ECOLOGY OF RED SNAPPER IN THE WESTERN GULF OF MEXICO: COMPARISONS AMONG ARTIFICIAL AND NATURAL HABITATS

A Dissertation

by

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This dissertation meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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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 goal of my study was to use concurrent comparisons of artificial reefs and natural habitats to provide key information to evaluate the utility of artificial reefs for reef fishes, in particular Red Snapper, in the western Gulf of Mexico (GOM).

In Chapter 1, I used remotely operated vehicle surveys to show fish communities differ 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 Chapter 2, I examined whether Red Snapper size structure and age and growth differ between artificial and natural habitats. Size and age distributions suggested natural banks supported more large and old individuals, and the logistic growth model suggested fish at artificial reefs reached larger sizes-at-age than those from other habitats.

In Chapter 3, I assessed vertical line gear performance and demonstrated differences in gear efficiency between artificial reefs and natural banks. The use of paired video revealed a high prevalence of gear saturation, which should be accounted for if vertical lines are used in providing indices of abundance.

In Chapter 4, I examined the effects of a newly created artificial reef using a before-after control-impact study. Following reef construction, juvenile Red Snapper abundance dramatically increased, and cohorts could be identified through time suggesting site fidelity. Because juvenile Red Snapper were present in high densities, appeared to be in good condition and growing quickly, and were no longer exposed to shrimp trawl mortality, the new reef likely enhanced the export of juveniles (i.e., production) to the adult population.

Collectively, my findings suggest artificial reefs can be a valuable tool for enhancing the Red Snapper population. Given the large area of natural habitats in the GOM, artificial reefs may also be an effective management option for diverting fishing effort away from a large portion of the stock. Furthermore, fish at artificial habitats appear to grow as well as those on natural habitats, and artificial reefs can provide nursery habitat to juveniles. To increase the role artificial reefs play in supporting the GOM Red Snapper stock, future research should identify reef designs that maximize growth, survival, and production.

DEDICATION

This work is dedicated to my wife, Meg, for her love, encouragement, and patience during this journey.

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INTRODUCTION

Artificial Reefs as Fish Habitat

Artificial reef development is a popular management tool used to enhance fish stocks, mitigate degradation or loss of natural habitats, and provide additional fishing and diving opportunities (Baine 2001; Baine and Side 2003; Dupont 2008). In the U.S. Gulf of Mexico (GOM), both state and federal agencies have developed active artificial reef programs (e.g., Rigs-to-Reefs, Ships-to-Reefs, etc.) with the primary focus of enhancing wild fish stocks. However, despite the popularity and support for artificial reef programs, our understanding of how artificial reefs affect marine fisheries is surprisingly limited. Generally, the uncertainty regarding the effects of artificial reefs on marine fisheries is driven by a lack of fishery-independent studies. Specifically, there have been limited standardized comparisons between artificial reefs and their natural counterparts, leaving significant knowledge gaps regarding the relative value and function of artificial reefs towards supporting fisheries productivity.

Artificial reefs provide habitat for many federally managed reef-associated fishes (Stanley and Wilson 1997; Gallaway et al. 2009). In the northern GOM, permitted artificial reefs such as decommissioned oil and gas platforms, Liberty ships, tanks, automobiles, and a variety of small concrete structures provide novel hard substrate for reef-associated fishes. In addition, oil and gas platforms have served as artificial reefs since oil and gas exploration intensified around the 1950s, and they currently represent the largest unintentional artificial reef complex in the world (Stanley and Wilson 2003; Shipp and Bortone 2009). Together, these artificial reefs provide an additional 12-20 km^2 of reef habitat on a shelf dominated by mud and sand with little to no vertical relief (Gallaway and Cole 1997; Stanley and Wilson 2003; Gallaway et al. 2009; GMFMC 2012). Comparatively, an estimated 1285 km^2 of the northern GOM shelf between

Pensacola, Florida, and Brownsville, Texas, comprises natural reef habitat with vertical relief on the order of meters (Parker et al. 1983). Nonetheless, natural reef habitats are relatively scarce over the northern GOM shelf (Dufrene 2005; Gallaway et al. 2009), thus artificial reef habitat may provide disproportionately valuable habitat to a variety of marine life.

Several studies have observed elevated catches and increased densities of ecologically and economically important fishes on artificial reefs (Love et al. 2005; Patterson et al. 2014); but whether or not these observed increases represent an actual increase in regional stock biomass (i.e., production hypothesis) or simply a redistribution of existing biomass (i.e., attraction hypothesis) remains a topic of active discussion (e.g., Grossman et al. 1997; Gallway et al. 2009; Shipp and Bortone 2009; Cowan et al. 2011; Claisse et al. 2014). The ability of an artificial reef to enhance production may depend on a variety of species- or life stage-specific behaviors and life-history traits, which in turn may be influenced by several aspects of artificial reef design including reef density, location, and spacing (Bohnsack 1989; Pickering and Whitmarsh 1997; Strelcheck et al. 2005; Brandt and Jackson 2013). Furthermore, even if artificial reefs are effective in enhancing production, these benefits may be diminished depending on the associated level of fishing mortality (Powers et al. 2003; Lindberg et al. 2006; Addis et al. 2016). Today, many scientists acknowledge that artificial reef function may vary from differing levels of attraction to enhanced production through time or space and that research should shift from the attraction-versus-production debate to better understanding the ecological performance of fish on artificial and natural reefs (Carr and Hixon 1997; Powers 2003; Love et al. 2006; Broughton 2012).

Red Snapper Life History and Management in the Gulf of Mexico

The Red Snapper (*Lutjanus campechanus*), is a large, long-lived, demersal reef fish belonging to the perciform family Lutjanidae (Allen 1985). The species is distributed over the continental shelf between the Yucatan Peninsula and North Carolina including the Gulf of Mexico (GOM; Hoese and Moore 1998). In the GOM, Red Snapper can live to be more than 50 years of age, corresponding to a maximum length and weight of approximately 1 m and 22.8 kg, respectively (Hoese and Moore 1998; Wilson and Nieland 2001; Allman and Fitzhugh 2007).

In the northern GOM, Red Snapper spawn offshore during a protracted spawning season lasting from May through September with a peak observed between June and August (Bradley and Bryan 1975; Collins et al. 1996). However, latitudinal variation has been documented, as Brulé et al. (2010) observed peak spawning in the early fall over the Campeche Bank of Mexico. Individuals may become sexually mature as early as 2 years of age; however, peak reproductive output is not realized until 12-15 years of age (Collins et al. 1996; Woods et al. 2003; Porch et al. 2007). Red Snapper are heterochronal, broadcast spawners with indeterminate annual fecundity, and estimates of 55.5 million eggs are reported for the average Red Snapper over its life-span (SEDAR 2005; Brulé et al. 2010). Red Snapper are “bet-hedgers” in that a single female will broadcast millions of eggs during her lifetime with each small egg having a low probability of survival (Cowan et al. 2011). This periodic life history strategy is successful in maintaining population stability through occasional strong year-classes, which occur when eggs and larvae encounter optimal conditions for growth and survival (Winemiller and Rose 1992, 1993; Houde 2008).

Following a 26-30 day planktonic egg and larval phase, early juveniles settle to low relief habitats consisting of soft sand and mud substrates and relic shell ridges (Rabalais et al. 1980;

Szedlmayer and Conti 1999; Rooker et al. 2004; Geary et al. 2007). Juvenile densities are highest at depths of 18-55 m (Gallaway et al. 1999). As juveniles grow, they display an ontogenetic shift in habitat use from these low relief habitats to more high relief (~1 m), structured habitat such as artificial and natural reefs (Szedlmayer and Lee 2004; Wells et al. 2008a; Gallaway et al. 2009). Several studies have suggested that the amount of suitable habitat for age 0-1 Red Snapper is a primary limiting factor (Gallaway et al. 2009; Szedlmayer 2011).

By age 2, Red Snapper recruit to even higher relief habitat including large natural reefs, rock outcroppings, offshore petroleum platforms, and large artificial reefs with some estimates suggesting that 70-80% of age 2 Red Snapper in the northern GOM reside at oil and gas platforms (Stanley 1994; Gitschlag et al. 2003; Nieland and Wilson 2003). After recruitment to high relief reef habitat, generally moderate to high estimates of site fidelity are reported (Szedlymayer and Schroepfer 2005; Strelcheck et al. 2007; Topping and Szedlmayer 2011). Red snapper are thought to reside at these high relief habitats for much of their adult life; however, some evidence suggests that older fish (i.e., greater than age 10) may begin to spend more time over soft mud bottoms as predation risk is thought to decrease substantially at these sizes (Nieland and Wilson 2003; Mitchell et al. 2004; Gallaway et al. 2009).

Generally, Red Snapper are opportunistic feeders consuming fishes, benthic crustaceans, squids, and pelagic zooplankton (McCawley et al. 2006), but similar to habitat use, ontogenetic shifts in Red Snapper diet are evident. For example, Wells et al. (2008b) documented diet shifts from zooplankton, mysid shrimp, and squid in juvenile Red Snapper to benthic crustaceans and fishes in adults. Some studies (e.g., McCawley et al. 2006; Wells et al. 2008b) have suggested that Red Snapper feed from sand and mud bottoms away from reefs, while others (e.g., Szedlmayer and Lee 2004) have suggested their diets consist mainly of reef-associated prey.

There is evidence that Red Snapper in the northern GOM act as a metapopulation with semi-isolated populations over the short term but with limited connectivity over the long term (Saillant et al. 2010). Additionally, regional and sub-regional differences in age, growth, and reproduction are evident (Fischer et al. 2004; Jackson et al. 2007; Saari 2011; Kulaw 2012). For example, Fischer et al. (2004) found that Red Snapper from Texas grew more quickly and reached smaller maximum sizes than fish from Louisiana or Alabama. At the habitat-level, Saari (2011) found that Red Snapper from shelf-edge banks off Louisiana had slower growth rates than those from standing platforms.

