) frequencies of Red Snapper captured at natural banks (white), artificial reefs (gray), and standing platforms (black) in the western Gulf of Mexico from 2012-2014. Length and weight frequencies are grouped into 50-mm bins and 0.5-kg bins, respectively (e.g., 350 = 350 – 399 mm TL).**

**Age** - Otolith-derived ages were estimated for 1,143 Red Snapper. After the first read, agreement between readers was 84.3% with an ACV of 2.63 and an APE of 1.86%. The second read increased agreement to 93.0% with an ACV and APE of 1.12 and 0.8%, respectively. Consensus on the remaining 80 otolith sections was achieved in the third joint reading. Red Snapper ages ranged from 2 to 30 years; however, age-3 to age-7 individuals comprised the vast majority of fish sampled (90.6%; Figure 10A). Only five individuals were older than 10 years. Mean age was not significantly different among habitats ( $F_{2,6} = 1.31$ ,  $P = 0.338$ ), averaging 5.04 years (SE = 0.22) at artificial reefs, 5.22 years (SE = 0.15) at standing platforms, and 5.77 years (SE = 0.20) at natural banks. Age frequency distributions differed among all habitats (artificial vs. natural:  $G = 161.75$ ,  $df = 9$ ,  $P < 0.001$ ; artificial vs. standing:  $G = 43.55$ ,  $df = 9$ ,  $P < 0.001$ ; natural vs. standing:  $G = 45.72$ ,  $df = 9$ ,  $P < 0.001$ ). A general pattern included a greater proportion of young fish at artificial reefs and standing platforms than at natural banks. For example, 7.0% of individuals from natural banks were age-2 and age-3 fish, compared to 15.2% of individuals from standing platforms and 25.4% of individuals from artificial reefs (Figure 10A). In contrast, a greater proportion of fish  $\geq$  age-6 was observed at natural banks (42.2%) compared to standing platforms (32.7%) or artificial reefs (27.1%). All age frequency distributions displayed relatively sharp declines from the age-7 to age-8 bins. Artificial reefs and standing platforms also showed sharp declines after age-5; however, this decline was not displayed in the natural bank age frequency (Figure 10A). Cohort frequency distributions for all

habitats displayed evidence of a strong 2009 year-class which constituted 34 – 40% of the fish sampled from each habitat (Figure 10B). Despite overall similarities between cohort frequencies, some differences among habitats were evident including strong representation of the 2007 year-class at natural banks and the 2011 year-class at artificial reefs that were not observed at the other habitats.

The ancillary evaluation of mean TL, TW, and age among sites suggested means for all three variables differed ( $P < 0.001$ ). Tukey contrasts revealed that fish sampled at Baker Bank were significantly longer (mean = 600.5 mm; SE = 6.4), heavier (mean = 2.89 kg; SE = 0.08), and older (mean = 6.5 yrs; SE = 0.1) than fish from any of the other sites. In addition, 80% of the Red Snapper sampled at Baker Bank were age-6 or older, and most were derived from the 2007 year-class (34%).



**Figure 10. Histograms displaying age (A) and cohort (B) frequencies of Red Snapper captured with vertical lines at natural banks (white), artificial reefs (gray) and standing platforms (black) in the western Gulf of Mexico from 2012-2014. >20 includes all individuals age-20 or older.**

**Growth** - Among the four models fit to TL-at-age and TW-at-age data, the logistic growth model best fit the data for each habitat (Table 5; Table 6). The Gompertz model was the second most supported model, although the logistic model consistently had at least twice the support as the Gompertz model (based on  $w_i$ ). Generally, both the two parameter and three parameter von Bertalanffy models had considerably less support (Table 5; Table 6). Based on  $AIC_c$ , the logistic model was selected to compare growth among habitats.

**Table 5. Growth models fit to length-at-age data for Red Snapper collected at artificial reefs, natural banks, and standing platforms in the western Gulf of Mexico (3P VB = three parameter von Bertalanffy model; 2P VB = two parameter von Bertalanffy model). Parameter estimates for each model ( $L_{\infty}$  = mean asymptotic TL;  $g$  = instantaneous rate of growth [Gompertz];  $k$  = growth coefficient [3P VB or 2P VB] or rate parameter [Gompertz];  $t_0$  = theoretical age at a length of zero [3P VB or 2P VB] or inflection point of the curve [Logistic]) are displayed with bootstrapped 95% confidence intervals in parentheses. Within each habitat, models are sorted by modified Akaike's Information Criteria (AICc), Akaike difference ( $\Delta_i$ ), and Akaike weights ( $w_i$ ).**

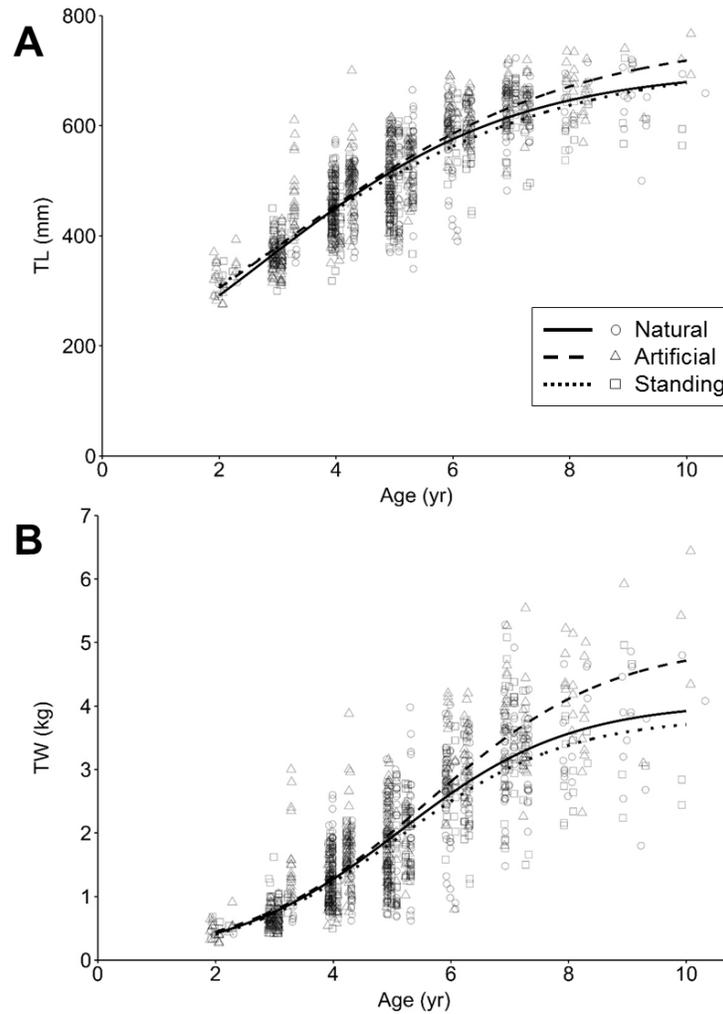
		$L_{\infty}$	$g$	$k$	$t_0$	AICc	$\Delta_i$	$w_i$
<b>Artificial</b>								
Logistic		761.70	0.40	-	3.01	4257.00	0.00	0.74
		(719.79, 822.74)	(0.34, 0.47)	-	(2.75, 3.41)			
Gompertz		816.65	0.27	1.72	-	4259.41	2.41	0.22
		(754.95, 914.76)	(0.21, 0.33)	(1.60, 1.91)	-			
3P VB		950.99	-	0.14	-0.62	4263.25	6.25	0.03
		(830.44, 1209.36)	-	(0.09, 0.20)	(-1.37, -0.08)			
2P VB		832.00	-	0.20	-	4266.87	9.87	0.01
		(790.09, 880.82)	-	(0.18, 0.22)	-			
<b>Natural</b>								
Logistic		702.69	0.46	-	2.74	4181.74	0.00	0.54
		(666.88, 754.54)	(0.37, 0.57)	-	(2.53, 3.01)			
Gompertz		727.77	0.35	1.91	-	4183.37	1.64	0.24
		(682.10, 798.80)	(0.26, 0.44)	(1.58, 2.45)	-			
2P VB		790.71	-	0.21	-	4184.16	2.42	0.16
		(747.75, 841.04)	-	(0.19, 0.24)	-			
3P VB		778.45	-	0.23	0.12	4186.09	4.35	0.06
		(711.83, 904.06)	-	(0.15, 0.31)	(-0.76, 0.73)			
<b>Standing</b>								
Logistic		715.93	0.39	-	2.70	3868.16	0.00	0.76
		(670.04, 787.15)	(0.31, 0.48)	-	(2.41, 3.17)			
Gompertz		754.60	0.28	1.59	-	3870.97	2.81	0.19
		(692.54, 865.09)	(0.20, 0.36)	(1.43, 1.86)	-			
3P VB		836.34	-	0.17	-0.67	3874.32	6.16	0.04
		(732.88, 1079.12)	-	(0.09, 0.24)	(-1.76, 0.06)			
2P VB		751.53	-	0.23	-	3876.15	7.99	0.01
		(713.69, 795.53)	-	(0.21, 0.26)	-			

**Table 6. Growth models fit to weight-at-age data for Red Snapper collected at artificial reefs, natural banks, and standing platforms in the western Gulf of Mexico (3P VB = three parameter von Bertalanffy model; 2P VB = two parameter von Bertalanffy model). Parameter estimates for each model ( $W_\infty$  = mean asymptotic TW;  $g$  = instantaneous rate of growth [Gompertz];  $k$  = growth coefficient [3P VB or 2P VB] or rate parameter [Gompertz];  $t_0$  = theoretical age at a length of zero [3P VB or 2P VB] or inflection point of the curve [Logistic]) are displayed with bootstrapped 95% confidence intervals in parentheses. Within each habitat, models are sorted by modified Akaike's Information Criteria (AICc), Akaike difference ( $\Delta_i$ ), and Akaike weights ( $w_i$ ).**

		$W_\infty$	$g$	$k$	$t_0$	AICc	$\Delta_i$	$w_i$
Artificial	Logistic	4.99	0.64	-	5.61	707.74	0.00	0.46
		(4.55, 5.64)	(0.56, 0.74)	-	(5.26, 6.09)			
	Gompertz	6.41	0.31	5.47	-	709.10	1.36	0.23
		(5.44, 8.13)	(0.25, 0.38)	(4.72, 6.65)	-			
	2P VB	8.14	-	0.20	-	709.16	1.41	0.23
	(7.13, 9.45)	-	(0.18, 0.21)	-				
3P VB	7.95	-	0.20	0.06	711.16	3.42	0.08	
	(6.25, 11.73)	-	(0.14, 0.27)	(-0.73, 0.66)				
Natural	Logistic	4.05	0.69	-	5.13	741.18	0.00	0.67
		(3.70, 4.55)	(0.57, 0.83)	-	(4.81, 5.57)			
	Gompertz	4.53	0.41	6.52	-	743.61	2.43	0.20
		(3.97, 5.44)	(0.31, 0.53)	(4.81, 9.66)	-			
	3P VB	4.88	-	0.31	0.80	745.16	3.98	0.09
	(4.16, 6.23)	-	(0.22, 0.42)	(-0.08, 1.43)				
2P VB	5.87	-	0.23	-	746.52	5.34	0.05	
	(5.16, 6.75)	-	(0.21, 0.26)	-				
Standing	Logistic	3.83	0.69	-	5.09	639.52	0.00	0.99
		(3.47, 4.36)	(0.57, 0.83)	-	(4.75, 5.58)			
	Gompertz	4.45	0.38	5.74	-	649.48	9.96	0.01
		(3.81, 5.58)	(0.28, 0.49)	(4.44, 8.07)	-			
	2P VB	5.45	-	0.24	-	652.64	13.12	0.00
	(4.76, 6.34)	-	(0.21, 0.26)	-				
3P VB	4.97	-	0.27	0.37	653.87	14.35	0.00	
	(4.06, 6.92)	-	(0.18, 0.37)	(-0.62, 1.06)				

Visually, logistic models of TL-at-age among the three habitats were quite similar until around age-6 when growth curves for natural banks and standing platforms began to increase at a slower rate than artificial reefs (Figure 11A). There was no evidence that models differed between natural banks and standing platforms (Table 7). However, likelihood ratio tests suggested the TL-at-age model for artificial reefs was significantly different than the models for natural banks or standing platforms ( $P < 0.05$ ; Table 7). Although no significant differences were found in subsequent likelihood ratio tests for equal parameters between artificial and natural banks, the smaller  $L_\infty$  for natural banks (702.7 mm) may have been driving the overall model difference as this estimate was not contained within the 95% CI of  $L_\infty$  for artificial reefs (Table 5). Between artificial reefs and standing platforms, the hypothesis of equal  $L_\infty$  and  $g$  parameters was rejected ( $\chi^2 = 12.54$ ,  $P = 0.002$ ; Table 7), suggesting separate  $L_\infty$  and  $g$

parameters were warranted. Similar to natural banks, the estimate of  $L_{\infty}$  for standing platforms (715.9 mm) was lower than estimated  $L_{\infty}$  for artificial reefs (761.7 mm) and was not contained in the 95% CI [719.8, 822.7].



**Figure 11. Logistic growth models of Red Snapper TL-at-age (A) and TW-at-age (B) data fitted separately by habitat type. Data are displayed for natural banks (circles and solid curve), artificial reefs (triangles and dashed curve), and standing platforms (squares and dotted line).**

Logistic models of TW-at-age were quite similar among all habitats from age-2 through age-5 or age-6, at which point the artificial growth curve continued to increase but at faster rate than curves for natural banks or standing platforms (Figure 11B). Like the TL-at-age models, no differences in TW-at-age models for natural banks and standing platforms was observed, and all three model parameters for these two habitats were similar (Table 6; Table 7). The TW-at-age model for artificial reefs was significantly different than the models for either natural banks or standing platforms ( $P < 0.001$ ; Table 7). Likelihood ratio tests indicated that the  $W_{\infty}$  estimate for

artificial reefs (4.99 kg) was significantly greater than  $W_{\infty}$  estimates for natural banks (4.05 kg) or standing platforms (3.83 kg; Table 6). Confidence intervals confirmed this difference as the 95% CI for  $W_{\infty}$  at artificial reefs did not overlap with 95% CIs for natural bank or standing platform  $W_{\infty}$  estimates (Table 6). Borderline significance (i.e.,  $P = 0.083$  for artificial vs. natural and  $P = 0.059$  for artificial vs. standing) was also observed for the  $t_0$  parameter and the estimate for artificial reefs (5.61) was not contained within the 95% CIs for natural banks or standing platforms.