The GOM Red Snapper stock has been exploited for over a century and currently supports economically valuable commercial and recreational fisheries (SEDAR 2013; Hood et al. 2007). The fishery began in the mid-19th century off the Florida panhandle; however, as early as the 1880s, evidence of stock depletion was reported (Collins 1887; Camber 1955). Commercial landings peaked at 14 million pounds in the 1960s with stock collapse occurring in the late 1980s (Hood et al. 2007; Porch et al. 2007). Federal management of the GOM Red Snapper stock began in 1976 with the implementation of the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA). As required by the MSFCMA, the Gulf of Mexico Fishery Management Council (GMFMC) drafted the Reef Fish Fishery Management Plan (FMP) in 1981 (Red Snapper are included in the reef fish management unit) and cited declining landings in the commercial and recreational fisheries for Red Snapper (GMFMC 1981). The first stock assessment for GOM Red Snapper, conducted in 1988, officially declared that the stock was overfished and experiencing overfishing (Goodyear 1988).

The GOM Red Snapper stock is currently overfished but no longer undergoing overfishing and in a rebuilding phase expected to be completed by 2032 (SEDAR 2013). The management of this stock is highly controversial given the diverse perceptions and values of the various stakeholders, scientists, and managers along with the numerous regulatory measures imposed on the recreational and commercial fisheries (Hood et al. 2007; Cowan et al. 2011). Hood et al. (2007) cited three primary factors influencing slow recovery including: 1) the stock had been fished to very low levels—1% of 20% spawning potential ratio (SPR), 2) the GMFMC choosing less conservative catch limits to balance the need to rebuild while minimizing negative social and economic impacts to the directed fisheries, and 3) the high level of mortality imposed on juvenile Red Snapper by commercial shrimp trawling. Other factors such as mortality of regulatory discards also slow recovery (Nieland et al. 2007; Curtis et al. 2015). Nevertheless, the stock is rebuilding rapidly.

Dissertation Purpose and Chapter Outline

Accurate evaluation of stock status requires an understanding of stock dynamics at regional or even sub-regional levels such as among habitats as these finer scale dynamics ultimately influence overall stock productivity (Pulliam 1988; Pulliam and Danielson 1991; Cadrin and Secor 2009; Kerr et al. 2010). Specifically, assessments of abundance and vital rates (e.g., growth, mortality, recruitment) can aid management by identifying important regions or habitats that may disproportionately contribute to stock maintenance or recovery. To date, limited simultaneous comparisons of Red Snapper abundance (Patterson et al. 2014), growth (Saari 2011), reproduction (Kulaw 2012; Glenn 2014), recruitment, or diet (Wells et al. 2008b; Simonsen et al. 2015; Tarnecki et al. 2015) have been conducted at natural and artificial habitats. In fact, most information on Red Snapper life history and ecology has been derived from artificial habitats or unknown locations from fishery-dependent sources (although a majority of the commercial fishery is carried out over artificial habitats; SEDAR 2009). As such, determining the relative value of artificial reefs to Red Snapper productivity is hindered without a natural baseline for comparison (i.e., concurrent demographic data from natural habitats).

In this dissertation, I present results from four separate studies designed to quantify Red Snapper demographics and provide insight into the relative value of artificial and natural habitats for Red Snapper in the western GOM. In Chapter 1, I use video-based data from a remotely operated vehicle (ROV) to compare fish community structure and provide estimates of Red Snapper density between artificial and natural habitats. In Chapter 2, I evaluate whether Red Snapper size structure, age, and growth differ between decommissioned platform artificial reefs, standing oil and gas platforms, and natural banks in the region. In Chapter 3, I assess vertical line gear performance at artificial reefs and natural banks and demonstrate the utility of a paired video survey to compliment traditional catch data. In Chapter 4, I examine the effects of a constructing a new artificial reef on Red Snapper and other reef associated fishes using a before-after control-impact (BACI) study. I conclude with a summary of key findings and implications of each chapter and discuss future avenues of research.

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CHAPTER I:

A COMPARISON OF FISH COMMUNITY STRUCTURE AT MESOPHOTIC ARTIFICIAL REEFS AND NATURAL BANKS IN THE WESTERN GULF OF MEXICO

Abstract

Oil and gas platforms along the northwestern Gulf of Mexico (GOM) shelf have served as artificial reefs since oil and gas exploration intensified in the 1950s. As these structures are decommissioned, they must be removed; however, some are converted to permanent artificial reefs. Despite the potential effects these artificial habitats may have on marine fisheries, investigations assessing fish communities inhabiting these structures relative to natural habitats are rare. During fall 2012, remotely operated vehicle 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 (*Lutjanus campechanus*) 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 like Red Snapper by diverting fishing pressure from 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.

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 (e.g., Claisse et al. 2015).

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, 2000; Wilson and Stanley 2003, 2006; Love and York 2005; Love et al. 2005, 2006; Reubens et al. 2013). Whether these observed increases in fish densities represent increased production (i.e., stock enhancement) or simply re-distribution (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, 2015). 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 coralgal 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 paper, I present the first comparative study of reef fish community structure among RTR artificial reefs and drowned coralgal 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. My specific objectives were to: 1) compare and contrast fish community structure between RTR artificial reefs and the nearby natural bank habitats and 2) estimate Red Snapper densities at these artificial reefs and natural bank habitats. Considering the social and economic importance of Red Snapper in the region, I discuss these density estimates with respect to the known area of the artificial and natural habitats surveyed and highlight the implications for artificial reef development and Red Snapper management in the GOM.

Study Area

The study area encompassed five artificial reef sites and five natural banks interspersed along the Texas shelf in the western GOM (Figure 1-1). The region is characterized by a gently sloping shelf, terrigenous sediments consisting of silt and clay muds, and a generally low availability of natural hard substrates with vertical relief ≥1 m (Parker et al. 1983; Rezak et al. 1985). 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 1-1). 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 natural banks in the northern GOM, which formed atop diapiric salt intrusions, the South Texas Banks have been classified as drowned remnant coralgal 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 1-1). 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).

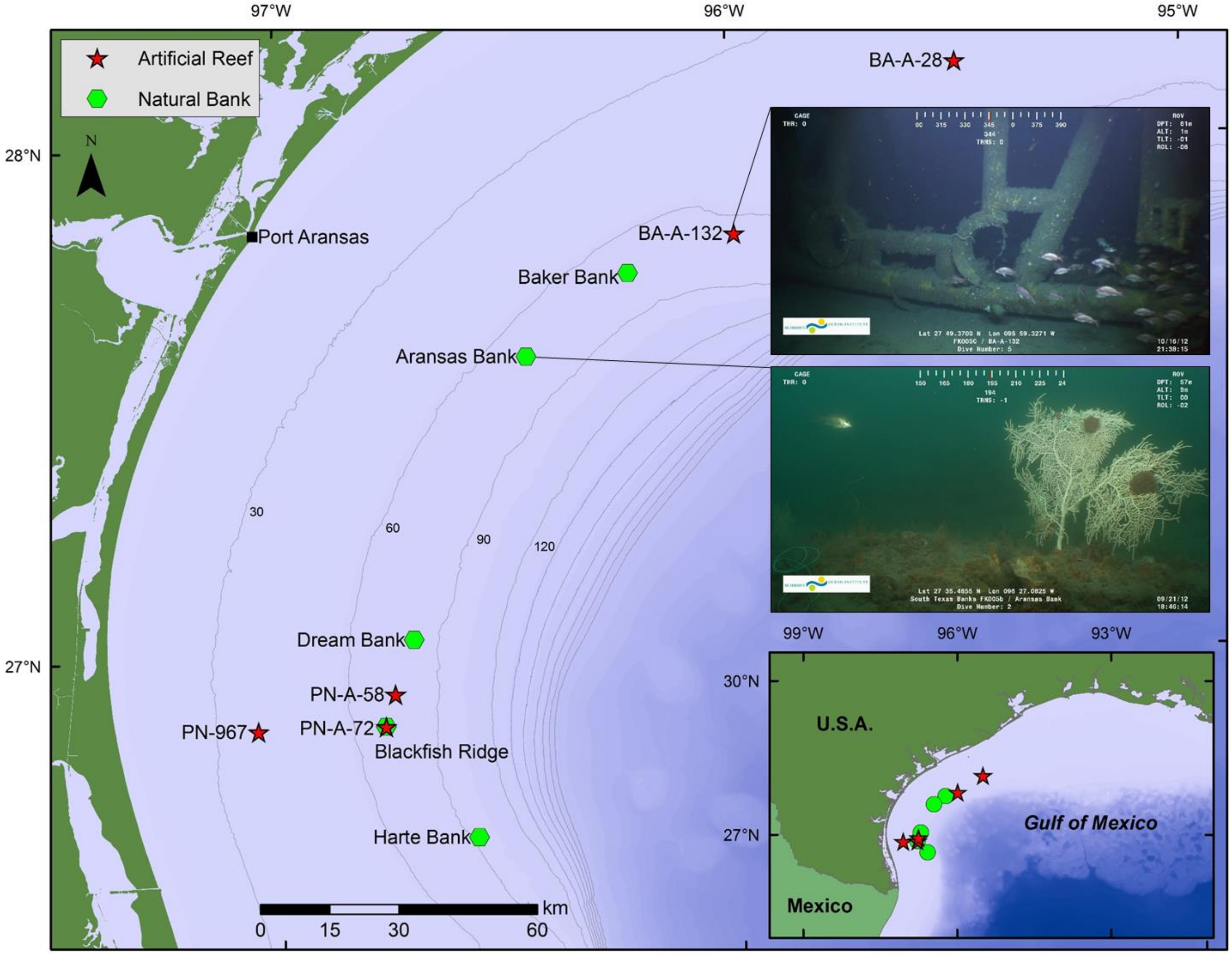

Figure 1-1. Map of artificial reefs (red stars) and natural banks (green circles) surveyed using the Global Explorer ROV in September and October 2012. Bathymetric contours (gray lines) are displayed in 30 m intervals. Inset map (bottom right) shows study location relative to the western GOM region. Inset pictures provide examples of each type of habitat type.

Table 1-1. 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^2)
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

Methods

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® 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.