**Table 7. Results of likelihood ratio tests comparing logistic growth model parameter estimates between artificial reefs, natural banks, and standing platforms in the western Gulf of Mexico. Comparison are presented for length-at-age data (left) and weight-at-age data (right). Significant P values ( $\alpha = 0.05$ ) are denoted in bold.**

Comparison	Null hypothesis	$\chi^2$	df	$P$	Comparison	Null hypothesis	$\chi^2$	df	$P$
<b>TL Models</b>					<b>TW Models</b>				
Artificial vs. Natural	Coincident curves	8.86	3	<b>0.031</b>	Artificial vs. Natural	Coincident curves	26.62	3	<b>&lt;0.001</b>
	Equal $L_{\infty}$	3.35	1	0.067		Equal $W_{\infty}$	7.64	1	<b>0.006</b>
	Equal $g$	1.22	1	0.269		Equal $g$	0.39	1	0.532
	Equal $t_0$	2.01	1	0.156		Equal $t_0$	3.01	1	0.083
	Equal $L_{\infty}$ and $g$	5.18	2	0.075		Equal $W_{\infty}$ and $g$	18.09	2	<b>&lt;0.001</b>
	Equal $L_{\infty}$ and $t_0$	3.35	2	0.187		Equal $W_{\infty}$ and $t_0$	20.49	2	<b>&lt;0.001</b>
	Equal $g$ and $t_0$	2.22	2	0.330		Equal $g$ and $t_0$	5.39	2	0.068
Artificial vs. Standing	Coincident curves	22.18	3	<b>&lt;0.001</b>	Artificial vs. Standing	Coincident curves	22.18	3	<b>&lt;0.001</b>
	Equal $L_{\infty}$	1.54	1	0.214		Equal $W_{\infty}$	11.95	1	<b>&lt;0.001</b>
	Equal $g$	0.03	1	0.872		Equal $g$	0.46	1	0.497
	Equal $t_0$	1.75	1	0.186		Equal $t_0$	3.57	1	0.059
	Equal $L_{\infty}$ and $g$	12.54	2	<b>0.002</b>		Equal $W_{\infty}$ and $g$	28.49	2	<b>&lt;0.001</b>
	Equal $L_{\infty}$ and $t_0$	1.76	2	0.416		Equal $W_{\infty}$ and $t_0$	43.86	2	<b>&lt;0.001</b>
	Equal $g$ and $t_0$	4.21	2	0.122		Equal $g$ and $t_0$	6.21	2	<b>0.045</b>
Natural vs. Standing	Coincident curves	5.47	3	0.140	Natural vs. Standing	Coincident curves	5.37	3	0.146
	Equal $L_{\infty}$	-	-	-		Equal $W_{\infty}$	-	-	-
	Equal $g$	-	-	-		Equal $g$	-	-	-
	Equal $t_0$	-	-	-		Equal $t_0$	-	-	-
	Equal $L_{\infty}$ and $g$	-	-	-		Equal $W_{\infty}$ and $g$	-	-	-
	Equal $L_{\infty}$ and $t_0$	-	-	-		Equal $W_{\infty}$ and $t_0$	-	-	-
	Equal $g$ and $t_0$	-	-	-		Equal $g$ and $t_0$	-	-	-

**Discussion** - Accurate evaluation of stock status requires an understanding of stock dynamics at regional or even sub-regional levels such as habitat as these finer scale dynamics ultimately influence overall stock productivity (Pulliam 1988; Pulliam and Danielson 1991; Cadrin and Secor 2009; Kerr et al. 2010). Our study provides new information on Red Snapper

demographics at the habitat level and suggests that differences in length, weight, and age frequencies and growth exist among artificial reefs, standing platforms, and natural banks in the western GOM region. We documented proportionally more relatively large, old Red Snapper at natural banks than either standing platforms or artificial reefs. Saari (2011) also reported differences in length and weight frequencies from similar habitats off of Louisiana; however, more large fish (e.g.,  $\geq 550$  mm TL) were sampled from artificial reefs (toppled RTR structures; 60%) than standing platforms (42%) or natural banks (27%), and no differences in age frequencies among habitats were reported. In contrast, nearly 50% of Red Snapper sampled from natural banks in this study were  $\geq 550$  mm TL compared to 36% at artificial reefs and 35% at standing platforms. These differences between studies may be influenced by the types of habitats surveyed in each study. For example, while artificial reefs in both studies consisted of RTR structures located in similar depths (60 – 80 m), the natural banks surveyed by Saari (2011; Alderdice, Bouma, Jakkula, and Rezak-Sidner banks) are classified as shelf-edge banks and are geologically distinct from the South Texas Banks surveyed in this study (e.g., result of salt diapirism vs. relict coralgall reefs; Rezak et al. 1985). The shelf-edge banks also occur in much deeper water than the banks in this study (e.g., ambient depths from 90 – 150 m compared to 72 – 84 m for the banks in this study) and are located in much closer proximity to the Mississippi River and its associated productivity (Grimes 2001), which may also contribute to the observed differences between Saari (2011) and our study. Regardless, the lack of similar trends among habitats in Louisiana (Saari 2011) and Texas (this study) highlights the complex nature of sub-regional stock dynamics for Red Snapper in the GOM.

Our study employed a standardized, fishery-independent vertical line survey (e.g., Gregalis et al. 2012), which permitted estimates of Red Snapper relative abundance (i.e., CPUE) among the three habitats. A key assumption when using CPUE data to estimate relative abundance is that CPUE is proportional to true abundance (Quinn and Deriso 1999). Because Red Snapper can form dense aggregations (Stanley et al. 1997), gear saturation may have been a potential issue affecting estimates of relative abundance as SEAMAP vertical lines used in this study consist of only 10 hooks per backbone. Vertical line relative abundance in our study was similar among artificial reefs, standing platforms, and natural banks surveyed—a finding that is inconsistent with previous studies that have demonstrated higher densities of Red Snapper at artificial habitats than natural habitats (Patterson et al. 2014; Streich et al. in press). For example, ROV transects conducted at artificial reefs and natural banks in the same region estimated Red Snapper density was nearly eight times greater at artificial reefs (Streich et al. in press). These previous studies relied on video-based surveys, which are generally less affected by gear saturation and may provide less biased indices of abundance given adequate environmental conditions (e.g., visibility; Harvey et al. 2012; Ajemian et al. 2015b). Several studies have successfully paired traditional fishery sampling gear with visual- or video-based surveys to quantify gear bias and selectivity (Cappo et al. 2004, Harvey et al. 2012; Patterson et al. 2012; Bacheler et al. 2013; Robinson et al. 2015), and given the potential for gear saturation and other

biases, a paired video-based survey that evaluates the efficacy of vertical line gear in estimating relative abundance among the habitats sampled here is warranted.

The limited number of older fish (i.e., > age-10) in our study is likely attributable to a combination of gear selectivity and ontogenetic changes in Red Snapper habitat selection (Allman et al. 2002; Mitchell et al. 2004; Allman and Fitzhugh 2007; Gallaway et al. 2009). Previous studies of Red Snapper growth have relied on other sampling means to obtain large fish including tournaments that target larger individuals (Patterson et al. 2001; Fischer et al. 2004) or landings from the commercial fishery, where the longline sector also selects for larger and older individuals (Schirripa and Legault 1999; Allman and Fitzhugh 2007). In addition, Red Snapper may rely less on structured “reef” habitat as they grow older, possibly spending more time over open, soft bottoms as they reach a size refuge from predation (Gallaway et al. 2009). This hypothesized shift in habitat use is supported by an abundance of significantly older Red Snapper (median age = 12 yrs; range = 3 – 53 yrs) sampled during research longline surveys conducted away from structured habitats in the western GOM (Mitchell et al. 2004), and may partially explain the decline from ages 7 – 9 in the age frequencies observed in our study (Figure 10). Fishermen commonly target structured habitats like artificial reefs (Grossman et al. 1997; Garner and Patterson 2015; Schuett et al. 2016; Simard et al. 2016); therefore, another feasible explanation is that the structured habitats we sampled may not support as many older fish simply due to higher fishing mortality at structured habitats compared to the open, soft bottom habitats. It is also important to remember that GOM Red Snapper remain in an overfished state (SEDAR 2013) and only recently have habitat-specific (i.e., natural vs. artificial habitats), fishery-independent comparisons of Red Snapper demographics been conducted (Saari 2011; Kulaw 2012; Glenn 2014; this study). As such, the “normal” age structure among these habitats is unknown. Thus, this study represents the first attempt to describe the age structure among habitats in the western GOM, but continued monitoring will be required to assess how age structure changes among these habitats as the stock recovers.

While habitat differences were the overarching focus of this study, our ancillary analysis of site-to-site differences in Red Snapper mean TL, TW, and age among sites revealed that Baker Bank supported larger and older fish than any of the other sites. Furthermore, most of these fish were age-6 or age-7 individuals from the 2007 year-class. Previous studies suggest that processes influencing Red Snapper year-class strength operate at large spatial scales as strong year-classes are represented in fishery landings consistently among all regions of the GOM (Allman and Fitzhugh 2007; Saari et al. 2014). Although our data displayed evidence of a strong 2009 year-class at all habitats, the strong representation of the 2007 year-class was only observed at Baker Bank and likely contributed significantly to the predominance of larger and older fish at natural banks compared to artificial reefs or standing platforms. Given the similarity in water quality data (thermocline presence and depth, DO, salinity) and the proximity of all sites sampled in our study, this difference in year-class representation suggests that site-specific factors such as fishing mortality and/or habitat-area (i.e., footprint) are also important drivers of apparent year-class strength. For example, Baker Bank had the largest footprint of any site we sampled (1.33

km<sup>2</sup> compared to 0.31 – 0.50 km<sup>2</sup> at the other natural banks and  $< 6.73 \times 10^{-3}$  km<sup>2</sup> at artificial reefs and standing platforms), which may effectively reduce fishing effort per unit area thereby allowing greater survival to older ages. An alternative explanation could be that sites with a greater habitat area provide greater resources-per-capita (e.g., Frazer and Lindberg 1994), which would potentially support larger Red Snapper and could even be selected for by larger individuals (i.e., habitat selection). Clearly, additional studies, similar to that of Strelcheck et al. (2005), are necessary to evaluate these hypotheses that relate the effects of habitat size and habitat type on Red Snapper demographics.

Fitting multiple growth models to size-at-age data and selecting the best model using information theory has been recommended and is increasingly common in peer-reviewed literature as the traditional VBGM may not always accurately represent size-at-age data (Katsanevakis 2006; Katsanevakis and Maravelias 2008; Natanson and Gervelis 2013; Ainsley et al. 2014; Natanson et al. 2014; Dippold et al. 2016). We fit four types of growth models to size-at-age data for Red Snapper from the three habitat types and found little support for either parameterization of the VBGM. Our results suggest the logistic model was the best in describing growth of Red Snapper among all habitats for both TL-at-age and TW-at-age data. Other studies of Red Snapper growth have used the VBGM, and that model may adequately fit size-at-age data, especially when older fish are present in the sample (Patterson et al. 2001; Wilson and Nieland 2001; Fischer et al. 2004). Few fish  $>$  age-10 were sampled in this study ( $n = 5$ ), and a different growth model may have been justified if more old Red Snapper had been sampled; however, given the data, use of the logistic model was justified in our study.

Logistic growth curves fit to size-at-age data from each habitat suggested that growth at artificial reefs was different than growth at natural banks or standing platforms. Among TL-at-age and TW-at-age models, evidence suggested that larger estimates of asymptotic mean size (i.e.,  $L_{\infty}$  and  $W_{\infty}$ ) at artificial reefs were driving the differences. Although Saari (2011) used the two parameter VBGM to describe growth, some similar patterns in growth were observed among habitats. For example, estimates of  $L_{\infty}$  and  $W_{\infty}$  at natural banks were lowest, suggesting Red Snapper at natural banks reach smaller maximum sizes on average. In addition, lower estimates of  $t_0$  (i.e., the inflection point of the logistic curve) at natural banks and standing platforms in this study imply that the instantaneous growth rate was beginning to slow earlier at these two habitats than at artificial reefs, which may indicate earlier maturation at natural banks and standing platforms. Because few old fish were present in our samples, parameter estimates derived from our growth curves should be interpreted with caution. In particular, estimates of asymptotic mean size may have been poorly estimated, as fewer age-9 and age-10 individuals from each habitat were sampled. Estimates of  $L_{\infty}$  and  $W_{\infty}$  from all habitats were generally smaller than those estimated by Saari (2011); however, this pattern is consistent with previous findings that suggest Red Snapper in the western GOM reach smaller mean asymptotic sizes than those from the northern GOM (Fischer et al. 2004; Saari et al. 2014). Nevertheless, confidence in the patterns we observed could be strengthened with additional samples that included more old individuals.

Despite the putative differences in growth among habitats, predicted mean TL-at-age was similar throughout the range of ages compared (e.g., predicted mean TL-at-age-10 was only 40 mm greater at artificial reefs than at standing platforms or natural banks). Differences in predicted mean TW-at-age displayed a more significant divergence between artificial reefs and standing platforms or natural banks. As a demonstration, consider three average Red Snapper, each residing at one of the three habitats examined and weighing approximately 1.25 kg. The fish residing at an artificial reef would weigh approximately 3.54 kg by age-7, about 0.5 kg heavier than its counterparts on a natural bank or standing platform. By age-10, the fish at the artificial reef would reach approximately 4.71 kg, nearly 1 kg heavier than the fish residing at the natural bank or standing platform. This example assumes that most fish display relatively long term residency at a particular habitat type, an assumption that may have limited support based on the findings of previous studies (see review by Patterson 2007). For example, tag-recapture studies conducted off the Texas coast have found that 52% (Diamond et al. 2007) to 94% (Fable 1980) of tagged Red Snapper were recaptured at their original tagging location although the mean time at liberty was only about half a year. Diamond et al. (2007) reported that fish traveled an average distance of 9.8 km and up to 58.3 km, and Curtis (2014) reported that acoustically tagged individuals moved from 2.7 km to 13.1 km, which would potentially allow fish to move between sites in our study given the distances between sites (mean = 20.6 km; SE = 2.0; range = 2 – 52 km). Interestingly, Diamond et al. (2007) stated that fish that moved from natural habitats tended to be recaptured at natural habitats and fish moving from artificial habitats tended to be recaptured at artificial habitats. Thus, while our example of habitat-specific growth is simplified and reliant on long term residency at a particular habitat, it demonstrates the potential effects of habitat differences on Red Snapper growth.

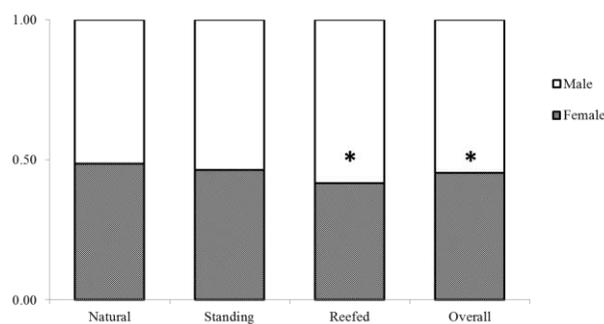
Collectively, our study indicates that differences in Red Snapper size and age structure and growth exist among habitats in the western GOM. These differences are perhaps not surprising given the disparate characteristics of each habitat type (e.g., footprint, relief, etc.) and documented differences in fish community structure between natural and artificial habitats across the GOM (Patterson et al. 2014; Streich et al., in press); however, the implications of these differences for GOM Red Snapper stock productivity remain uncertain at this time. For example, while growth appears to differ at artificial reefs (e.g., greater TW-at-age than standing platforms or natural banks), the effect of this difference is dependent upon associated reproductive potential. Reproductive potential is generally positively correlated with increasing size and age (Porch et al. 2007; Lowerre-Barbieri et al. 2015; Porch et al. 2015); therefore, if the observed increase in TW-at-age at artificial reefs corresponds to increased reproductive potential compared to fish at natural banks or standing platforms, artificial reefs may contribute more to stock-specific production on a per unit area basis. Similarly, the preponderance of larger, older individuals at natural habitats (especially Baker Bank) may indicate higher reproductive potential at natural habitats. Downey (2016) showed that gonadosomatic indices, spawning frequency, and batch fecundity were similar among these three habitats in our region; however, sample sizes

were too low to statistically evaluate these variables by age. Nevertheless, this finding hints that similar-aged fish have similar reproductive potential among the three habitats (Downey 2016).