Fish communities of both artificial reefs and natural banks were surveyed 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 1-1) necessitated some slight modifications to 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 is 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, an attempt to survey at least two structures was made 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. Direct observations from these ROV transects were to document the fish communities inhabiting the five natural banks surveyed. The ROV maintained a consistent camera tilt, viewing angle (105°), and height above the seafloor (~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 (~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.—I began my 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). A one-way design was used 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). This analysis was followed by hierarchical agglomerative clustering (via CLUSTER) and similarity profile (SIMPROF) testing to determine whether it was appropriate to interpret the resulting nMDS groupings. A SIMPER analysis was performed to determine which species were responsible for the variation among resulting groups. Because species do not arrive independently in samples

(Clarke et al. 2006), I also performed an inverse analysis (e.g., Field et al. 1982) to determine if species were positively associated in samples (i.e., MinCounts fluctuate in proportion across samples). Prior to beginning this analysis, Type 2 SIMPROF was used to test the null hypothesis that species were not associated with each other (Somerfield 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 (Somerfield 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 surveys spanned two distinct habitats with varying physical characteristics, I 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 1-1) potentially influenced the fish communities we observed. Abiotic data were normalized and converted to a resemblance matrix based on Euclidean distance measures. A RELATE test was used to assess the agreement between the biotic and abiotic resemblance matrices. Given a significant RELATE test, I 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.—I estimated Red Snapper density on artificial reefs and natural banks within the study area using standardized transects from the previously described ROV community surveys. Abundance estimates were standardized 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). These criteria were chosen 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^2). Because there were 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). A non-parametric bootstrap test for equality (n = 1000) was used 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^2) times the mean density on artificial reefs (# of fish/m^2)].

Results

Community Analyses

Video-based surveys from the ROV deployments resulted in 22.2 hours of footage. Surveys 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 1-2). The highest species richness was observed 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 1-1). Salinity was similar at both habitats and averaged 36.5 psu.

Table 1-2. Record of various taxa observed during ROV surveys at five natural banks and five artificial reef sites along the Texas Shelf in fall 2012.

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

Table 1-2 (continued).

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
Pomacentridae	Brown Chromis	*Chromis multilineata*							X			
	Purple Reeffish	*Chromis scotti*	X	X	X	X						
	Sunshinefish	*Chromis insolata*	X	X	X	X						
	Yellowtail Reeffish	*Chromis enchrysura*	X	X	X	X						
	Bicolor Damselfish	*Stegastes partitus*								X		
	Damselfish sp.	*Stegastes 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								
	Cubbyu	*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	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	1.730	1.960	1.790
Eveness (J')			0.741	0.679	0.659	0.874	0.760	0.581	0.740	0.577	0.678	0.563

Interestingly, no single species was observed at all 10 sites; however, five species were observed at ≥ 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 1-2). 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 Reeffish (*Chromis scotti*), Sunshinefish (*C. insolata*), and Yellowtail Reeffish (*C. enchrysura*). 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 (H') was generally higher at natural banks (mean = 2.31; SE = 0.09) than artificial reefs (mean = 1.98; SE = 0.14; Table 1-2). The highest diversity was observed 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 (*Lujanus 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 1-3). 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 1-3. 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.

	Site									
Common name	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 1-2). 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 1-4). 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 1-2). 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 Reeffish, 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).

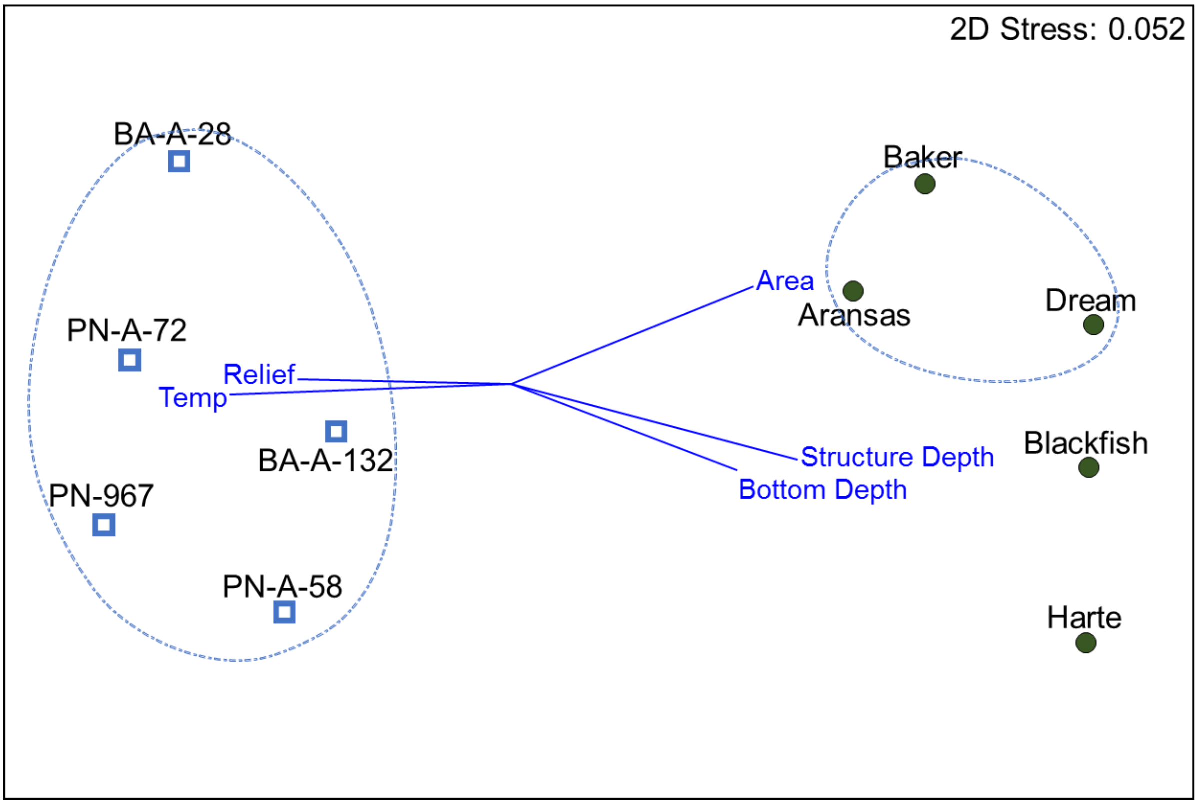

Figure 1-2. Non-metric multidimensional scaling (nMDS) ordination using square-root transformed MinCounts and Bray-Curtis similarities from ROV surveys of artificial reefs (blue squares) and natural banks (green circles). Significant groups determined with SIMPROF ($P < 0.005$) are denoted by the dashed circles. The relationship of the five habitat variables tested with Bio-Env are displayed in the blue vector plot.

Table 1-4. 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	$\text{Mean}_{\text{Artificial}}$	$\text{Mean}_{\text{Natural}}$	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 Reeffish	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

The inverse analysis indicated that there was strong evidence of association among species observed in the community 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 1-3). The first group (e.g., A in Figure 1-3) 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 1-3) 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 1-3), 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 1-3) 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 ($\rho = 0.68$).

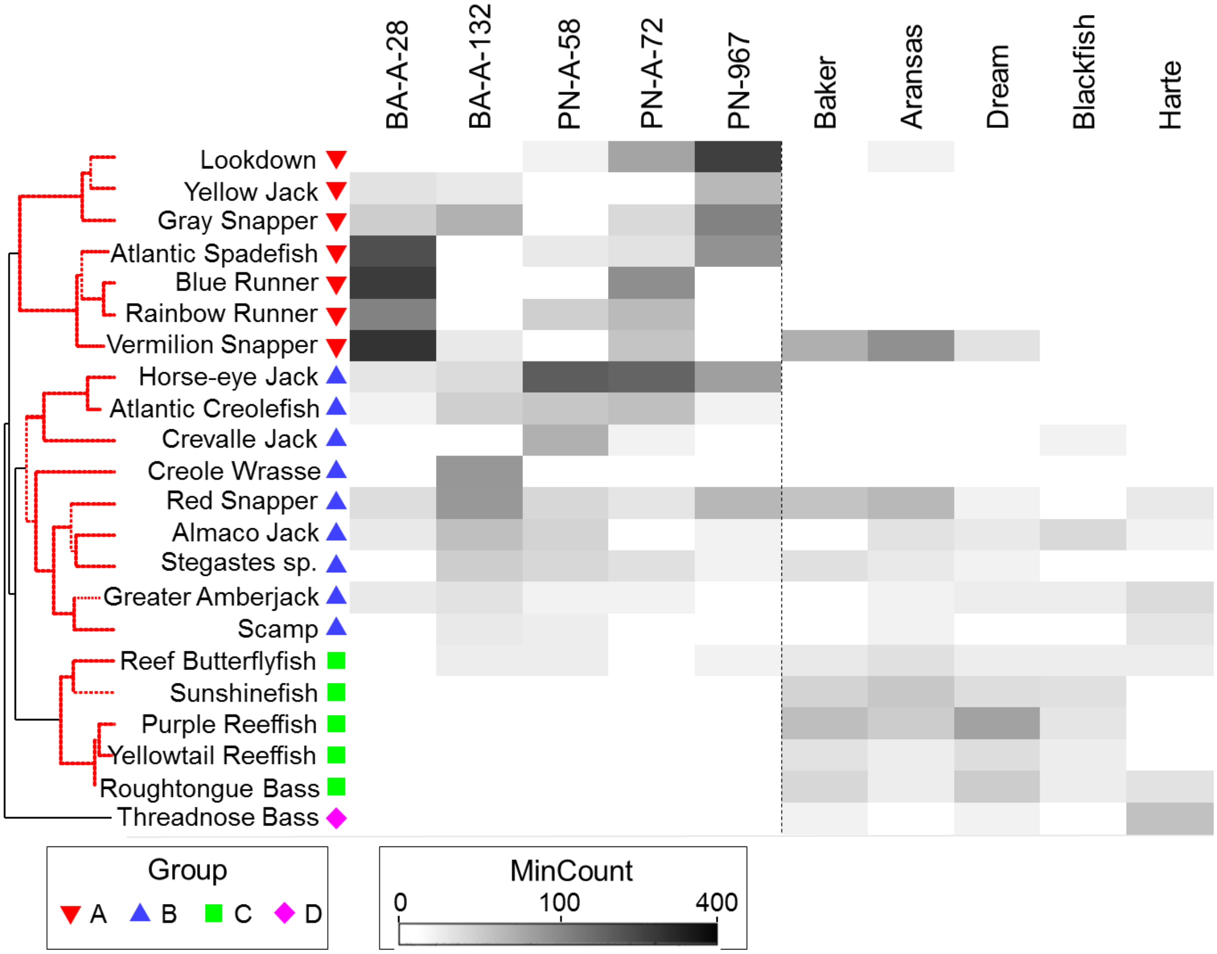

Figure 1-3. Shade plot of square-root transformed species counts (only species accounting for > 5% of the total counts in any one sample are shown) by sample site. The linear gray scale shows back-transformed MinCounts. The dendrogram on the left displays the hierarchical clustering of species groups 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).

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^2; 95% CI [0.103 – 0.315]) was nearly 7.8 times greater than density at natural banks (mean = 0.022 fish/m^2; 95% CI [0.005 – 0.047]; Figure 1-4A). 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 1-4). Estimated densities from individual transects at artificial reefs ranged from a low of 0.03 fish/m^2 at BA-A-28 to as high as 0.49 fish/m^2 at BA-A-132. Among natural banks, Blackfish Ridge had the lowest estimated density (0 fish/m^2), while Aransas Bank had the highest estimated density (0.06 fish/m^2; Figure 1-4B). 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 1-5). 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.

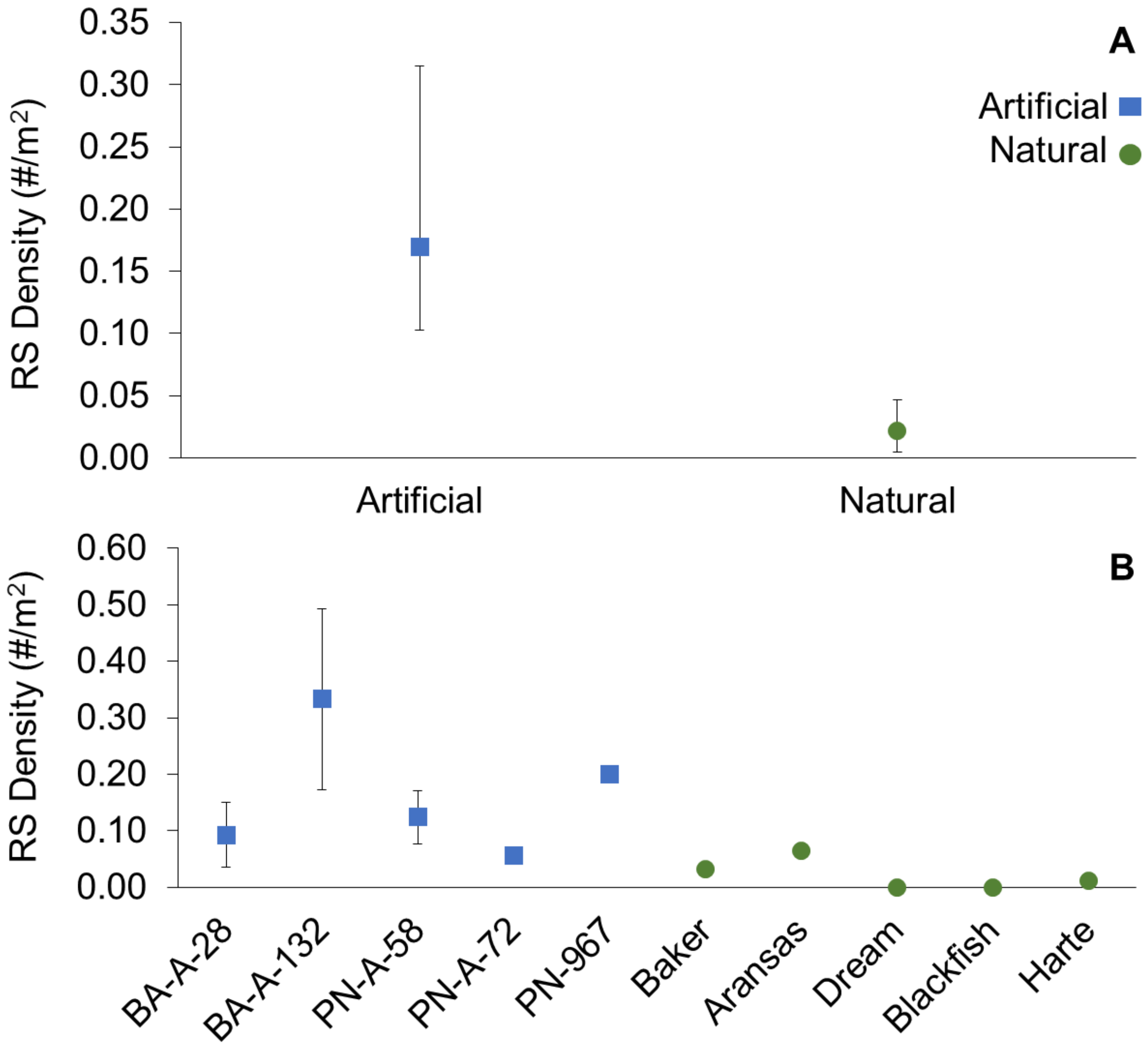

Figure 1-4. Red Snapper (RS) density estimates (# of individuals/m2) from ROV transects on artificial reefs (squares) and natural banks (circles) in the western GOM in fall 2012. Density is displayed by (A) habitat (error bars represent bootstrapped 95% confidence intervals) and by (B) site to display variation in individual estimates (error bars representing standard error are displayed for sites that had two transects).

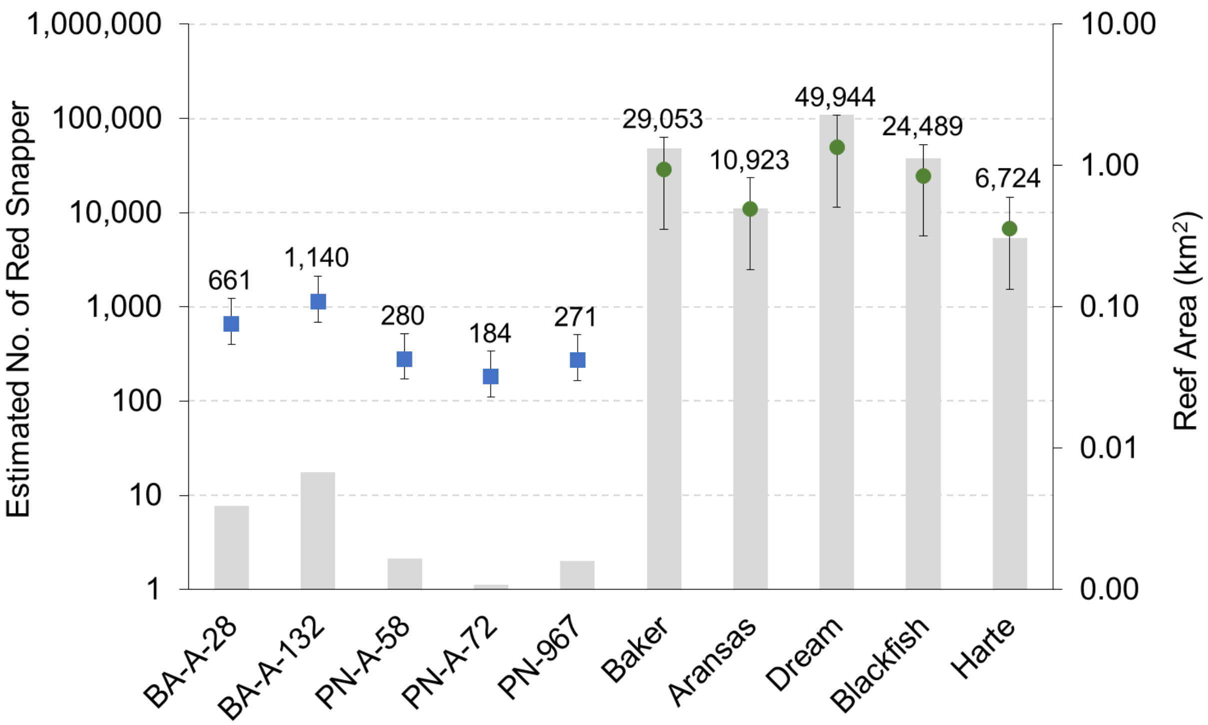

Figure 1-5. Estimated total abundance of Red Snapper (based on habitat density estimate multiplied by reef area; error bars represent bootstrapped 95% confidence interval) at artificial reefs (squares) and natural banks (circles). Reef area (gray bars) is plotted on the secondary y-axis. Note that both 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). This 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. Analyses suggest that fish communities at artificial reefs were different than fish communities at natural habitats, a finding that supports 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, the 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, continued monitoring of these habitats is needed 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 were not observed 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.

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).

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 Reeffish, Yellowtail Reeffish, 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, 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 this bank was surveyed, its terrace did extend out of the nepheloid layer. Nevertheless, lower MinCounts of several pomacentrid damselfishes were observed 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, low abundances of potential predators like Red Snapper were observed at both of these sites. While effects of the nepheloid layer probably influenced the communities 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 the study region, Ajemian et al. (2015b) noticed a similar transition in fish communities around the 60 m isobath. In this study, 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. For example, with the exception of BA-A-28, PN-967, and Harte Bank, the sites surveyed were located in bottom depths of 61-82 m rather than a wide range of depths across the shelf. While 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, I observed many of these species in highest abundances at BA-A-28 and PN-967, two artificial reefs with the shallowest structure depths. While I recognize that bottom depth and vertical relief of a site influence structure depth, these data support previous studies indicating 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, future video-based surveys designed for assessing fish community structure at these habitats could 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. Several species groups were identified that occurred in similar fashion throughout the samples. For example, species in the reef-dependent group (i.e., group C in Figure 1-3; 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 the samples suggests that their association is not by chance (Somerfield 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; Somerfield and Clark 2013).

My 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 my density estimates must be made with the following considerations. First, the 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), these estimates are likely a conservative underestimate of true density. For example, Red Snapper were observed 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 I excluded density estimates from this site, the resulting mean Red Snapper density at artificial reefs (0.115 fish/m^2) was still 5.2 times greater than the density estimated at natural banks (0.022 fish/m^2). Second, 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, my 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 this estimate of 7.8 fold. 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, estimates appear low, and this may be attributable to the presence of nearby RTR structures at some of the 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. My estimates of Red Snapper density and subsequently total abundance at the five natural banks in this study suggest that at least 121,100 (likely more) Red Snapper inhabited these sites at the time of the survey (see Figure 1-5). Assuming the average weight of Red Snapper from natural banks in the study area (2.3 kg; estimated from fishery-independent vertical line surveys; M. K. 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 the survey was performed in 2012.

The 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^2 [Table 1] divided by the estimated natural reef habitat in northern GOM = 1578 km^2 [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^2), 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 this 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, due to a relatively small sample size and restricted geography, the estimates presented here should be interpreted with caution; 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. Future surveys could increase replication and geographic coverage of both natural and artificial reefs to gain better estimates across the northern Gulf of Mexico. While this study provides new information necessary for evaluating the effects of RTR artificial reefs in the western GOM compared to natural bank habitats, 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. 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.