These results would imply that RTR artificial reefs, standing platforms, and natural banks may all contribute similarly to stock-specific production on a per unit area basis; however, the relative importance of each habitat to overall stock recovery and maintenance will depend on the distribution of fish at each habitat type (Pulliam 1988; Pulliam and Danielson 1991). Studies estimating Red Snapper abundance among habitats are limited, but some have demonstrated that absolute abundance is likely significantly greater on natural habitats simply due to their larger habitat area (Streich et al., in press). Finally, due to typical study design logistics (e.g., boat time, distance/time between sites), sample sites in this study were located within a relatively confined area in the western GOM. Should future studies examine differences in Red Snapper demographics among habitats, we recommend increasing spatial coverage and replication at the habitat level (i.e., more sites per habitat) to better evaluate the patterns and hypotheses described here and to refine our understanding of how different habitats contribute to the maintenance of the GOM Red Snapper stock.

### **Red Snapper Fecundity - Artificial Reefs and Natural Banks (Obj. 2)**

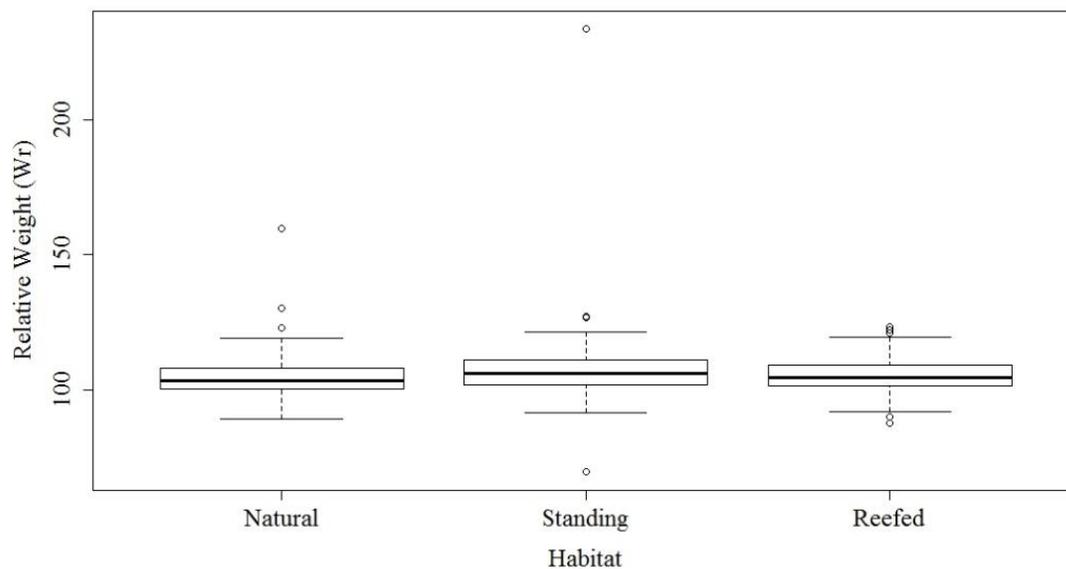
**Overview** - A total of 1585 Red Snapper were collected. Of these, 863 were male, 717 were female, and 5 had indeterminate sex. The ratio of males to females across all habitats was significantly different ( $\chi^2 = 13.49$ ,  $p = 0.0002$ ; Figure 12). Separate chi-square tests for each habitat type revealed fewer females than males on reefed habitats ( $\chi^2 = 16.45$ ,  $p = 5e-16$ ; Figure 12), and similar ratios on both natural ( $\chi^2 = 0.33$ ,  $p = 0.56$ ) and standing habitats ( $\chi^2 = 2.49$ ,  $p = 0.11$ ; Figure 12).



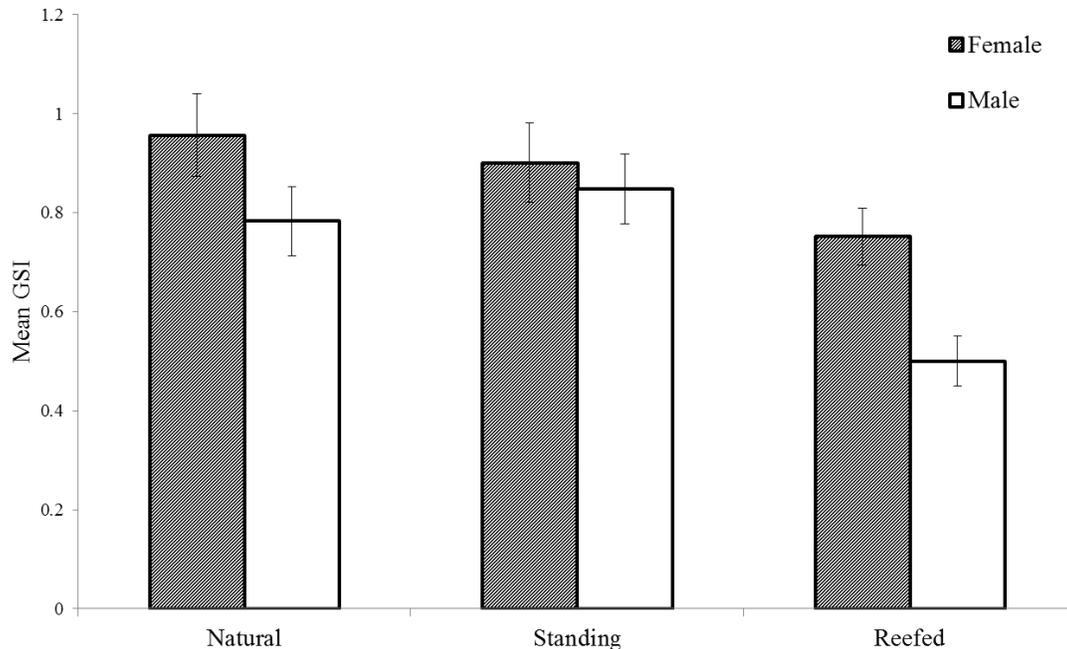
**Figure 12. Male:Female ratio of Red Snapper collected in the northwestern Gulf of Mexico by habitat type (natural = 505, standing = 491, reefed = 584 and overall = 1580). Chi-square analysis was used to test Male:Female ratios on each habitat, an asterisk (\*) denotes significance at  $p < 0.05$ .**

**Fecundity/Spawning Condition** - Out of the 717 total female Red Snapper, 544 were collected during the spawning season from natural ( $n = 175$ ), standing ( $n = 177$ ), and reefed ( $n = 192$ ) habitats and were included in spawning season analyses. Ages of females collected during the spawning season ranged from 2 to 14 years with TLs of 276 to 767 mm and were generally similar among habitat types. Red Snapper from natural habitats were 2 to 10 years old with TLs ranging from 294 to 739 mm, individuals from standing habitats were 2 to 14 years old with TLs of 300 to 694 mm, and individuals collected from reefed habitats were 2 to 14 years old with TLs ranging from 276 to 767 mm. The mean age (natural = 6.2, standing = 5.0, reefed = 5.8) and TLs (natural = 549, standing = 503, reefed = 545) of female Red Snapper collected during the spawning season was similar among habitats (age  $p = 0.19$ , TL  $p = 0.28$ ).

Since condition can affect reproductive output of fish we used  $Wr$  to assess the condition of female Red Snapper from each habitat type. The  $Wr$  on natural ( $104 \pm 8$ ), standing ( $107 \pm 16$ ), and reefed ( $105 \pm 10$ ) habitats was not significantly different ( $p = 0.35$ ; Figure 13). The similarity in  $Wr$  indicates the fish on each habitat are in similar condition and therefore should have the same reproductive capabilities.



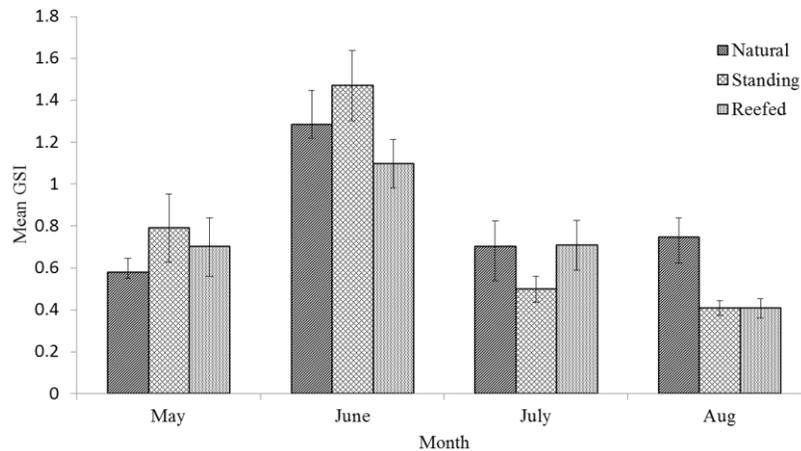
**Figure 13.** The condition index, relative weight ( $Wr$ ), for Red Snapper collected on natural, standing and reefed habitats in the northwestern Gulf of Mexico.  $Wr$  among habitats was tested using nested ANOVA (Site within Habitat) and no statistical differences were found ( $p = 0.25$ ).



**Figure 14. Mean gonadosomatic index (GSI) of male and female Red Snapper collected during the spawning season (May – August) from natural, standing, and reefed habitats in the northwestern Gulf of Mexico. Mean GSI was tested for each sex among habitats using nested ANOVA (Site within Habitat) and no statistical differences were found (females  $p = 0.65$ , males  $p = 0.12$ ).**

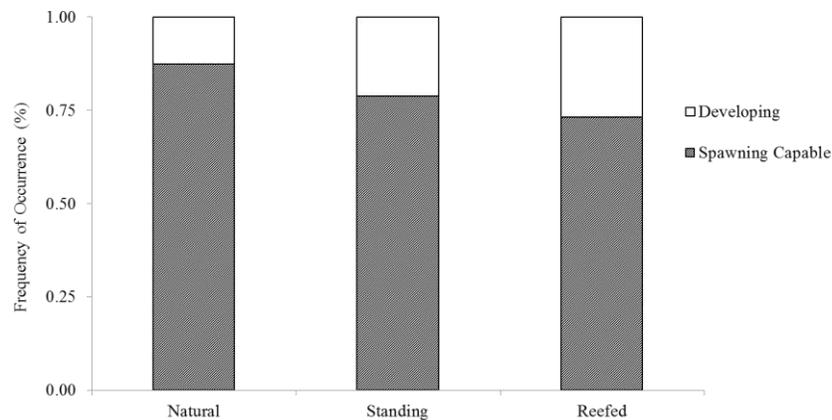
To examine the overall effort put into reproduction by Red Snapper among habitats, we calculated GSI to compare among habitats. There was no difference found among habitats for male or female Red Snapper. The mean GSI of Females collected from natural ( $0.956 \pm 0.084$ ), standing ( $0.901 \pm 0.080$ ), and reefed ( $0.752 \pm 0.058$ ) habitats were not significantly different ( $p = 0.65$ ; Figure 14). The differences in the GSI of males collected from natural ( $0.783 \pm 0.070$ ), standing ( $0.848 \pm 0.071$ ), and reefed ( $0.500 \pm 0.051$ ) habitats were also not significant ( $p = 0.12$ ; Figure 14).

Female GSI values at all habitats were low in May (natural = 0.578, standing = 0.790, reefed = 0.700), increased to a peak in June (natural = 1.284, standing = 1.469, reefed = 1.097), before decreasing in July (natural = 0.701, standing = 0.498, reefed = 0.707) and in August (natural = 0.745, standing = 0.408, reefed = 0.406). In July, female GSI values on standing reefs were lower than on both natural and reefed habitats, while in August both standing and reefed GSI values appeared lower than natural areas. However, these differences were not significant and overall there were no significant differences in female GSI among habitats within each month of the spawning season ( $p = 0.47$ ; Figure 15).



**Figure 15. Mean GSI per month and habitat of female Red Snapper collected during the spawning season in the northwestern Gulf of Mexico. The effects of habitat within each month on mean GSI was tested using nested ANOVA (Site within Habitat) and there were no significant differences among habitats within each month ( $p = 0.47$ ). The effect of month on mean GSI was also tested and was found to be significant ( $p < 0.0001$ ).**

A total of 526 females were assigned a reproductive stage and percent spawning capability was determined by habitat type to be: 87% at natural banks, 79% at standing platforms, and 73% at reefed platforms (Figure 16). The percentage of spawning capable individuals among habitat types was not significantly different from one another ( $\chi^2 = 1.24$ ;  $p = 0.53$ ).

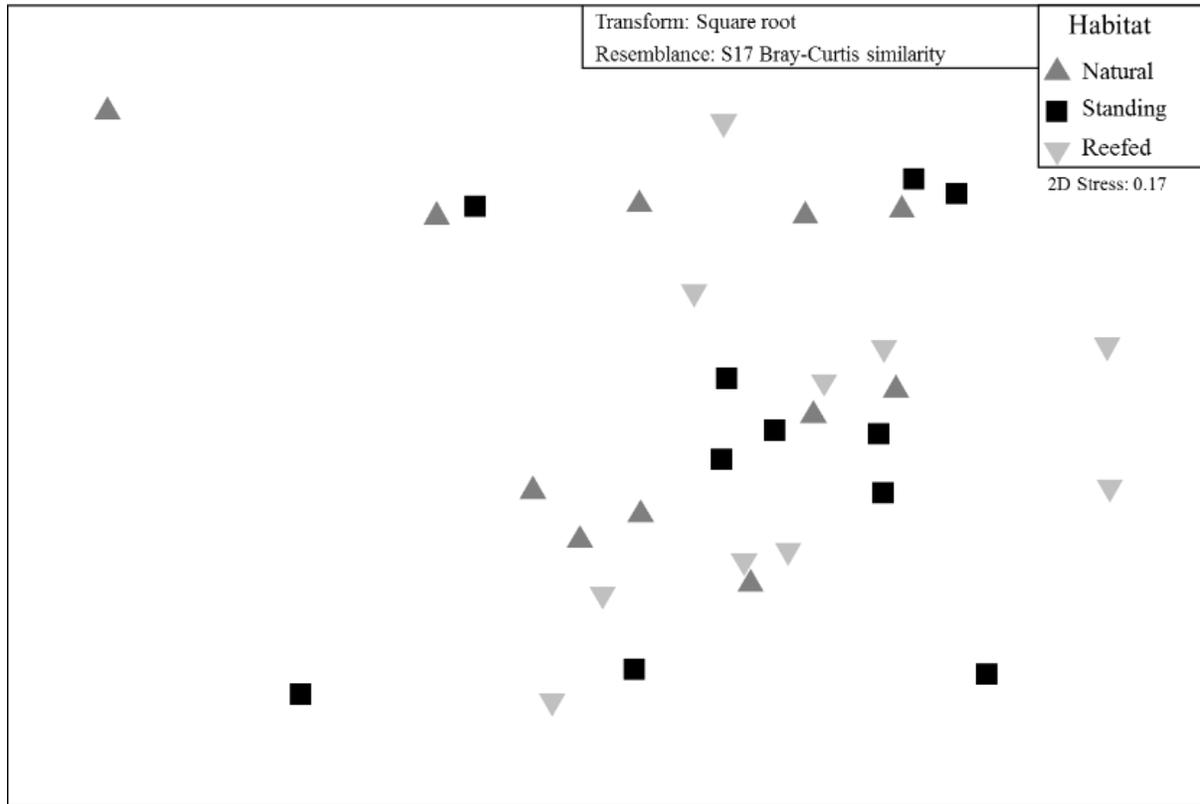


**Figure 16. The percent Frequency of Occurrence (%FO) of spawning capable female Red Snapper collected in the northwestern Gulf of Mexico on natural, standing, and reefed habitats. Spawning capable refers to individuals exhibiting vitellogenic or more advanced oocytes. The %FO among habitats was compared using chi-square and there were no significant differences identified ( $\chi^2 = 1.24$ ,  $p = 0.53$ ).**

The MDS plot did not reveal a discernable pattern among habitat types (Figure 17). Further analysis by PERMANOVA statistically confirmed that there was not a significant difference among the three habitat types in terms of the distribution of most advanced oocyte stages ( $p = 0.194$ ).