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CHAPTER II:

A COMPARISON OF SIZE STRUCTURE AND AGE AND GROWTH OF RED SNAPPER (*Lutjanus campechanus*) AMONG ARTIFICIAL AND NATURAL HABITATS IN THE WESTERN GULF OF MEXICO

Abstract

Red Snapper support economically important fisheries in the Gulf of Mexico (GOM) and have been classified as overfished since the first stock assessment in 1988. Although the stock is now showing signs of recovery, management could benefit from a better understanding of regional or even habitat-level differences in stock demographics, as these dynamics ultimately determine overall stock 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, decommissioned platform artificial reefs, 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 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. This study

highlights the potential benefits of artificial reefs to Red Snapper and indicates that all habitats could contribute similarly to stock productivity on a per unit area basis.

Introduction

The Red Snapper (*Lutjanus campechanus*) 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-19th 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, I 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, I 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 2-1). 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 to many of the other shelf-edge banks in the Gulf (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 and maintain similar 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).

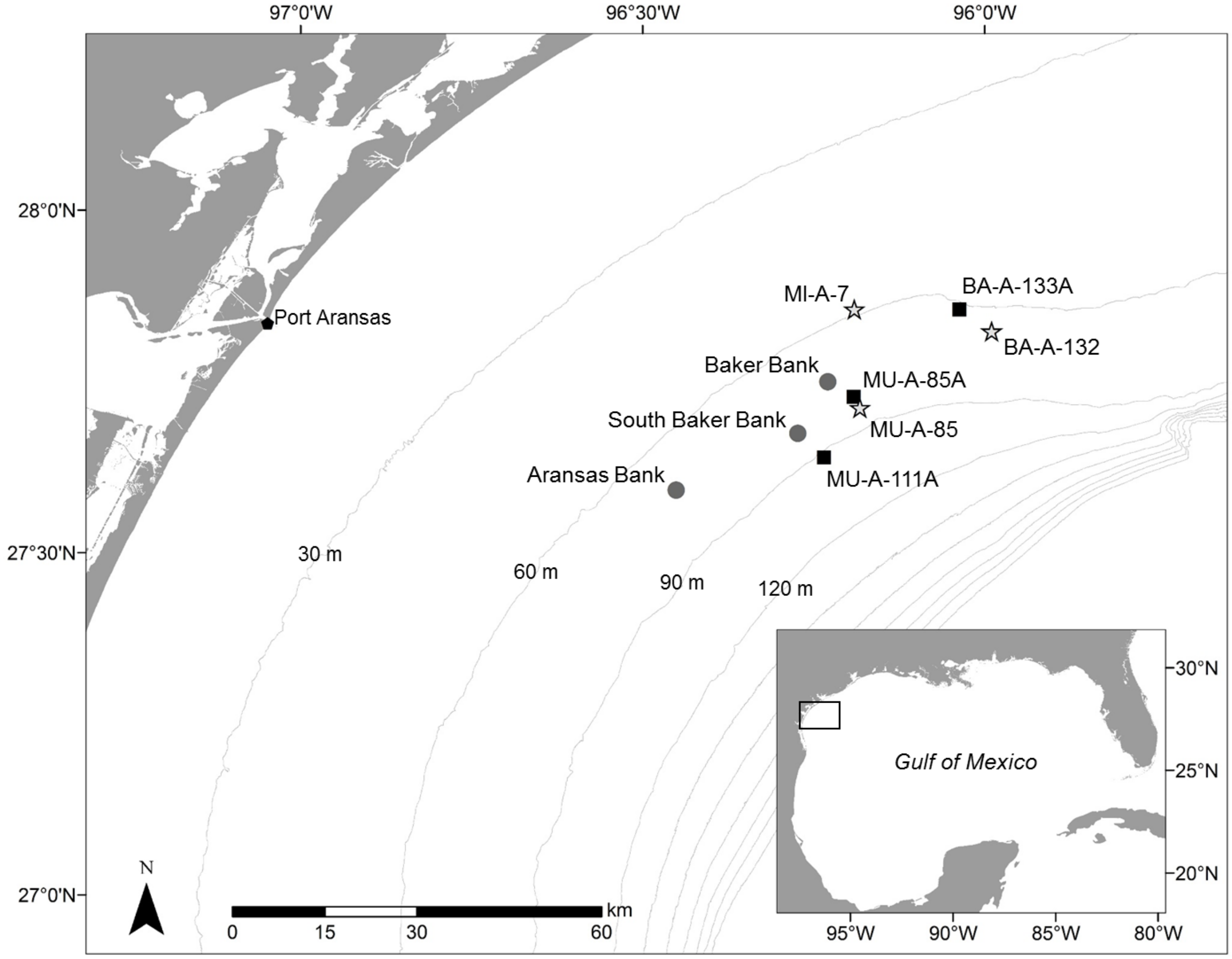

Figure 2-1. Map of the study area depicting locations of artificial reefs (stars), natural banks (circles), and standing platforms (black squares) that were sampled with fishery-independent vertical line surveys from 2012-2014. Gray contour lines represent relevant bathymetry within the study area (30-m isobaths), while the inset map shows the location of the study area relative to the Gulf of Mexico.

Methods

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. Three replicate sets (i.e., 3 drops of each hook size in each set; 9 drops total) were conducted 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^2 compared to ~ 1 km^2, 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^{-1}), 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, 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 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. Precision between readers was assessed using the average coefficient of variation (SD / mean × 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 30th had their age advanced one year if the section displayed a large translucent edge. For fish captured after June 30th, age was equal to the opaque annulus count. Thus, annual age cohorts were based on calendar year rather than time since spawning (Jerald 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:

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

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^{-1}), 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, I 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:

$$\mathrm{TW} = a\mathrm{TL}^{b},$$

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_∞ 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_∞ 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:

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

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

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:

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

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

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 ≤ 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_∞ between habitats) or two parameters (e.g., equal L_∞ and k between habitats) were similar between habitats were sequentially tested.

Results

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.

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 2-2A). 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 2-2A). 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 2-2B). 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 2-2B). 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 [1.80×10^{-8}, 2.64×10^{-8}]) and $b = 2.92$ (95% CI [2.89, 2.95]).

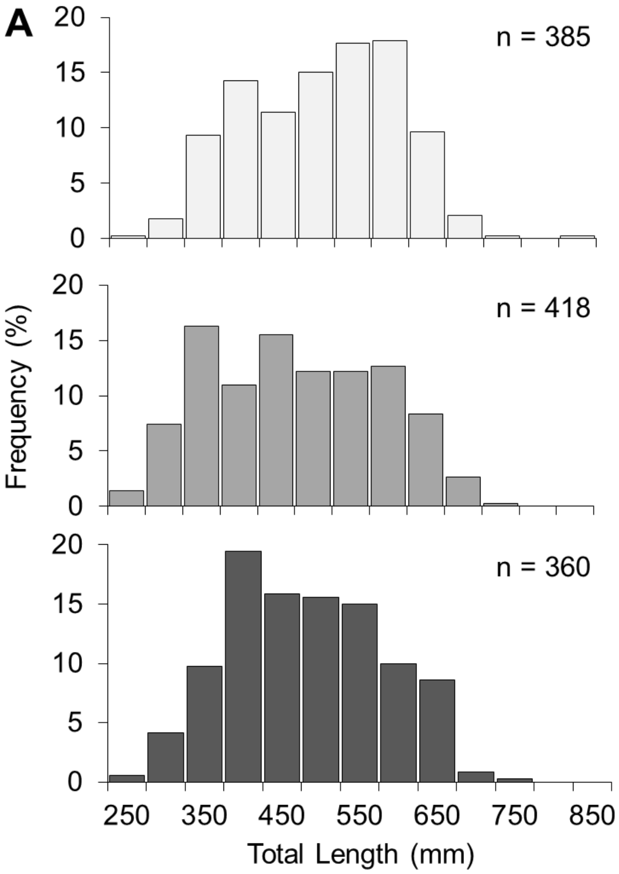

Figure 2-2. Length (A) and weight (B) frequencies of Red Snapper captured at natural banks (light gray), artificial reefs (gray), and standing platforms (dark gray) in the western Gulf of Mexico from 2012-2014. Length and weight frequencies are grouped into 50-mm bins and 0.5-kg bins, respectively (e.g., 350 = 350 – 399 mm TL).

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%. Visual assessment of an age-bias plot indicated no obvious bias between reader 1 and reader 2 age assignments. 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 3A). 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 3A). 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 2-3A). 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 2-3B). 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%).

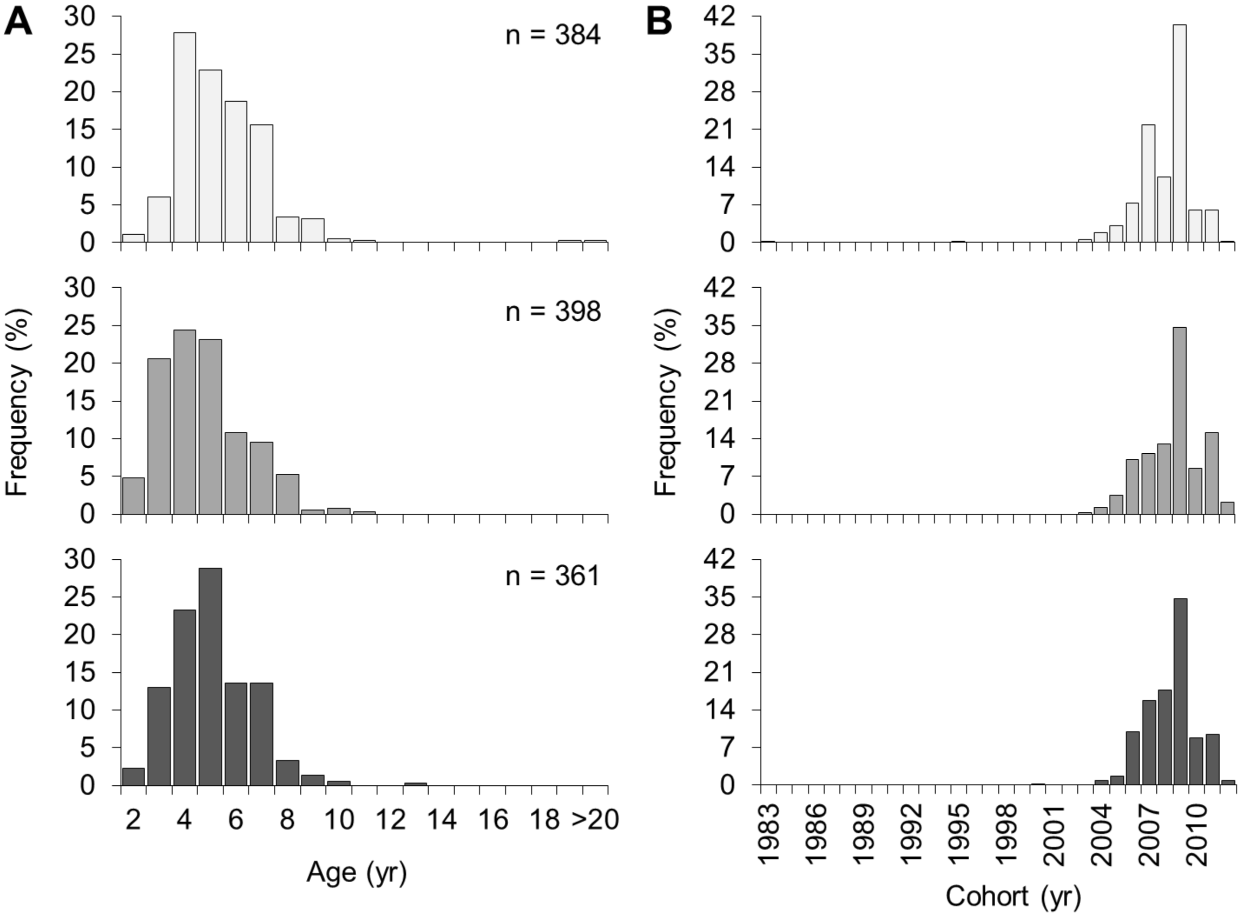

Figure 2-3. Histograms displaying age (A) and cohort (B) frequencies of Red Snapper captured with vertical lines at natural banks (green), artificial reefs (red) and standing platforms (blue) in the western Gulf of Mexico from 2012-2014. >20 includes all individuals age-20 or older.

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 2-1; Table 2-2). 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 2-1; Table 2-2). Based on AIC_c, the logistic model was selected to compare growth among habitats.

Table 2-1. 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_∞ = 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 (AIC$_c$), Akaike difference (Δ_i), and Akaike weights (w_i).

		L_∞	g	k	t_0	AICc	Δ_i	w_i
Artificial								
	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)	-			
Natural								
	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)			
Standing								
	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 2-2. 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_∞ = 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 (AIC$_c$), Akaike difference (Δ_i), and Akaike weights (w_i).

		W_∞	g	k	t_0	AICc	Δ_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 slow at a faster rate than artificial reefs (Figure 2-4A). There was no evidence that models differed between natural banks and standing platforms (Table 2-3). 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 2-3). Although no significant differences were found in subsequent likelihood ratio tests for equal parameters between artificial and natural banks, the smaller L_∞ 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_∞ for artificial reefs (Table 2-1). Between artificial reefs and standing platforms, the hypothesis of equal L_∞ and g parameters was rejected ($\chi^2 = 12.54$, $P = 0.002$; Table 2-3), suggesting separate L_∞ and g parameters were warranted. Similar to natural banks, the estimate of L_∞ for standing platforms (715.9 mm) was lower than estimated L_∞ for artificial reefs (761.7 mm) and was not contained in the 95% CI [719.8, 822.7].

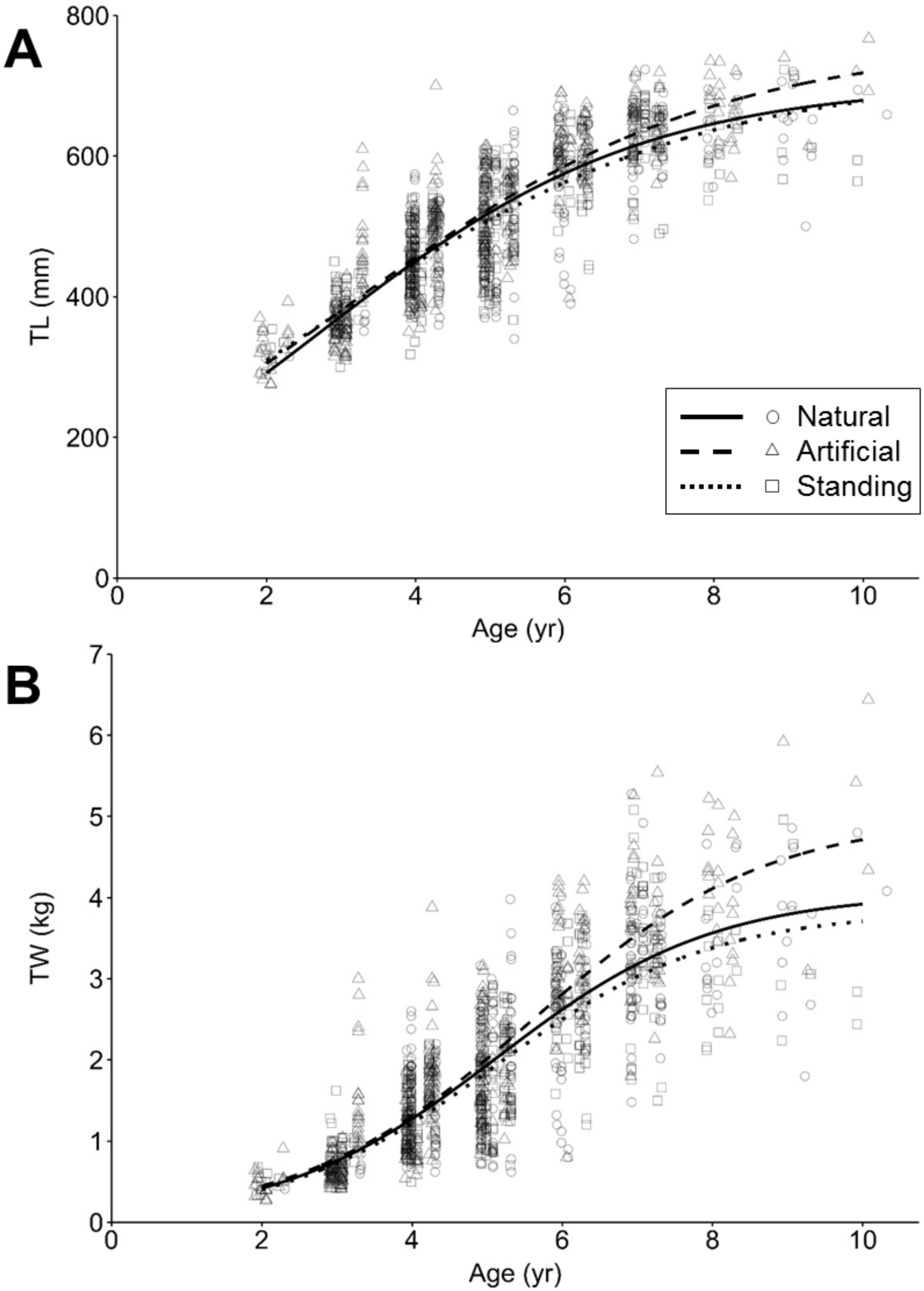

Figure 2-4. Logistic growth models of Red Snapper TL-at-age (A) and TW-at-age (B) data fitted separately by habitat type. Data are displayed for natural banks (circles and solid curve), artificial reefs (triangles and dashed curve), and standing platforms (squares and dotted line).

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 2-4B). 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 2-2; Table 2-3). 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 2-3). Likelihood ratio tests indicated that the W_∞ estimate for artificial reefs (4.99 kg) was significantly greater than W_∞ estimates for natural banks (4.05 kg) or standing platforms (3.83 kg; Table 2-3). Confidence intervals confirmed this difference as the 95% CI for W_∞ at artificial reefs did not overlap with 95% CIs for natural bank or standing platform W_∞ estimates (Table 2-2). The estimate for the t_0 parameter was not significantly different among habitats (i.e., $P = 0.083$ for artificial vs. natural and $P = 0.059$ for artificial vs. standing); however, the estimate for artificial reefs (5.61) was not contained within the 95% CIs for natural banks or standing platforms.

Table 2-3. 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 (α = 0.05) are denoted in bold.

Comparison	Null hypothesis	χ^2	df	*P*	Comparison	Null hypothesis	χ^2	df	*P*
	TL Models					**TW Models**			
Artificial vs.	Coincident curves	8.86	3	**0.031**	Artificial vs.	Coincident curves	26.62	3	**<0.001**
Natural	Equal L_∞	3.35	1	0.067	Natural	Equal W_∞	7.64	1	**0.006**
	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_∞ and g	5.18	2	0.075		Equal W_∞ and g	18.09	2	**<0.001**
	Equal L_∞ and t_0	3.35	2	0.187		Equal W_∞ and t_0	20.49	2	**<0.001**
	Equal g and t_0	2.22	2	0.330		Equal g and t_0	5.39	2	0.068
Artificial vs.	Coincident curves	22.18	3	**<0.001**	Artificial vs.	Coincident curves	22.18	3	**<0.001**
Standing	Equal L_∞	1.54	1	0.214	Standing	Equal W_∞	11.95	1	**<0.001**
	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_∞ and g	12.54	2	**0.002**		Equal W_∞ and g	28.49	2	**<0.001**
	Equal L_∞ and t_0	1.76	2	0.416		Equal W_∞ and t_0	43.86	2	**<0.001**
	Equal g and t_0	4.21	2	0.122		Equal g and t_0	6.21	2	**0.045**
Natural vs.	Coincident curves	5.47	3	0.140	Natural vs.	Coincident curves	5.37	3	0.146
Standing	Equal L_∞	-	-	-	Standing	Equal W_∞	-	-	-
	Equal g	-	-	-		Equal g	-	-	-
	Equal t_0	-	-	-		Equal t_0	-	-	-
	Equal L_∞ and g	-	-	-		Equal W_∞ and g	-	-	-
	Equal L_∞ and t_0	-	-	-		Equal W_∞ 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 among 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). My 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. I 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., ≥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 ≥550 mm TL compared to 36% at artificial reefs and 35% at standing platforms. These differences between studies may be influenced by the habitat types 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 coralgal 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 this 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.