Batch fecundity estimates and annual fecundity estimates were calculated for all hydrated females ( $n = 71$ ), and time-calibrated spawning frequency was calculated for fish exhibiting spawning markers (V, H, & POF;  $n = 421$ ). On natural habitats BFE was  $133,552 \pm 130,409$  ova, with a SFE of 9.9 days, which results in 15.2 spawns per season. On natural habitats AFE was  $2,029,474 \pm 505,297$  ova (Table 8). The BFE for standing habitats was  $84,018 \pm 78,377$  ova and a SFE of 7.9 days resulting in 19.0 spawns per season. On standing habitats AFE was  $1,599,580 \pm 398,906$  ova (Table 8). Reefed habitats had a BFE of  $77,601 \pm 69,309$  ova, a SFE of 10.2 days, and spawned 14.7 times during the season; resulting in an AFE of  $1,138,724 \pm 321,443$  ova (Table 8). Although apparent numerical differences exist, BFE ( $p = 0.64$ ), SFE ( $\chi^2 = 0.539$ ,  $p = 0.76$ ), and AFE ( $p = 0.39$ ) were not significantly different among habitat types (Table 8).

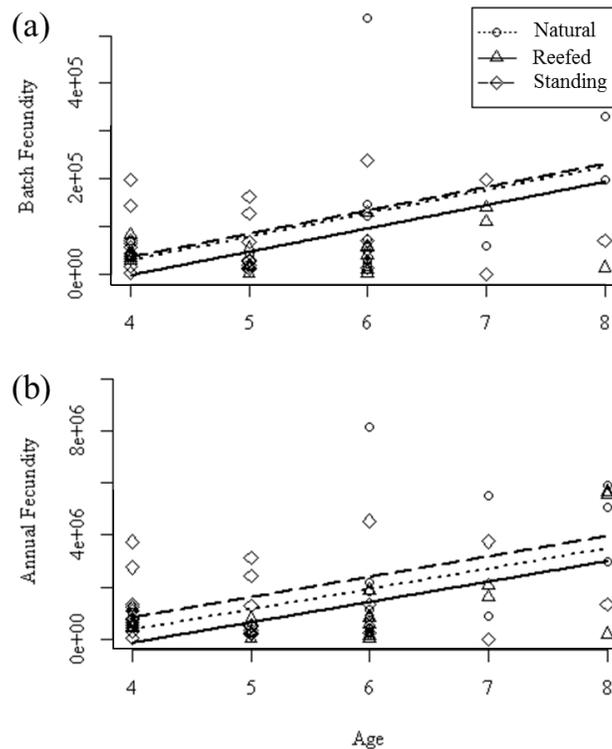
ANCOVAs were restricted to the ages 4 through 8, where at least one individual per age exhibited hydrated oocytes for BFE and AFE to be determined. Both BFE and AFE showed an increasing trend with age for Red Snapper between 4 and 8 years (Figure 18A and B). Age was significant in predicting both BFE ( $p = 3.19 \times 10^{-5}$ ), while habitat type was not ( $p = 0.48$ ; Figure 18A). A similar trend was apparent for AFE where age was a significant predictor ( $p = 0.0001$ ; Figure 18B) but not habitat ( $p = 0.21$ ; Figure 18B).



**Figure 17.** A multidimensional scaling (MDS) ordination of oocyte stage distribution by habitat type of female Red Snapper collected in the northwestern Gulf of Mexico. Oocyte stages were grouped by sample site and date, square root transformed, and a Bray-Curtis similarity calculated on the resulting oocyte composition.

**Table 8.** Overview of female reproductive characteristics from Red Snapper collected in the northwestern Gulf of Mexico on natural, standing, and reefed habitats from May – August in the years 2013-2015 combined. Spawning frequency (SFE) is reported in days. Batch fecundity (BFE) and annual fecundity (AFE) are reported as mean  $\pm$  standard error (SE).

Habitat	n	SFE	Spawns/Season	BFE $\pm$ SE	AFE $\pm$ SE
Natural	21	9.9	15.2	133552 $\pm$ 130409	2029474 $\pm$ 505297
Standing	27	7.9	19.0	84018 $\pm$ 78377	1599580 $\pm$ 398906
Reefed	23	10.2	14.7	77601 $\pm$ 69309	1138724 $\pm$ 321443
All	71	9.3	16.2	96590 $\pm$ 89889	1577440 $\pm$ 237338



**Figure 18. Batch fecundity (A) and annual fecundity (B) by age and habitat of female Red Snapper collected in the northwestern Gulf of Mexico. Differences in BFE and AFE per age were tested among habitats using ANCOVA. There were no statistical differences in BFE ( $p = 0.480$ ) or AFE ( $p = 0.21$ ) among habitat types by age; while age was significant in predicting BFE ( $p = 3.19 \times 10^{-5}$ ) and AFE ( $p = 0.0001$ ).**

**Discussion** - This study investigated the reproductive differences between Red Snapper collected from natural and artificial habitats in the northwestern Gulf. Red Snapper on artificial habitats exhibited similar reproductive capabilities and characteristics to those from natural reefs. The GSI values showed the spawning season on the three habitat types was similar during each month of the season, and no differences among habitats for GSI averaged over the entire season. Further, females collected during the spawning season exhibited similar spawning behavior in terms of fecundity and spawning frequency among all habitat types with the percentage of mature females and the distribution of oocyte stages not different among habitats. Together, these results suggest that artificial and natural reefs offer comparable value to Red Snapper in terms of reproductive output. Thus, fish on artificial reefs are contributing similarly to the population in the western Gulf as the fish located on natural reefs.

While our study showed that reproductive characteristics were similar among habitat types, other studies have shown differences in Red Snapper reproductive characteristics between natural and artificial habitats. Kulaw (2012) found that natural banks yielded the highest GSI out of the habitats, although SFE was not found to be significant; however, this study was

characterized by low sample size of hydrated females ( $n = 8$ ), and their numbers did not allow for statistical comparisons of BFE and AFE between habitats. Glenn (2014) also found the reproductive potential of Red Snapper at artificial reefs to differ significantly from natural reefs located on the Louisiana shelf edge. A GSI value greater than 1 are generally associated with spawning, and Glenn (2014) observed these “spawning” values only in June on artificial reefs (Grimes 1987; Collins et al. 1996). This was interpreted as a truncated spawning season for fish found on artificial habitat. However, in this study similar GSI patterns were observed for all habitat types.

Additionally, spawning capable and hydrated females were identified during all months of the spawning season, at times with GSI values  $< 1$ , which correlates with GSI values above 0.5 indicating the onset of vitellogenesis as found by Fitzhugh et al. (2004). Glenn (2014) also found mean BFE to be lower on the artificial reef site than on the natural sites; however, these results were based on a relatively small sample size (e.g., only nine hydrated females were identified; two from natural reefs and seven from the artificial site), and an unequal size distribution of hydrated fish; one of the two fish from natural sites was the largest fish sampled and exhibited the highest fecundity. These results here with a much larger representation of fish showed similar spawning characteristics using increased sample size, fish of similar lengths, and an equal distribution among habitat types (natural = 21, standing = 27, reefed = 23).

Additionally, during site location and fish collection, a directed effort was made to control for depth and proximity of habitat types, and these geographic differences may have confounded some of the previous finding with regard to habitat differences. For example, site selection in these previous studies was limited due to the distribution of natural habitat along the Louisiana shelf edge which resulted in site depths ranging from 55–160 m (Kulaw 2012; Glenn 2014). Contrastingly, depth of the sites selected for this study ranged from 60-90 m. Therefore, reproductive differences identified between habitats may also be related to physical differences of sample location rather than habitat type and large difference in reproductive potential have been observed across the Gulf (Porch et al. 2015).

We found no statistical differences in fish condition, TL, and age among habitats during the spawning season which suggests the similarities in reproductive characteristics among habitats did not have differing influences from age and length. In previous studies, the differences between Red Snapper reproduction found on artificial and natural reefs were attributed to several factors, but that was not what was observed here. For example, Kulaw (2012) found differences in fish size and age among habitats. In addition, natural banks had a larger slope on length-weight regressions than artificial habitats, which can be interpreted as the fish being in better condition. However, it was acknowledged that bias was possible due to seasonal fluctuation and significant differences in TL among habitats (Kulaw 2012).

Reproductive differences were also attributed to poor nutritional condition of the fish located on the artificial reef site based on a concurrent diet study (Glenn 2014; Schwartzkopf 2014) and previous literature stating reduced fecundity can be linked to poor diet and condition (Marteinsdottir and Begg 2002; Rideout et al. 2006). Nevertheless, for this study fish condition

was similar among natural vs. artificial reefs. The differences between this study and other Gulf studies are not simply an artifact of demographic differences among samples analyzed because fish ages and sizes were similar between studies. For example, the size range of this study (276 to 767 mm) is similar to the ranges reported by Kulaw (2012; 235-864 mm) and Glenn (2014; 327 – 793 mm). Additionally, the age range of female Red Snapper (2-14 years) was also similar to the age range reported by Kulaw (2012; 1 – 12 years) and Glenn (2014; 3 – 17 years). This reinforces the speculation that Red Snapper in the western Gulf may have varied reproductive capacities than fish from the northern Gulf (Lyczkowski-Shultz and Hanisko 2007; Porch et al. 2015).

Comparing the reproduction of Red Snapper across the Gulf reveals apparent regional or demographic differences among semi-distinct populations. Increased GSI values and spawning individuals were identified from May through August which is widely reported to be within the spawning season for this species throughout the Gulf (Futch and Bruger 1976; Collins 1996; Wilson 1994; Woods 2003). Hydrated fish were identified at age 2, similar to past studies in the Gulf (Woods 2003; Fitzhugh et al. 2004). In the western Gulf, higher larval concentration and possible spawning potential has been found compared to the eastern Gulf (Lyczkowski-Shultz and Hanisko 2007). Interestingly, BFE, SFE and AFE calculated in this study were generally lower than previous estimates in the Gulf. Both the minimum and maximum BFE values throughout the Gulf were reported from Florida and ranged from a minimum of 458 to a 1,704,736 (Collins et al. 1996). In Alabama, BFE values were 304,996 (Woods 2003). In Louisiana, BFE values ranged from 219,258 to 704,563 with a low value of 41,878 for artificial habitats (Kulaw 2012; Glenn 2014). Batch fecundity in this study was found to be 96,590, which is toward the lower end of the ranges reported in previous studies. Spawning frequency is also highly variable throughout the Gulf with spawning events estimated between 14.7 (this study) to 44 events in Alabama (Woods 2003). These patterns translate to AFE as well because AFE depends upon BFE and SFE in the calculation. However, the method used to preserve the sampled ovaries could also be a contributing factor in observed differences between studies as frozen gonads have been shown to tend to slightly exaggerate batch fecundity estimates and affect the ability to detect spawning markers (Porch et al. 2015). Although BFE and SFE for the western Gulf were lower than other areas in this study, Porch et al. (2015) found the western Gulf, including the western Louisiana shelf and central to south Texas shelf, to be the areas with highest spawning activity which would match with a greater larval abundance. These results indicate that spawning behavior of Red Snapper is highly variable among geographic areas in the Gulf which might influence conclusions about the reproductive potential of the population.

In summary, the influence of habitat on reproduction appears to be variable among regions throughout the Gulf. Red Snapper in this study had similar reproductive characteristics among natural banks, standing platforms, and reefed platforms. These results suggest when examined in light of other research show that Red Snapper reproduction is widely variable and may be dependent on location in the Gulf of Mexico and supports the idea that the Red Snapper

population in the Gulf of Mexico is comprised of several semi-isolated populations (Gold and Saillant 2007).

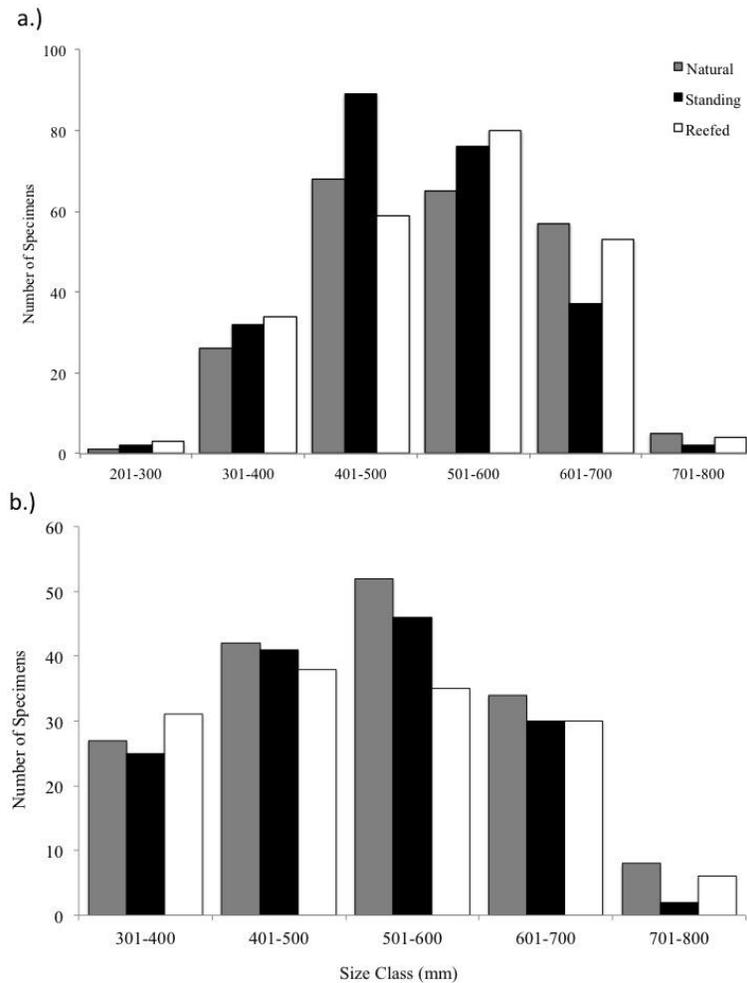
Certainly, this work refining reproductive characteristics of Red Snapper in the ns GOM has several management implications. Artificial reefs appear to offer similar value to Red Snapper reproduction as natural habitat in the western Gulf of Mexico. With thousands of platforms off the Texas coast that are scheduled for decommissioning and removal or donation to the TPWD Rigs-to-Reefs program, the identification of an artificial reef's value should be an important component of the decision making process. Minimally, the use of platforms as artificial reefs does not appear to negatively affect the population, in terms of reproduction, and there is evidence that removing platforms may be detrimental (Peabody and Wilson 2006; Gallaway et al. 2009, Streich et al. in press). If the influence of habitat on other factors can be determined to be equal to natural reefs, then artificial reefs may be a valid method for creating additional habitat for Red Snapper populations in the western Gulf. Furthermore, there is evidence from this study as well as others throughout the Gulf that indicate there are demographic differences in Red Snapper populations located in separate areas of the Gulf. This suggests that fishery managers should consider regional differences in Red Snapper populations when making management decisions.

Other factors besides habitat type can potentially affect reproductive potential, such as distance from shore or water depth. These should be considered in future studies in an effort to better understand Red Snapper reproduction in the western Gulf of Mexico, and to identify best practices for reefing. Additionally, age and size can affect fecundity and maturation. For example, there is some evidence that fecundity and spawning behavior in older fish begins to decrease (Fitzhugh et al. 2004), however, Porch et al. (2015) determined that fish SFE does not decrease at older ages, and confirmed increasing size and age increased spawning frequency up to age 35. This study did not address the effect of age, due to limited sample sizes of these very old age classes. The lack of older Red Snapper captured in the large-scale study (n = 1585) support the conclusion of Porch et al. (2015) that even if older fish exhibit senescence, it is unlikely to be an important factor considered in stock assessments as these older fish are rare. However, the lack of older larger fish is often cited as evidence for an unrecovered population (Cowan et al. 2011), and the contribution of older fish is often cited as a reason for their greater importance to the population (Palumbi 2004; Birkland and Dayton 2005). If these older fish do not contribute as much to the population, then they may not play as important a role in management decisions. In light of this a wider range of sizes and ages is needed, especially of larger sizes and ages, to identify how much the older ages contribute to the population.

### **Red Snapper Trophic Ecology - Artificial Reefs and Natural Banks (Obj. 3)**

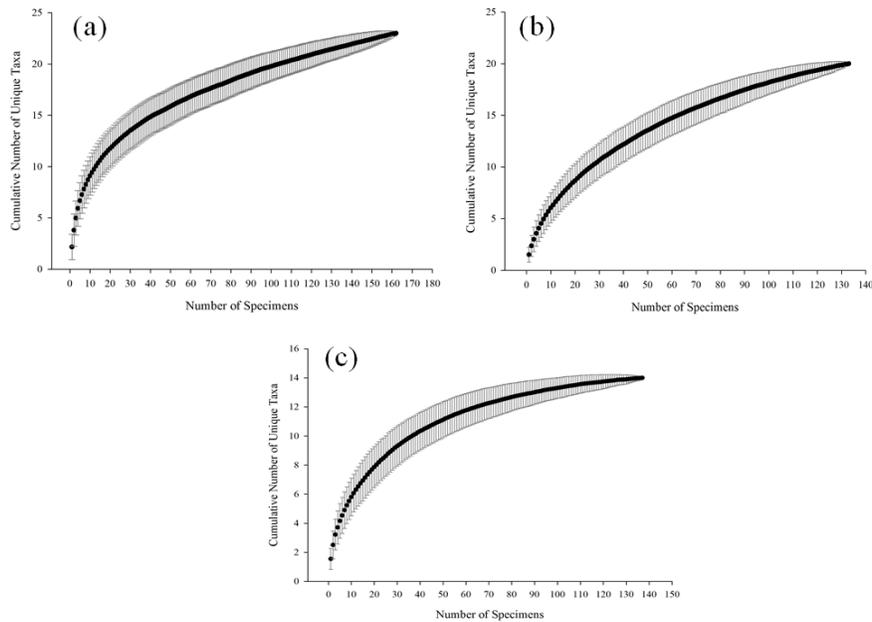
For trophic analysis, a total of 1585 fish sized from 275-767 mm TL with an age range of 2-13 years were collected from natural (505), standing (494), and reefed (586) habitats.

**Diet** - There were 333 empty stomachs, 558 distended stomachs, and 694 containing prey. Identifiable prey was obtained from 533 stomachs from 2013-2014 and only these fish were included in the statistical analysis of diet composition among habitat types (Figure 19A).



**Figure 19. Histogram of Red Snapper *Lutjanus campechanus* used in a.) diet and b.) stable isotope analysis by size class (100 mm bins) and habitat, including natural reefs (natural), standing oil and gas platforms (standing), and reefed platforms (reefed).**

A total of 33 prey categories were identified across all habitats, excluding unidentified content (UIC), which was not considered in statistical analyses. The species accumulation curves for all habitats approached an asymptote, indicating the sample size was likely sufficient to describe the prey groups consumed on these habitats (Figure 20). Prey taxa were grouped by class for ease of analysis and interpretation. Overall, the majority of the stomach composition by %W was made up of Osteichthyes (63.51%) and Malacostraca (27.67%); the remaining prey categories made up less than 10% of the diet each (Table 9).



**Figure 20. Cumulative prey curves plotting mean ( $\pm$ SE) of unique prey items and number of specimens sampled for Red Snapper *Lutjanus campechanus* ( $n = 560$ ) collected from natural (a), standing (b), and reefed (c) habitats in the northwestern Gulf of Mexico during 2013-2015.**

There were a total of 30 taxa identified from natural habitats (Figure 21). By Class, Osteichthyes (46.30%) made up the greatest percentage of Red Snapper diet by weight followed by Malacostraca (39.91%), and Hydrozoa (10.12%). Congridae, Ophichthidae, Carangidae, Anguilliformes, and unidentified fish (Osteichthyes) were the major prey items found in Class Osteichthyes. Within Malacostraca, the major taxa include *Portunus* spp., *Portunus spinimamus*, unidentified crabs (Decapoda), and unidentified crustaceans (Malacostraca). The remaining classes made up less than 2% of the diet by weight. Seven taxa were unique to natural habitats including Achelata, *Calamus leucosteus*, *Cavolinia tridentata*, Clupeidae, Haemulidae, Holothuroidea, and Tanaidacea (Table 9).

**Table 9. Diet of Red Snapper *Lutjanus campechanus* (n = 560) collected in the northwestern Gulf of Mexico by prey class, and lowest possible taxon showing percent frequency of occurrence (%FO), percent number (%N), and percent weight (%W) excluding unidentified content, and percent Index of Relative Importance (%IRI). Values are reported for**

Class	Lowest Possible Taxon	Overall				Natural				Standing				Reefed			
		%FO	%N	%W	%IRI												
<b>Bivalvia</b>	Bivalvia	<b>0.25</b>	<b>0.08</b>	<b>&lt;0.01</b>	<b>0.06</b>	<b>0.20</b>	<b>0.04</b>	<b>&lt;0.01</b>	<b>0.03</b>	<b>0.64</b>	<b>0.31</b>	<b>0.01</b>	<b>0.29</b>	-	-	-	-
<b>Cephalopoda</b>		<b>1.01</b>	<b>0.47</b>	<b>2.14</b>	<b>0.39</b>	<b>1.18</b>	<b>0.32</b>	<b>0.90</b>	<b>0.28</b>	<b>0.96</b>	<b>0.78</b>	<b>3.97</b>	<b>0.79</b>	<b>0.83</b>	<b>0.35</b>	<b>2.09</b>	<b>0.35</b>
	Octopoda	0.25	0.11	0.29	0.09	0.59	0.16	0.64	0.14	-	-	-	-	-	-	-	-
	Teuthida	0.76	0.36	1.86	0.30	0.59	0.16	0.25	0.14	0.96	0.78	3.97	0.79	0.83	0.35	2.09	0.35
<b>Chondrichthyes</b>	Rajidae	<b>0.08</b>	<b>0.03</b>	<b>0.12</b>	<b>0.02</b>	-	-	-	-	-	-	-	-	<b>0.28</b>	<b>0.09</b>	<b>0.46</b>	<b>0.08</b>
<b>Gastropoda</b>		<b>5.74</b>	<b>32.60</b>	<b>0.43</b>	<b>25.21</b>	<b>8.04</b>	<b>45.62</b>	<b>0.95</b>	<b>38.99</b>	<b>2.88</b>	<b>2.49</b>	<b>&lt;0.01</b>	<b>2.32</b>	<b>4.97</b>	<b>2.08</b>	<b>0.04</b>	<b>1.89</b>
	<i>Atlanta spp.</i>	4.05	2.05	0.02	1.59	4.31	1.43	0.01	1.22	2.56	2.34	<0.01	2.18	4.97	2.08	0.04	1.89
	<i>Cavolinia tridentata</i>	1.60	30.52	0.41	23.60	3.73	44.19	0.94	37.77	-	-	-	-	-	-	-	-
	<i>Janthina janthina</i>	0.08	0.03	<0.01	0.02	-	-	-	-	0.32	0.16	<0.01	0.15	-	-	-	-
<b>Holothuroidea</b>	Holothuroidea	<b>0.08</b>	<b>0.03</b>	<b>&lt;0.01</b>	<b>0.02</b>	<b>0.20</b>	<b>0.04</b>	<b>&lt;0.01</b>	<b>0.03</b>	-	-	-	-	-	-	-	-
<b>Hydrozoa</b>	Siphonophora	<b>1.94</b>	<b>0.63</b>	<b>5.32</b>	<b>0.67</b>	<b>3.33</b>	<b>0.67</b>	<b>10.12</b>	<b>1.33</b>	<b>1.92</b>	<b>0.93</b>	<b>2.72</b>	<b>0.96</b>	-	-	-	-
<b>Malacostraca</b>		<b>51.27</b>	<b>51.27</b>	<b>27.67</b>	<b>43.20</b>	<b>55.88</b>	<b>37.50</b>	<b>39.91</b>	<b>40.08</b>	<b>39.42</b>	<b>31.31</b>	<b>13.49</b>	<b>31.16</b>	<b>54.97</b>	<b>62.97</b>	<b>23.50</b>	<b>60.24</b>
	Amphipoda	4.65	3.23	0.70	2.55	4.71	1.74	1.58	1.65	4.17	2.80	0.01	2.61	4.97	4.86	0.01	4.41
	Achelata	0.08	0.03	<0.01	0.02	0.20	0.04	0.01	0.03	-	-	-	-	-	-	-	-
	Decapoda	7.35	17.08	3.20	13.61	8.63	18.35	4.39	16.51	5.45	3.12	3.34	3.23	7.18	12.23	0.88	11.22
	Hippidae	0.08	0.03	0.07	0.02	-	-	-	-	-	-	-	-	0.28	0.09	0.27	0.08
	Isopoda	0.42	0.14	0.02	0.11	0.39	0.08	0.03	0.07	0.32	0.16	<0.01	0.15	0.55	0.17	<0.01	0.16
	Malacostraca	14.02	4.79	7.51	5.53	15.88	3.41	9.72	6.39	11.54	5.61	5.95	6.46	13.54	4.60	5.50	5.58
	<i>Ogyrides spp.</i>	0.17	0.08	<0.01	0.06	-	-	-	-	0.32	0.16	<0.01	0.15	0.28	0.17	<0.01	0.16
	<i>Farfantepenaeus spp.</i>	0.42	0.14	2.73	0.13	0.39	0.08	1.32	0.08	-	-	-	-	0.83	0.26	8.66	0.37
	<i>Portunus Gibbesii</i>	0.34	0.22	0.84	0.17	0.39	0.20	0.88	0.18	0.32	0.31	0.77	0.29	0.28	0.09	0.86	0.08
	<i>Portunus spinicarpus</i>	3.89	2.79	7.77	2.68	7.45	3.65	15.13	5.65	1.28	0.62	1.17	0.61	1.10	0.52	2.87	0.53
	<i>Portunus spinimanus</i>	0.08	0.03	0.13	0.02	-	-	-	-	-	-	-	-	0.28	0.09	0.51	0.08
	<i>Portunus spp.</i>	1.77	0.93	2.50	0.80	2.94	1.11	4.65	1.26	0.64	0.31	0.83	0.30	1.10	0.35	0.75	0.33
	Stomatopoda	17.82	21.74	2.12	17.46	14.71	8.80	2.21	8.24	15.38	18.22	1.41	17.36	24.31	39.46	2.87	37.15
	Tanaidacea	0.08	0.03	<0.01	0.02	0.20	0.04	<0.01	0.03	-	-	-	-	-	-	-	-
	<i>Speocarcinus lobatus</i>	0.08	0.03	0.08	0.02	-	-	-	-	-	-	-	-	0.28	0.09	0.34	0.08
<b>Osteichthyes</b>		<b>38.01</b>	<b>13.96</b>	<b>63.51</b>	<b>29.69</b>	<b>28.04</b>	<b>6.34</b>	<b>46.30</b>	<b>18.08</b>	<b>53.85</b>	<b>31.46</b>	<b>79.80</b>	<b>64.33</b>	<b>38.40</b>	<b>12.84</b>	<b>73.91</b>	<b>37.28</b>
	Anguilliformes	1.52	0.63	3.12	0.57	0.98	0.28	1.94	0.28	2.24	1.56	3.12	1.58	1.66	0.52	5.24	0.64
	Carangidae	0.17	0.08	1.92	0.07	0.20	0.04	2.36	0.04	0.32	0.31	2.81	0.31	-	-	-	-
	Clupeidae	0.08	0.03	0.09	0.02	0.20	0.04	0.20	0.03	-	-	-	-	-	-	-	-
	Congridae	0.25	0.08	9.82	0.11	0.20	0.04	9.41	0.08	0.64	0.31	18.27	0.50	-	-	-	-
	Haemulidae	0.08	0.03	0.01	0.02	0.20	0.04	0.02	0.03	-	-	-	-	-	-	-	-
	<i>Orthopristis chrysoptera</i>	0.08	0.03	2.31	0.02	-	-	-	-	0.32	0.16	7.46	0.19	-	-	-	-
	<i>Pristipomoides aquilonaris</i>	0.08	0.03	0.41	0.02	-	-	-	-	0.32	0.16	1.31	0.15	-	-	-	-
	<i>Hoplunnis spp.</i>	0.34	0.11	3.03	0.10	-	-	-	-	0.64	0.31	1.21	0.30	0.55	0.17	10.73	0.27
	Ophichthidae	0.84	0.27	10.34	0.36	0.78	0.16	7.94	0.28	0.64	0.31	5.77	0.36	1.10	0.35	20.33	0.74
	Ophidiidae	0.17	0.05	0.02	0.04	-	-	-	-	0.64	0.31	0.05	0.29	-	-	-	-
	Osteichthyes	34.29	12.59	31.29	28.33	25.29	5.71	21.80	17.29	48.08	28.04	39.81	60.65	35.08	11.80	37.61	35.64
	<i>Calamus leucosteus</i>	0.08	0.03	1.16	0.02	0.20	0.04	2.63	0.05	-	-	-	-	-	-	-	-
<b>Ostracoda</b>	Ostracoda	<b>0.17</b>	<b>0.05</b>	<b>&lt;0.01</b>	<b>0.04</b>	<b>0.20</b>	<b>0.04</b>	<b>&lt;0.01</b>	<b>0.03</b>	-	-	-	-	<b>0.28</b>	<b>0.09</b>	<b>&lt;0.01</b>	<b>0.08</b>
<b>Polychaeta</b>	Polychaeta	<b>0.17</b>	<b>0.05</b>	<b>&lt;0.01</b>	<b>0.04</b>	<b>0.20</b>	<b>0.04</b>	<b>&lt;0.01</b>	<b>0.03</b>	-	-	-	-	<b>0.28</b>	<b>0.09</b>	<b>&lt;0.01</b>	<b>0.08</b>
<b>Thaliacea</b>	Thaliacea	<b>1.27</b>	<b>0.82</b>	<b>0.81</b>	<b>0.65</b>	<b>2.75</b>	<b>1.15</b>	<b>1.82</b>	<b>1.09</b>	<b>0.32</b>	<b>0.16</b>	<b>&lt;0.01</b>	<b>0.15</b>	-	-	-	-

On standing habitats, a total of 25 taxa were identified. By Class, Osteichthyes (79.80%) was the leading prey category in Red Snapper diets. Malacostraca (13.49%) is the next category followed by Cephalopoda (3.97%), and Hydrozoa (2.72%). Carangidae, *Hoplunnis spp.*, *Pristimoides aquilonaris*, and unidentified fish were identified within Osteichthyes. Unidentified crustaceans (Malacostraca) and crabs (Decapoda) were the major taxa identified in Class Malacostraca along with low amounts of Stomatopoda and *Portunus spinicarpus*. The cephalopods consisted of squid (Teuthida) and Hydrozoa of Siphonophora. The remaining Classes made up less than 1% of the diet on standing habitats. Four taxa were unique to standing habitats including *Janthina janthina*, Ophidiidae, *Orthopristis chrysoptera*, and *Pristipomoides aquilonaris* (Table 9).