This 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 this 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 this 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 likely 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 this study (Figure 3). 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, my 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, my analysis of site-to-site differences in Red Snapper mean TL, TW, and age among sites revealed that Baker Bank supported conspicuously more 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 my 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 this 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 sampled (1.33 km^2 compared to 0.31 – 0.50 km^2 at the other natural banks and $< 6.73 \times 10^{-3}$ km^2 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; Gervelis and Natanson 2013; Ainsley et al. 2014; Natanson et al. 2014; Dippold et al. 2016). In this study, I 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. My 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 this 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_∞ and W_∞) 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_∞ and W_∞ 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 these samples, parameter estimates derived from these growth curves should be interpreted with some 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_∞ and W_∞ 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 I 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 the above 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, this 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 the study 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, studies should increase the spatial coverage and replication at the habitat level (i.e., more sites per habitat) to better evaluate the patterns and hypotheses described here. This will aid in the determining the prevalence of unique sites (e.g., Baker Bank) and ultimately refine our understanding of how different habitats contribute to the maintenance of the GOM Red Snapper stock.

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CHAPTER III:

AN EVALUATION OF VERTICAL LINE GEAR PERFORMANCE AMONG ARTIFICIAL AND NATURAL HABITATS IN THE WESTERN GULF OF MEXICO WITH ADDITIONAL COMPARISONS FROM PAIRED UNDERWATER VIDEO

Abstract

Given the difficulty of sampling in deep marine environments, gear efficiency is often assumed to be constant over various conditions encountered during sampling; however, this assumption is rarely verified and has the potential to bias studies. To test these assumptions, I used fishery-independent vertical line surveys to evaluate whether gear efficiency and selectivity is similar while assessing reef fish populations at oil and gas platforms, artificial reefs, and natural banks in the western Gulf of Mexico. During the study, 192 vertical line sets were conducted with cameras placed on a subset of these deployments to validate any gear bias and efficiency among these habitat types. Red Snapper (*Lutjanus campechanus*) accounted for 2,033 (93%) of the catch. No difference in Red Snapper CPUE among habitats was detected. When evaluating fish size, 8/0 and 11/0 hooks sampled significantly larger Red Snapper at natural banks than artificial habitats, a finding likely attributable to a greater proportion of large fish at natural banks. While CPUE was similar among all hooks at standing platforms and artificial reefs, CPUE at natural banks was lower for shallower hooks and increased towards the bottom hooks along the vertical line backbone. At all three habitats, Red Snapper TL decreased from shallow to deep hook positions. Paired camera deployments revealed other factors affecting efficiency such as bait removal and depredation of the catch. Vermilion Snapper (*Rhomboplites aurorubens*) were effective at removing bait while avoiding capture. Perhaps related to this

observation, Red Snapper CPUE was negatively correlated with the Vermilion Snapper video index of abundance. Video confirmed gear saturation was prevalent (70% of deployments), occurring more frequently on artificial habitats. Furthermore, an interesting bias occurred, where the effective time fished was shorter at artificial habitats as the number of available baited hooks declined rapidly. Collectively, these results point towards higher relative abundance at artificial habitats; however, the prevalence of saturation indicates CPUE is likely not proportional to true abundance; thus these biases hinder the ability to detect differences at the scale examined in this study using vertical line. Vertical line surveys should evaluate the prevalence of saturation as inferences regarding relative abundance may be compromised when this information is unknown.

Introduction

For many exploited fish populations, stock assessments and management commonly rely on fishery-dependent data. However, such data can often be biased by fisher behavior (e.g., targeting of specific portions of the population), management regulations, and gear selectivity (Hilborn and Walters 1992). Fishery-independent sampling can control for some of these issues and efficiently provide indices of abundance and other biological data over a variety of spatial and temporal scales, which is critical for effective management (Yoccoz et al. 2001). However, fishery-independent methods may still suffer from the same inherent catchability and size selectivity biases because the gears used are often nearly identical to the gear used in the fishery (e.g., longlines, traps; Ellis and DeMartini 1995; Harvey et al. 2012; Santana-Garcon et al. 2014). Thus, evaluations of gear performance that can help to identify survey biases are needed, and if possible, should be conducted under a range of environmental conditions and at various habitats that may be encountered during sampling.

Fishery-independent surveys commonly supply indices of abundance that are derived from catch per unit effort (CPUE). The usefulness of these indices relies on the assumption that changes in CPUE reflect proportional changes in actual abundance (Hilborn and Walters 1992; Quinn and Deriso 1999). Furthermore, this approach assumes that gear efficiency (i.e., catchability) remains constant across space, time, habitat types, and environmental conditions, which is often not the case nor verified (Hilborn and Walters 1992; Rozas and Minello 1997; McAuley et al. 2007). Certain gears such as longlines may be particularly prone to violating this assumption, because efficiency declines as the number of hooks remaining unoccupied and baited declines during the soak time (Somerton and Kikkawa 1995). Identifying and accounting for such bias is crucial for estimating the relationship of the survey index with true population abundance; however, estimates of true population size are difficult to obtain. Nevertheless, with recent advances in remote monitoring (e.g., remote underwater video) and the use of paired gear comparisons, calibration and refinement of surveys designed to index abundance can be achieved (Rodgeveller et al. 2011; Bacheler et al. 2013a, 2014; Parker et al. 2016).

In the U.S. Gulf of Mexico (GOM), recent stock assessments for Red Snapper (*Lutjanus campechanus*) have recommended additional fishery-independent sampling to elucidate regional and sub-regional (e.g., habitat) differences in Red Snapper demographics (SEDAR 2013). Accordingly, a vertical line survey was recently developed to characterize the spatial and temporal distribution of commercially and recreationally important reef fish species (Gregalis et al. 2012; SEAMAP 2013). One particular goal of the survey includes generating an index of abundance for Red Snapper at both unstructured and structured (i.e., natural hard bottom and artificial structure) habitat types while also providing fishery-independent biological data on size structure, age, growth, and reproduction (Gregalis et al. 2012; SEAMAP 2013). While this gear is likely the most efficient to use under these conditions, there are nuances with gear efficiency and selectivity that can influence assessments. For example, Gregalis et al. (2012) evaluated the performance of vertical lines to sample reef fish at artificial (e.g., military tanks and reef pyramids) and unstructured habitats (i.e., bare substrate) off the coast of Alabama. They showed that peak catch rates occurred with five minute soak times and demonstrated the species selectivity of vertical lines using a paired remotely operated vehicle (ROV) survey. Vertical line hook size selectivity has also been estimated for Red Snapper and Vermilion Snapper (*Rhomboplites aurorubens*) at natural habitats in the GOM (Campbell et al. 2014). While these two studies have provided important information on the performance and selectivity of vertical lines, vertical line gear performance among habitat types remains unknown. This is particularly important given that the survey spans natural and artificial habitats—two habitats that can have dramatically different physical characteristics (e.g., vertical relief, habitat area). If vertical lines fish differently at one habitat than the other, data generated from the survey (i.e., CPUE index of abundance; size structure) may not be comparable across habitats. For example, because the gear fishes vertically in the water column, the efficiency or size selectivity of shallower hooks may be different at natural habitats given their greater distance from the structure.

The goal of this study was to evaluate the performance of vertical lines, following Southeast Area Monitoring and Assessment Program (SEAMAP) specifications, to survey Red Snapper at three ‘reef’ habitats commonly found over the western GOM shelf. While other studies using vertical line gear have uncovered important data concerning Red Snapper population dynamics, the aim with this work was provide information necessary for calibrating vertical line estimates of relative abundance. Given the previous work of Gregalis et al. (2012) and Campbell et al. (2014), I was specifically interested in testing the effects of hook size and hook position on the Red Snapper vertical line index of abundance (i.e., CPUE) and size among habitat types. Finally, I used paired video deployments to compare an alternative video-based index of abundance with the vertical line index of abundance, and also evaluate vertical line bias and efficiency between habitats.

Study Area

Vertical line surveys were conducted at natural banks, standing oil and gas platforms (hereafter "standing platforms"), and artificial reefs off the south Texas coast in the western GOM (Figure 3-1). With the exception of the structured habitats sampled in this study, the continental shelf in the region is dominated by open expanses of terrigenous sediments consisting of silt and clay muds and a low availability of natural hard substrates with vertical relief $\geq$1 m (Parker et al. 1983; Rezak et al. 1985). A persistent nepheloid layer of varying thickness covers the Texas continental shelf, likely influencing the ecology of these habitats (Shideler 1981; Rezak et al. 1985; Tunnell et al. 2009). Artificial reefs in this study were developed under the Texas Parks and Wildlife Department's Artificial Reef Program and consisted of decommissioned oil and gas structures (i.e., Rigs-to-Reefs structures) or Liberty ships (two sites). Natural banks in this study were part of a group of geomorphic features collectively known as the South Texas Banks (Rezak et al. 1985). Generally, the natural banks offered less vertical relief (mean = 15 m; range = 12-17 m) than either artificial reefs (mean = 22.8 m; range = 5-53 m) or the standing platforms, which extended from the water's surface to depth. In addition, the areal extent (i.e., footprint) of artificial reefs and standing platforms surveyed was much less than that of natural banks (~ 0.001 km^2 compared to ~ 0.75 km^2, respectively). Nevertheless, all of these habitat types are well-known to harbor large populations of Red Snapper.