There were 22 taxa identified from the diet of Red Snapper on reefed habitats. By Class, Osteichthyes contributed the most (73.91%), followed by Malacostraca (23.50%), and cephalopoda (2.09%). Prey items identified in Osteichthyes included mainly unidentified fish, and eel taxa such as Ophichthidae, *Hoplunnis spp.*, and Anguilliformes. Within Malacostraca, *Farfantepenaeus spp.*, *Portunus spinicarpus*, Stomatopoda, and unidentified crustaceans were the most common prey identified. The remaining Classes made up less than 1% each of the diet on reefed habitats. Three unique taxa were identified on reefed habitats including *Speocarcinus lobatus*, *Portunus spinimanus*, and *Hippidae sp.* (Table 9).

Multivariate analysis using PERMANOVA revealed differences among habitat types ( $p=0.001$ ) and size classes ( $p = 0.004$ ); there was also a significant interaction between habitat and size class ( $p = 0.011$ ; Table 10).

**Table 10. Results from a two way crossed PERMANOVA on diet composition among habitat and size class (100 mm bins) of Red Snapper collected from natural, standing, and reefed habitats in the northwestern Gulf of Mexico; df = degrees of freedom, SS = sum of squares, MS = mean sum of squares.**

Factor	df	SS	MS	Pseudo- <i>F</i>	<i>P (perm)</i>	Unique perms
Habitat	2	21,028	10,514	3.375	<b>0.001</b>	999
Size Class	5	33,348	6,669	2.141	<b>0.004</b>	998
Habitat * Size Class	10	46,294	4,629	1.486	<b>0.011</b>	998

Secondary testing by PERMDISP revealed significant differences in dispersion among habitats ( $p=0.003$ ), but not size class ( $p = 0.61$ ). Differences between size classes were found using pairwise comparisons by habitat type. Standing was different from natural and reefed in 301-400, all habitats were different in 401-500 and 501-600, and standing was different from natural at 601-700. No differences were observed in 701-800 (Table 11).

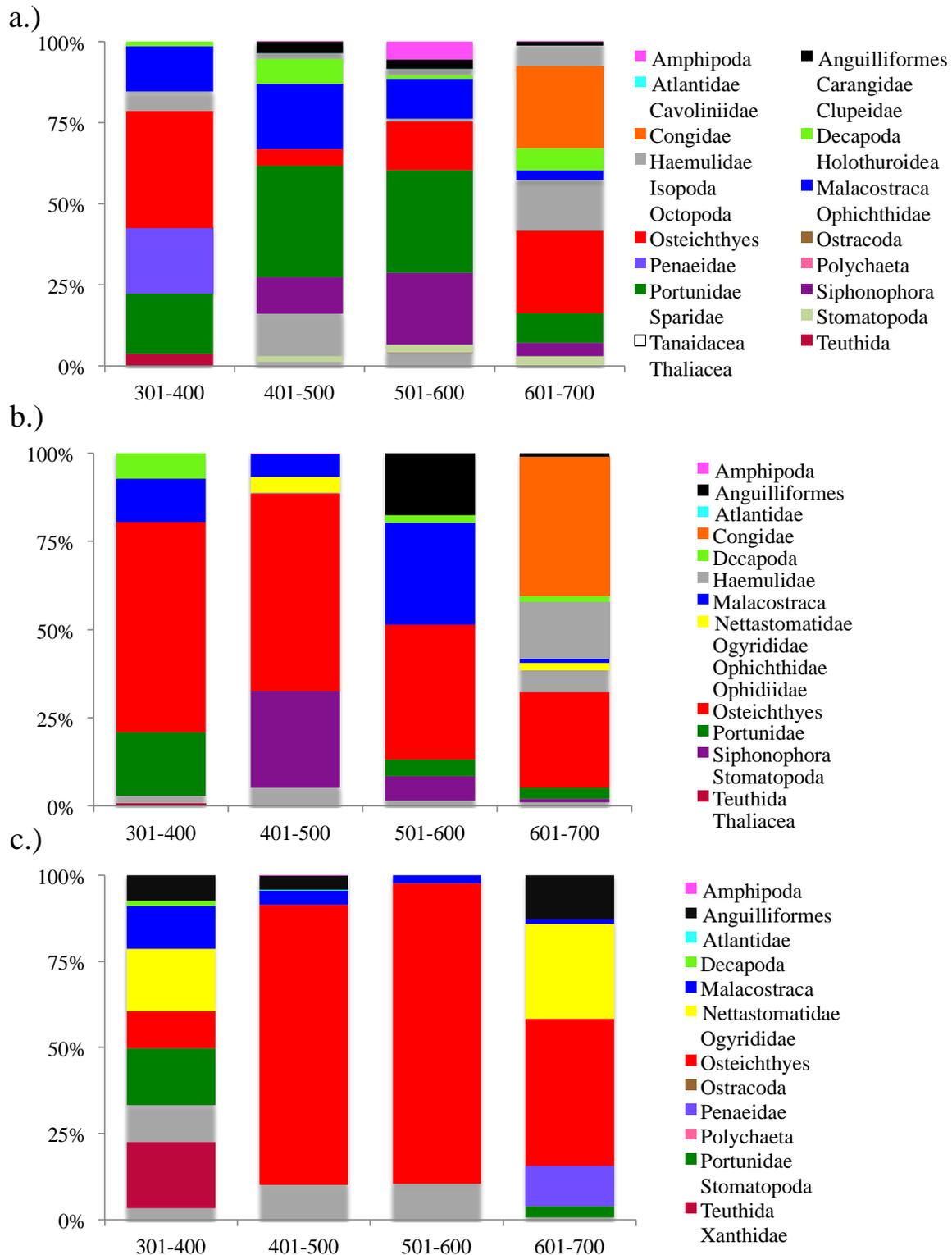
**Table 11. Post-hoc multiple comparisons of Red Snapper diet by size class and habitat (natural, standing, and reefed) with significance considered at  $p \leq 0.05$ .**

Factors	df	t	P(perm)	Unique perms
<b>301-400</b>				
Natural vs. Standing	32	1.602	<b>0.043</b>	999
Natural vs. Reefed	33	1.250	0.125	999
Standing vs. Reefed	35	1.600	<b>0.038</b>	998
<b>401-500</b>				
Natural vs. Standing	79	3.407	<b>0.001</b>	999
Natural vs. Reefed	77	2.914	<b>0.001</b>	998
Standing vs. Reefed	58	1.981	<b>0.009</b>	997
<b>501-600</b>				
Natural vs. Standing	77	2.039	<b>0.001</b>	999
Natural vs. Reefed	60	2.436	<b>0.002</b>	999
Standing vs. Reefed	47	1.672	<b>0.031</b>	999
<b>601-700</b>				
Natural vs. Standing	40	1.630	<b>0.022</b>	999
Natural vs. Reefed	46	1.298	0.097	998
Standing vs. Reefed	38	1.157	0.234	998
<b>701-800</b>				
Natural vs. Standing	3	0.485	0.899	10
Natural vs. Reefed	3	1.006	0.501	10
Standing vs. Reefed	2	0.516	0.652	3

SIMPER analysis of diet by habitat and size class showed that a higher percentage of Osteichthyes in standing and a lower percentage of Malacostraca in 501-601 and 601-700 was primarily driving the observed differences between habitats (Table 12).

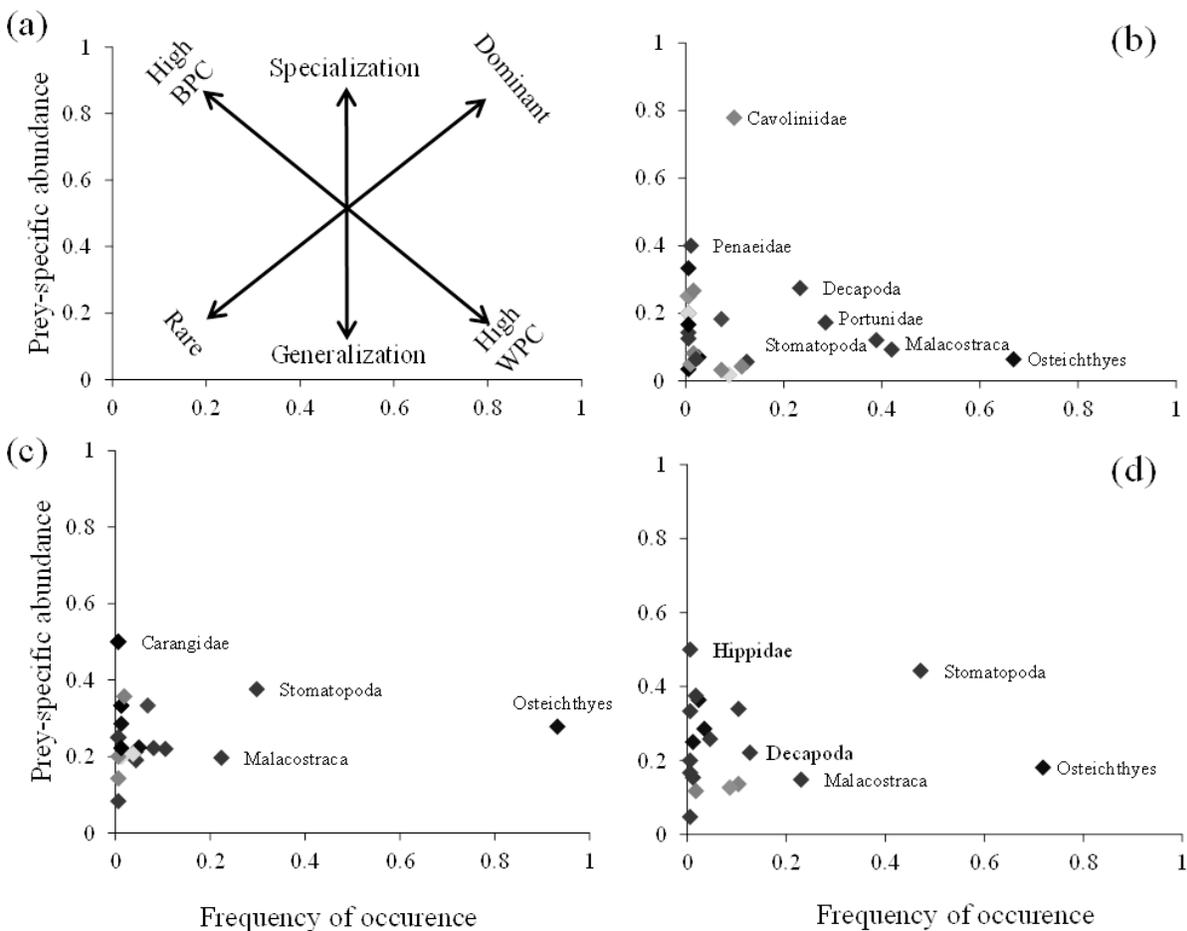
**Table 12. SIMPER analysis of Red Snapper diet (standardized weight) by habitat and size class (natural, reefed, and standing) collected from natural, standing, and reefed habitats in the northwestern Gulf of Mexico.**

Taxon	Abundance		Avg. Dissimilarity	SD	Contribution (%)	Cummulative Contribution(%)
<b>Size Class: 501-600</b>						
Average dissimilarity = 85.40						
	Natural	Reefed				
Osteichthyes	0.27	0.34	22.15	0.98	25.94	25.94
Portunidae	0.57	0	16.35	0.61	19.14	45.08
Stomatopoda	0.16	0.11	12.83	0.67	15.02	60.1
Malacostraca	0.32	0.02	10.92	0.55	12.79	72.89
Average dissimilarity = 87.66						
	Natural	Standing				
Osteichthyes	0.27	0.35	18.67	0.86	21.3	21.3
Malacostraca	0.32	0.29	16.34	0.7	18.64	39.94
Portunidae	0.57	0.06	15.24	0.62	17.38	57.32
Siphonophora	0.31	0.07	10.17	0.45	11.6	68.92
Stomatopoda	0.16	0.06	8.75	0.56	9.98	78.91
Average dissimilarity = 74.29						
	Reefed	Standing				
Osteichthyes	0.34	0.35	31.21	1.31	42.02	42.02
Malacostraca	0.02	0.29	15.17	0.57	20.42	62.44
Stomatopoda	0.11	0.06	13.6	0.71	18.3	80.74
<b>Size Class: 601-700</b>						
Average dissimilarity = 85.07						
	Natural	Standing				
Osteichthyes	0.59	0.89	26.49	1.01	31.14	31.14
Portunidae	0.33	0.19	9.25	0.6	10.88	42.01
Ophichthidae	0.32	0.13	7.55	0.42	8.87	50.89
Congidae	0.2	0.42	6.73	0.32	7.91	58.8
Siphonophora	0.2	0.06	6.24	0.45	7.34	66.14
Malacostraca	0.19	0.07	6.06	0.61	7.12	73.26



**Figure 21. Percent by weight of Red Snapper *Lutjanus campechanus* diet collected by size class (100 mm TL bins) from a.) natural, b.) standing, and c.) reefed habitats in the northwestern Gulf of Mexico, excluding unidentified content. Prey taxa are displayed as family or lowest taxon possible if family was not achieved.**

The feeding strategy diagrams created for natural, standing, and reefed habitats showed that prey items are mostly rare in the diet of Red Snapper and indicate generalization (Figure 22). Most prey items plotted toward the bottom left and close to the origin indicating that these prey items were preyed upon rarely and contributed little to the diet. On natural banks Cavoliniidae is high on the y-axis which indicates a high between phenotype component, meaning individual fish may specialize on this particular prey but at a low frequency. At all three habitat types Osteichthyes is close to the within phenotype component, which indicates that the Red Snapper overall tend eat fish at a high frequency. On standing and reefed habitats Stomatopoda was more frequent and at a higher abundance than at natural sites.

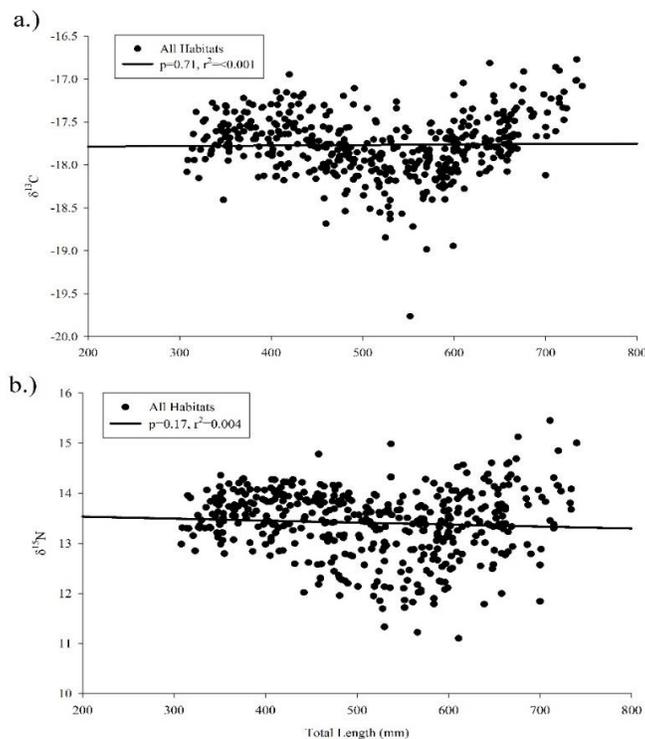


**Figure 22. Feeding strategy diagrams of Red Snapper collected from natural (b), standing (c), and reefed (d) habitats in the northwestern Gulf of Mexico. The interpretation guide (a) was adapted from Amundsen et al. 1996. Prey items are plotted by family or the next highest taxon identifiable.**

**Stable Isotope Analysis** - A total of 447 muscle samples were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ; 163 from natural, 145 from standing, and 139 from reefed (Table 13). The size distribution by habitat type was fairly equal (Figure 19B). There was no linear relationship between  $\delta^{13}\text{C}$  and TL ( $p=0.71$ ,  $r^2<0.001$ ) or  $\delta^{15}\text{N}$  and TL ( $p=0.17$ ,  $r^2=0.004$ ; Figure 23).

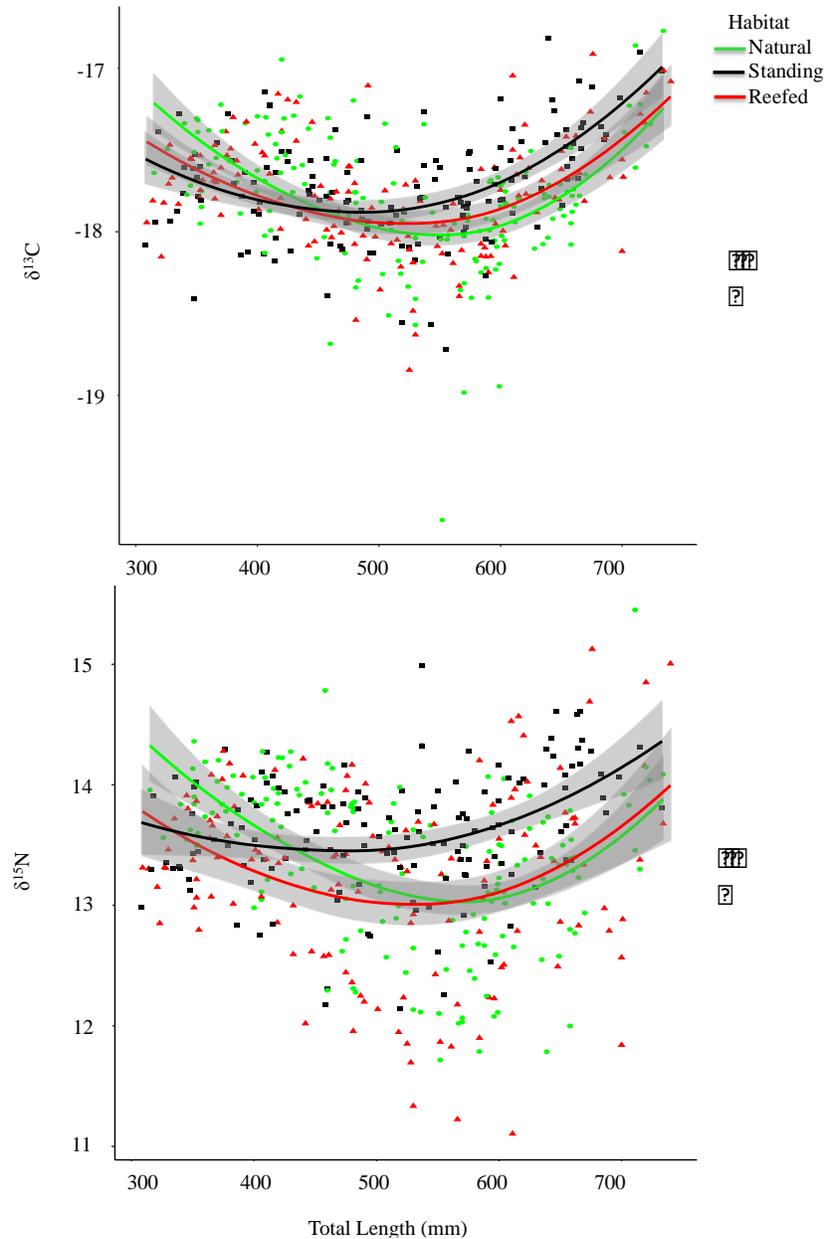
**Table 13. Sample size (n) of Red Snapper epaxial muscle tissue samples used in stable isotope analysis and mean isotope values ( $\pm\text{SE}$ ) of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) by habitat, including natural reefs (natural), standing oil and gas platforms (standing), and reefed platforms (reefed).**

Habitat	n	$\delta^{13}\text{C}$	$\pm\text{SE}$	$\delta^{15}\text{N}$	$\pm\text{SE}$
Natural	163	-17.81	0.39	13.36	0.67
Reefed	139	-17.77	0.34	13.26	0.77
Standing	145	-17.72	0.33	13.61	0.50
<b>Overall</b>	<b>447</b>	<b>-17.77</b>	<b>0.36</b>	<b>13.41</b>	<b>0.67</b>



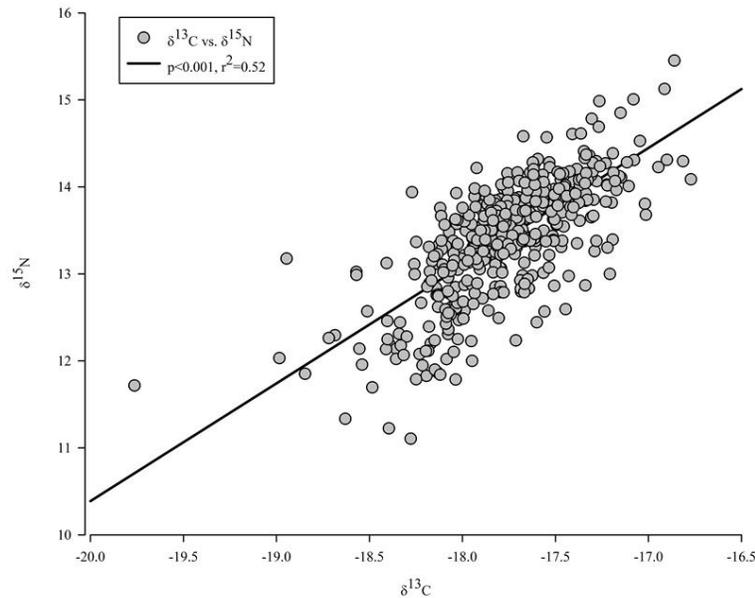
**Figure 23. Scatterplot and simple linear regression of Red Snapper  $\delta^{15}\text{C}$  (a) and  $\delta^{13}\text{N}$  (b) values and total length (mm), including natural reefs (natural), standing oil and gas platforms (standing), and reefed platforms (reefed).**

The non-linear relationship of isotope values and TL was visualized with a LOESS scatterplot; while the relationship was not linear, there are apparent trends within in each habitat (Figure 24).



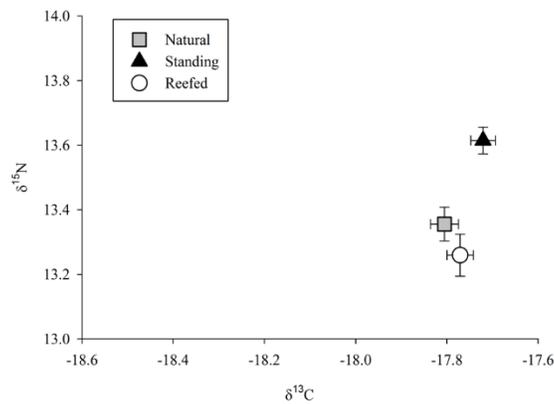
**Figure 24. Scatterplot of Red Snapper carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) values and total length (TL) with local polynomial regression (LOESS) curve overlay by habitat type natural reefs (natural), standing oil and gas platforms (standing), and reefed platforms (reefed).**

There was a positive relationship in isotopic space between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  for all habitats ( $p < 0.001$ ,  $r^2 = 0.52$ ; Figure 25).



**Figure 25. Scatterplot and simple linear regression of stable nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) ratios (mean  $\pm$ SE) with regression lines for western Gulf of Mexico Red Snapper.**

A significant effect of habitat and size class on isotope values was observed (MANOVA  $p < 0.001$ ; Table 14). Overall mean  $\delta^{15}\text{N}$  was higher at standing rigs (Figure 26). Subsequent univariate ANOVAs showed that by habitat  $\delta^{13}\text{C}$  did not differ significantly ( $p = 0.060$ ), but there were effects of size class ( $p < 0.001$ ) and a habitat and size class interaction ( $p < 0.001$ ; Table 14).  $\delta^{15}\text{N}$  was significantly different by habitat ( $p = 0.016$ ), size class ( $p < 0.001$ ), and the interaction was also significant ( $< 0.001$ ; Table 14).

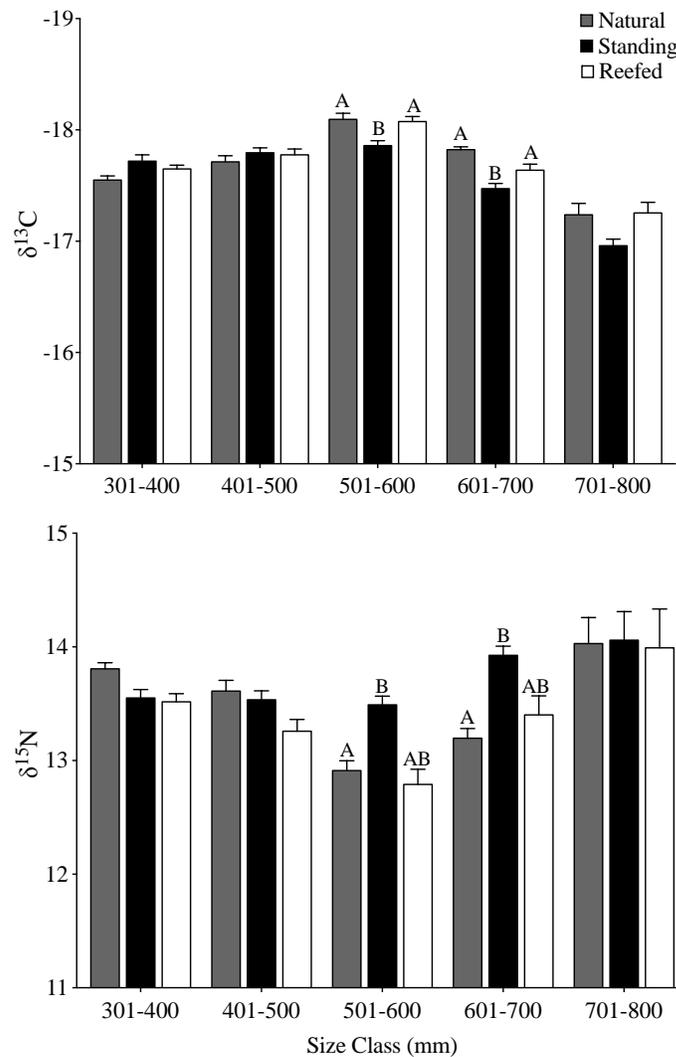


**Figure 26. Stable nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) ratios (mean  $\pm$ SE) of western Gulf of Mexico Red Snapper by habitat type: natural reefs (natural), standing oil and gas platforms (standing), and reefed platforms (reefed).**

**Table 14. Multivariate analysis of variance (MANOVA) table comparing  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of Red Snapper by habitat (natural, standing, and reefed) and size class (100 mm bins TL) showing main effects and interactions with significance considered at  $p \leq 0.05$  and individual univariate analysis of variance (ANOVA) for each factor showing response variables  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  separately.**

Factor	SS	df	F	P
<b>MANOVA</b>				
Habitat	-	4	8.103	<b>0.026</b>
Size Class	-	4	32.329	<b>&lt;0.001</b>
Habitat * Size Class	-	8	3.522	<b>&lt;0.001</b>
<b>ANOVA: <math>\delta^{13}\text{C}</math></b>				
Habitat	0.482	2	2.827	0.060
Size Class	14.700	4	3.675	<b>&lt;0.001</b>
Habitat * Size Class	2.359	8	4.141	<b>&lt;0.001</b>
<b>ANOVA: <math>\delta^{15}\text{N}</math></b>				
Habitat	2.851	2	4.173	<b>0.016</b>
Size Class	24.999	4	18.295	<b>&lt;0.001</b>
Habitat * Size Class	13.080	8	4.786	<b>&lt;0.001</b>

Post-hoc pairwise comparisons for  $\delta^{13}\text{C}$  by habitat and size class revealed that standing was slightly yet significantly lower than natural and reefed in 501-600 and 601-700 mm fish (Figure 27). Similarly,  $\delta^{15}\text{N}$  varied by size class with standing significantly more enriched than natural in 501-600 and 601-700 mm fish, but not significantly greater than fish from reefed habitats (Figure 27).



**Figure 27. Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope values  $\pm$  SE of Red Snapper by habitat, natural reefs (natural), standing oil and gas platforms (standing), and reefed platforms (reefed), and size class (100 mm bins), shared letters indicate similarity and differing letters indicate statistical significance.**

**Discussion** - Diet and stable isotope analysis of Red Snapper yielded insight into the trophic ecology of this important fishery species in the western GOM. This dual-pronged approach enabled analysis using short-term (stomach contents) and integrative measures of diet (stable isotopes). Interestingly, reefed and natural structures exhibited a similar isotopic signature, which suggests that these habitats are functioning similarly; however, standing had a significantly higher  $\delta^{15}\text{N}$  than individuals at reefed habitats for multiple size classes. Thus, habitat structure type may have certain consequences for the trophic ecology of Red Snapper.

Overall, Red Snapper appear to exhibit a mixed or opportunistic feeding strategy with varying degrees of generalization and slight individual specialization at all habitat types. An

examination of feeding strategy diagrams per habitat did not reveal a unique pattern for any of the habitats. Most prey items were located in the rare occurrence area of the feeding strategy diagram for every habitat type, which shows that regardless of habitat, Red Snapper are not specializing on any one particular prey item, instead preying on a variety of items as they are available. The prey items spreading up the y-axis, toward the between phenotype component, indicate that individuals within the population may simultaneously specialize on separate prey items (Amundsen et al. 1996; Ajemian and Powers 2012). As such, individual variation may play a large role in some of the noise observed in the dietary data. Some taxa are more easily identifiable due to persistent hard structures, such as Portunidae, Carangidae, Stomatopoda, and Cavoliniidae, which may have led to a slight inflation of the importance of these taxa to the diet of Red Snapper. Incorporation of DNA barcoding into diet content studies would reveal finer differences in diet and remove some of the bias due to the easily identifiable features of some taxa (Valdez-Moreno et al. 2012; Cote et al. 2013). The addition of these factors in future diet studies would increase clarity to the question of habitat influence on the diet composition of Red Snapper in the Gulf of Mexico.

Using fairly large sample sizes (~130 per habitat), we found that there are subtle differences in  $\delta^{15}\text{N}$  that could be attributed to habitat type, but importantly these differences depend on size class. As such, habitat-specific effects may not be interpretable without capturing a considerable ontogenetic component. Interestingly, we did not observe a linear relationship between TL and either carbon or nitrogen stable isotopes. However, based on the LOESS curve, ontogenetic trends were present for reefed and natural bank habitats but noticeably less for standing platforms. This suggest that active platforms may provide a unique and more consistent food resource over ontogeny.

There were subtle differences observed in Red Snapper trophic ecology that were attributed to habitat type. Similarly, the epifaunal communities occupying sediments around reefs in this area (including MU-A-85A) have been shown to support different prey communities, which were attributed to unmeasured, subtle, abiotic components (Montagna and Harper 1996). There are also documented effects of contaminants from oil and gas platforms impacting the available prey community (Peterson et al. 1996). Different epifaunal communities near platforms leaching contaminants into the water or sediment could have bottom up effects on the localized food web, thus resulting in varied isotopic signatures in Red Snapper at different sites within the same habitat type. This idea could be investigated farther by assessing the chemical burden of water and sediments from these sites or by testing for a molecular response of P450 induction in fish. Recent research in the GOM suggests that artificial light from platforms may result in higher  $\delta^{15}\text{N}$  due to the increased presence of prey fish. Future work should assess the physical parameters and biogeochemical ecology of natural and artificial reefs in the GOM in an effort to understand what may be driving these differences. Possible factors to investigate would be the total area of a site, vertical relief, substrate type, distance from shore, freshwater inputs from terrestrial environments, and water chemistry.

There is some debate as to whether Red Snapper are a resident or transient species. A lack of long-term residency on a particular site could explain the variation in observed trophic ecology. For example, Red Snapper are known to move between natural and artificial habitats throughout the course of a day or to be motivated by seasonal changes in temperature (Topping and Szedlmayer 2011; Piranio and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016), which could muddle any isotopic differences between habitat types. Furthermore, recent studies using advanced, fine-scale tracking methods show Red Snapper to be highly resident species that move on and off structure with 77% of tagged fish occupying a secondary habitat (Williams-Grove and Szedlmayer 2016). Thus, it is possible that Red Snapper may be moving between the natural and artificial reef sites used in this study. Large Red Snapper tagged within this study area have been shown to have movement ranges of up to 13.1 km making the prospect of traversing our study sites (range 2 – 52 km) feasible for the bigger size classes. This movement may be for optimal foraging, to avoid predation, or for spawning purposes.

This work supports the idea that artificial reefs may allow Red Snapper to take advantage of unique foraging opportunities in the western Gulf. Prey items unique to habitat were identified in the diet of fish on artificial reefs in the northwestern Gulf. These included *Fanfantepona* sp., Octopoda, Cavolinia, Achelata, Tanaidacea, Clupeidae, and Haemulidae on natural sites, *Janthina*, *Orthopristis*, *Pristipomoides*, *Hopplunis*, and Opiphiidae on standing, and Rajidae, *Portunus spinimanus*, and *Speocarcinus lobatus* on reefed. Furthermore, the value of artificial reefs may not be directly related to prey composition present on the reef, but to other opportunities provided by their placement. The lack of major differences in the trophic ecology of Red Snapper from natural and reefed oil and gas habitats in the western GOM suggest that these habitats are functioning similarly and thus may be an effective strategy for creating additional habitat for this important species. Habitat has been cited as a limiting factor for Red Snapper populations (Shipp and Bortone 2009), so maintaining artificial reefs may be beneficial for fishery managers as they strive to stabilize the population.

The results of this study have implications for management, as there are currently hundreds of oil and gas platforms off the Texas coast approaching decommissioning and removal. The Texas Parks and Wildlife Department Rigs-to-Reefs program offers an alternate to complete removal where decommissioned platforms can be donated and used as artificial reefs. It appears that Red Snapper using artificial reefs are not restricted as far as the prey selection or quality in the northwestern Gulf of Mexico. If the influence of artificial reefs on other important life history characteristics can be determined to be as beneficial as natural reefs, then reefing platforms may be a valid method for creating habitat for Red Snapper in the northwestern Gulf.

### **Overall Summary**

Our work involved the integration of several habitat-specific performance metrics of Red Snapper to best assess the stock enhancement value of multiple offshore habitats. With the rapid decommissioning of oil and gas platforms and subsequent conversion to artificial reefs (via “Rigs-

to-Reefs”), our project was developed to assess potential impacts of these “new” habitats on Red Snapper, with the assumption that the habitat from which fish were extracted contributed to the biological state in which we observed each individual. With notable exceptions, we found that individuals from reefed platforms performed similarly (trophic ecology, timing of reproduction) to those extracted from standing oil and gas platforms and natural banks. As such, continued allocation of decommissioned platform materials to Rigs-to-Reefs should not have negative impacts on Red Snapper overall. In fact, our finding of increased growth rates (beyond Age-6) on reefed platforms demonstrates a potential benefit of these types of habitats. However, it should be noted that the largest and oldest fish were consistently found on natural bank habitats. Thus, together, both artificial and natural habitats can play different yet complementary roles in enhancing the Gulf of Mexico Red Snapper stock.

Our findings did not show major differences in abundance based on vertical line data, although we suspect gear saturation may be limiting our ability to clearly assess differences. Based on video indices between reefed platforms and natural banks, we observed higher Red Snapper densities on reefed platforms, potentially due to the limited spatial extent of these structures. However, it is important to remember that some of these Rigs-to-Reefs artificial reef sites may include up to several dozen individual structures, and that may play a role in how fish perform at those sites (Lindbergh et al. 2006). Unfortunately, it was beyond the scope of this particular study to analyze populations on such smaller scales (i.e., structure to structure). However, future studies should strive to design sampling to address this component, perhaps using a stratified random approach if possible.

Many previous studies have demonstrated the influence of trophic ecology on performance parameters of demersal fishes, particularly in temperate systems. In the North Sea, the body condition of several benthic fisheries species apparently hinges upon the availability of Sand Eels (*Ammodytes marinus*), the primary prey for many of these species (Engelhard et al 2012). In Atlantic Cod (*Gadus morhua*), another temperate reef fish, reproductive capacity was shown to be correlated with food sources; individuals that consumed pelagic prey (i.e., capelin) were found to have better condition than those consuming benthic crustaceans (Sherwood et al. 2007). Much less is known about these linkages between habitat-specific performance metrics in subtropical fishes. In coral reef habitats, diet and condition has been known to vary on relatively small spatial scales (e.g., fore-reef vs. back-reef) for species of butterflyfish (Berumen et al. 2005). In the Gulf of Mexico, recent studies off Louisiana suggest that Red Snapper may fare better on natural reefs over artificial reefs due to enhanced trophic diversity (Simonsen et al. 2015) and improved condition (Schwartzkopf and Cowan 2016). However, comparisons were made with natural banks along the shelf-edge that were likely influenced by several additional factors due to increased depths and comparisons over large scales (100s of km). Off the Texas coast, where fish community assemblages are known to vary across similar depth gradients (Ajemian et al. 2015), we limited potential spatial impacts to a much finer scale (10s of km). As such, we feel confident in the habitat-specific analyses conducted in our project.

In our study, Red Snapper  $\delta^{13}\text{C}$  varied minimally by habitat, suggesting fish from all three habitats (standing platforms, reefed platforms, and natural banks) still derived carbon from similar sources. However, certain size classes (501-600 mm TL and 601-700 mm TL) on standing platforms showed higher  $\delta^{13}\text{C}$  values. In her recent thesis, Foss (2015) showed similar trends in standing platforms, which she indicated were characterized as having higher amounts of light and algae. These conditions may have played a role in our data as well, and warrants further investigation. Our finding of higher  $\delta^{15}\text{N}$  values on Red Snapper from standing platforms for the same two size classes is consistent with the only other habitat-specific trophic study from the Gulf of Mexico region (Simonsen et al. 2015). These differences may be attributed to the higher contribution of fish to the diet of Red Snapper as determined from stomach content analysis. Although not statistically significant, these fish also had the highest average condition and spawned most frequently, which suggests that feeding ecology may have influenced fish robustness. Interestingly, despite higher growth rates beyond Age-6 at reefed platforms, we could not find a trophic rationale for this departure from the other habitats.

Additional direct and indirect factors that were not accounted for in our experimental design may also impact fish condition and thus habitat-specific performance. For example, predator densities (e.g., sharks) may cause reef fish prey to seek additional shelter and thus limit foraging, which in turn may reduce overall condition (Sherwood et al. 2007). Moreover, since fish are known to exhibit compensatory response as densities increase, some of these habitats may be reaching carrying capacity, and may explain the absence of larger individuals on artificial habitats where Red Snapper densities are higher. These individuals likely have higher space requirements. Research into Red Snapper residency and site fidelity at these depths (60-90 m) should be explored, as it may lend further insights into habitat-specific performance. While we suspected high residency in these fish based on previous studies, we recognize that some of the larger individuals may have larger home ranges that may temporarily displace them from these habitats. This is supported by a lack of differences in diet and trophic ecology at larger size classes. A final consideration moving forward would be to better quantify habitat-specific fishing pressure. While we observed fishermen across all habitat types over the project period, we did not quantify fishing mortality that may also influence the interpretation of these results. Future work should attempt to quantify this potential factor that may influence biological parameters.

Collectively, our findings suggest artificial reefs can be a valuable tool for enhancing the Red Snapper population. With the rapid decommissioning of oil and gas platforms and subsequent conversion to artificial reefs (via “Rigs-to-Reefs”), our project was developed to assess potential impacts of these artificial habitats on Red Snapper. Generally, we found that individuals from reefed platforms performed similarly (trophic ecology, timing of reproduction) to fish from standing oil and gas platforms and natural banks. As such, continued allocation of decommissioned platform materials to Rigs-to-Reefs should have positive impacts on the Red Snapper stock overall. Given the large area of natural habitats in the GOM, and that the largest and oldest fish were consistently found on these natural banks, artificial reefs may also be an effective management option for diverting fishing effort away from a large portion of the spawning stock.

### **B. Significant problems**

We had no significant problems during the course of this project. We experienced a few minor but typical scheduling setbacks associated with inclement weather conditions, but these were taken into account during the planning phase and did not alter our overall goals and objectives or the proposed methodology to attain them. We chose to use Red Snapper as the model species, which were abundant at numerous size classes and locations. While we attempted to compare trophic differences of sympatric Snapper species (Gray and Vermillion Snapper) as well as Gray Triggerfish, for this study the availability of these other species among all habitat types and sites in the numbers needed for meaningful analyses were very limited. Thus, to make the most thorough and robust comparison of the relative habitat value of oil and gas platforms and natural habitats the primary focus remained on Red Snapper. Additionally, these key data are most needed for Red Snapper, as managers try to better assess their abundance in the Gulf of Mexico.

### **C. Need for additional work**

The work completed in this study has led to a greater understanding of how fish communities on artificial reef habitats compare to those found on natural banks. While effects of the nepheloid layer probably influenced the communities we observed, further investigation of proximity effects of artificial reefs on fish communities is warranted as new artificial reefs may fail to meet management objectives depending on their proximity to existing reef habitat. Additionally, our age and growth findings could be enhanced by increasing spatial coverage and replication at the habitat level (i.e., more sites per habitat) to better evaluate the patterns and hypotheses described here and to refine our understanding of how different habitats contribute to the maintenance of the GOM Red Snapper stock. Future studies should also focus on movement between these habitats and how that may influence the age and growth structure we observed in this study. While this study focused on Red Snapper, additional comparisons of species-specific life history traits (e.g., reproductive potential, age distribution, growth, mortality, site fidelity) at both artificial and natural habitats are needed to fully understand the value and function of natural and artificial reefs to other reef fish species. Moreover, some of these Rigs-to-Reefs artificial reef sites include up to several dozen individual structures, and that may play a role in how fish perform at those sites. While it was beyond the scope of this particular study to analyze populations on such a fine-scale (i.e., structure to structure), additional studies should strive to design sampling to address this component, perhaps using a stratified random approach if possible. A final consideration moving forward would be to better quantify habitat-specific fishing pressure. While we observed fishermen across all habitat types over the project period, we were not able to quantify fishing mortality, and how it may also influence the interpretation of these results. Future work should attempt to determine how fishing mortality might influence biological parameters

## VII. EVALUATION

### A. Attainment of project goals and objectives

The goals and objectives for this project were fully attained as proposed. No modifications were made to the project goals and objectives. Vertical longlines were used to collect Red Snapper from various size classes among standing and reefed oil and gas platforms, as well as natural bank habitats. The longline data was combined with video and ROV survey data to establish community structure at artificial reefs and natural banks. We were able to collect all necessary hard parts (otoliths) and tissues (muscle, gonads, stomachs) from Red Snapper from the longline samples to determine fecundity, size at age, and diet. The tremendous amount of data and analyses conducted allowed us to determine the potential benefits of artificial reefs to Red Snapper and indicates that all habitats could contribute similarly to overall stock productivity and health on a per unit area basis.

### B. Dissemination of project results

This project has been a subject of interest and anticipation for the general public and fisheries management communities. The culminated results of this study have resulted in at least five manuscripts that are in the final stages of completion or are already submitted and in review with peer-reviewed international journals. The first manuscript pertains to the estimates of species richness, size distribution, and relative abundance on artificial reefs using remotely operated vehicle (ROV) survey data (Streich et al. in revision). The second relates to comparative length at age estimates for Red Snapper on various habitat types (Streich et al. in press). The third manuscript details the differences in Red Snapper reproductive biology on natural vs. artificial reefs (Downey et al. in prep). The fourth manuscript will describe observed trophic ecology of Red Snapper using various habitats based on stable isotope and dietary data (Brewton et al. in prep). The final manuscript will combine all the various aspects of Red Snapper biology and abundance in a review of the fishery in the western Gulf of Mexico (Ajemian et al. in prep). Data obtained from this project resulted in the successful completions of one student's M.S. thesis (C. Downey; Graduated Dec. 2016) and a substantial component of another Ph.D. student's dissertation (M. Streich; Graduated Dec. 2016). Multiple presentations have been given at local and national scientific meetings including the American Fisheries Society Annual Meetings, American Society of Ichthyologists and Herpetologists, Benthic Ecology Meeting, and the Texas Bays and Estuaries Meeting. Finally, PI Stunz is on the Gulf of Mexico Fishery Management Council, and he has ensured these products will be conveyed in the management arena. The whitepaper and summary documents for those meetings are freely available upon request.

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