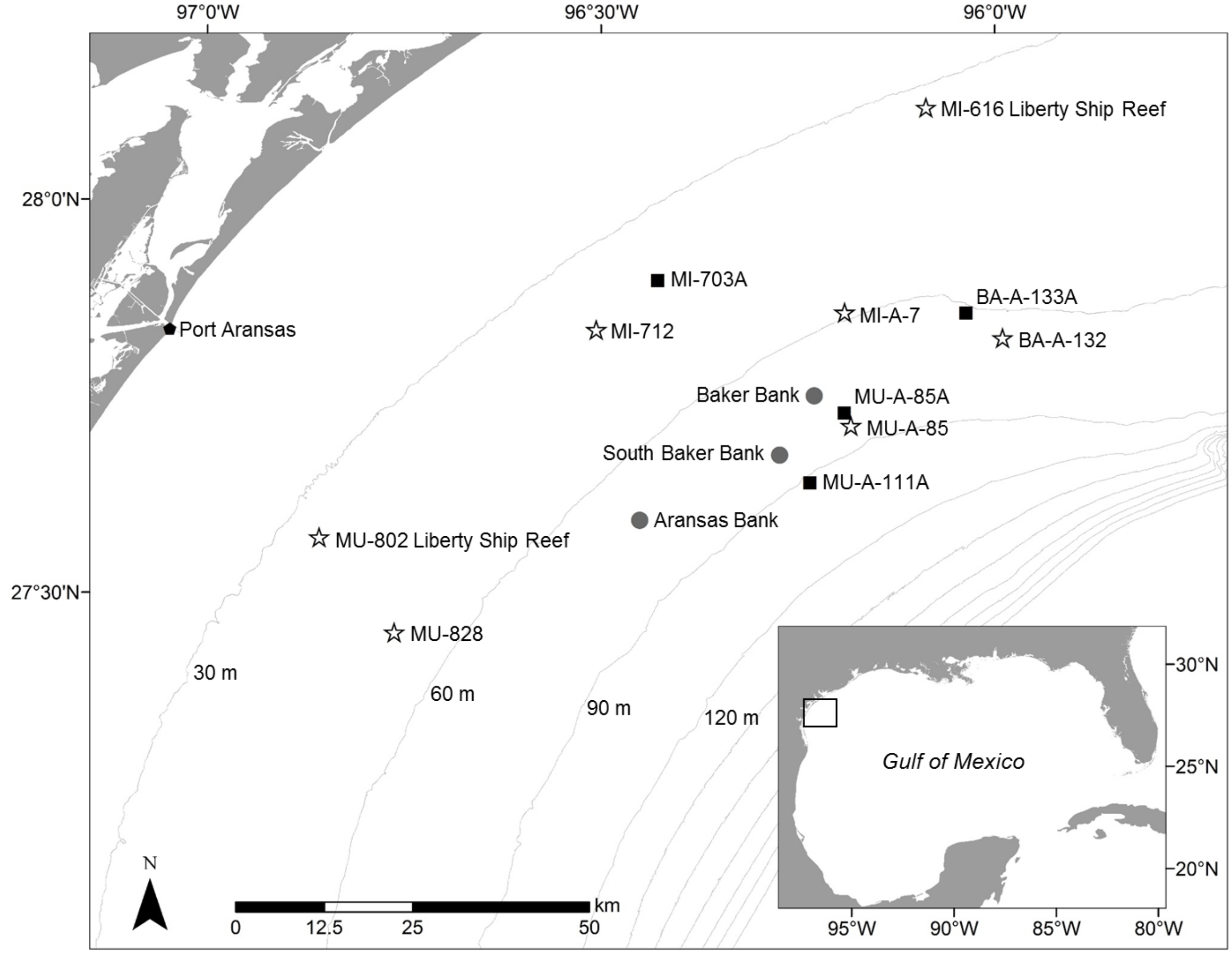

Figure 3-1. Locations of artificial reefs (stars), standing platforms (black squares), and natural banks (gray circles) surveyed with vertical longlines from 2012-2015 in the western Gulf of Mexico. Inset map displays study area within the Gulf of Mexico.

Methods

Sampling procedure.—Red Snapper were sampled with standardized vertical lines from October 2012 through August 2015. Vertical line gear followed specifications of 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 the side of the vessel and allowed to soak for 5 minutes. Hook sizes were then rotated in a random fashion, such that a different hook size was fished on the first, second, and third drop at a site. Three replicate sets were conducted 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, 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. Upon retrieval of the gear, the fate of each hook was recorded (e.g., fish, bait, no bait, no hook), and 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 other studies.

To further evaluate gear efficiency, a video camera (GoPro® Hero3+) was attached to random subset of vertical line deployments to estimate species frequency of occurrence, relative abundance, and record species interactions with the gear. The camera was attached to the terminal end of the mainline and faced downward towards the backbone (SEAMAP 2013). In the laboratory, video was downloaded from cameras and viewed by two independent viewers. Fish were identified to the lowest possible taxon, enumerated, and recorded each time they entered the field of view. Counts of the two viewers were compared and jointly reviewed only if the counts differed by >5%. For each survey, a MinCount was generated for each species that was observed during the five minute soak time. 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 abundance is widespread throughout the literature (Ellis and DeMartini 1995; Wells and Cowan 2007; Ajemian et al. 2015; Campbell et al. 2015). Video samples were excluded from further analyses if they were unreadable (e.g., too turbid, which was defined as being unable to see at least five hooks of the backbone). Hereafter, I refer to this paired dataset as vertical line-video data.

Data Analyses.—Catch per unit effort was calculated as the number of fish per hook per five minutes (fish·hook^{-1}·5 min^{-1}). Because the vertical line was deployed multiple times at a site, a linear regression was used to test for an effect of sequential deployments on CPUE at each habitat. To verify cameras had no effect on Red Snapper CPUE, Welch's *t*-test was used to compare CPUE from deployments with and without cameras. A nested ANOVA was used to test the interactive effects of hook size and habitat type on Red Snapper CPUE and total length (TL), with hook size (8/0, 11/0, 15/0), habitat (artificial, natural, standing), and their interaction as main effects. To account for variability among sites, site was nested within habitat. All data were assessed for normality and homogeneity of variance using normal probability plots and residual examination, and if necessary, were transformed prior to testing. If significant interactions were detected, post hoc ANOVAs were conducted to test the effect of each factor while holding the level of the other factor constant (e.g., testing hook size effect at natural habitats). Tukey's HSD was used if these post hoc ANOVAs detected significant effects of hook size or habitat. All tests were carried out using $\alpha = 0.05$.

To evaluate the possibility that physical differences in each habitat (e.g., immediate vertical relief) influence the performance of vertical lines, ANCOVA was used to test for a relationship between hook position (i.e., 1-10; shallow to deep) and mean Red Snapper CPUE or TL by habitat type. If vertical lines fished similarly at each habitat, I predicted that no patterns would exist in Red Snapper CPUE and TL by hook position (i.e., equal catchability per hook).

Using the vertical line-video data, I compared species frequency of occurrence and the Red Snapper video index of abundance (i.e., MinCount) between habitat types. Welch's *t*-test was used to test for differences in the mean Red Snapper video index of abundance between artificial reefs and natural banks. Interspecific interactions with the vertical line gear were also documented, and Pearson's correlation coefficient was used to assess association between Red Snapper CPUE and MinCounts of other species attracted to the vertical line. Because true abundance data were not available, I used the paired vertical line-video data to compare the Red Snapper video index of abundance (i.e., MinCount) to the vertical line index of abundance (i.e., CPUE). A linear relationship between the two indices was expected if they both indexed true abundance equally well (Bacheler et al. 2013b). To test whether the relationship between the two indices was linear or nonlinear, a linear model (log-transformed CPUE = b × log-transformed MinCount), a Beverton-Holt model (log-transformed CPUE = [a × log-transformed MinCount] / [b + log-transformed MinCount]), and an exponential model (log-transformed CPUE = $a^{\text{log-transformed MinCount}}$) were fit to the data for artificial reefs and natural banks. Akaike's information criterion (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989) was used to determine the best-fitting model for each habitat. The model with the lowest AIC_c indicated the best model; however, models within two AIC_c units of the best model were also considered to have strong support (Burnham and Anderson 2002). If the best-fitting model was the same for each habitat, a likelihood ratio test was used to determine if the relationship between indices could be described by a single curve (i.e., habitats pooled).

Longlines are prone to the effects of gear saturation (Beverton and Holt 1957; Somerton and Kikkawa 1995); therefore, I visually assessed if saturation occurred on each paired vertical line-video deployment of the gear. I considered saturation to occur if all 10 hooks were either occupied by a fish or no longer baited before the vertical line was retrieved. Fisher's exact test was used to determine if saturation occurred at equal frequencies at the two habitat types. Saturation (by the definition above) effectively reduced capture probability to zero; therefore, time of saturation was recorded and used to estimate the effective time fished for each deployment (i.e., effective time fished = saturation time – deployment start time). Welch's *t*-test was used to evaluate the null hypothesis of equal time fished between habitats. The time when the MinCount was observed for each deployment was also recorded and compared between habitats using Welch's *t*-test.

Results

Vertical line sampling.—Over the course of the study, 192 vertical line sets (573 backbones fished) were conducted, capturing 2,184 fish representing 20 species and 7 families. Red Snapper composed the vast majority of the catch (2,033 fish; 93.1% of catch; Table 3-1). Vermilion Snapper were the next most commonly captured species (3.6% of catch); none of the remaining species made up more than one percent of the catch. Red Snapper ranged in size from 251 to 855 mm TL, averaging 551 mm TL (SE = 6.9) at natural banks, 519 mm TL (SE = 5.8) at standing platforms, and 517 mm TL (SE = 6.3) at artificial reefs. Red Snapper CPUE averaged 0.355 fish·hook^{-1}·5 min^{-1} during the study. There was no evidence of enhanced catch with sequential deployments of the gear at artificial reefs (t = -0.20, df = 225, P = 0.843), natural banks (t = 0.88, df = 169, P = 0.380), or standing platforms (t = 0.73, df = 173, P = 0.466). Cameras were affixed to 166 backbones fished during the study. There was no evidence that camera presence affected Red Snapper CPUE (t = 0.59, df = 316, P = 0.556).

There was no evidence of an interactive effect of habitat and hook size on Red Snapper CPUE ($F_{4, 553}$ = 1.82, P = 0.123), indicating that the effect of hook size on CPUE was similar among habitat types. While mean CPUE was greater at artificial reefs (mean = 0.400 fish·hook^{-1}·5 min^{-1}; SE = 0.04) and standing platforms (mean = 0.367 fish·hook^{-1}·5 min^{-1}; SE = 0.05) than natural banks (mean = 0.293 fish·hook^{-1}·5 min^{-1}; SE = 0.06), these differences were not significant ($F_{2, 11}$ = 1.17, P = 0.347). Hook size did have an effect on Red Snapper CPUE ($F_{2, 553}$ = 10.58, P < 0.001), with 11/0 hooks having greater catch rates than either 8/0 or 15/0 hooks. Both habitat and hook size influenced Red Snapper TL but not in an additive fashion as their interaction was significant ($F_{4, 454}$ = 3.04, P = 0.017). Post hoc ANOVAs suggested that the effect of habitat was significant for the 8/0 hook ($F_{2, 149}$ = 7.09, P = 0.001) and 11/0 hook ($F_{2, 164}$

= 6.62, $P = 0.002$), but not for the 15/0 hook ($F_{2,\,152} = 2.07$, $P = 0.130$). The 8/0 hook sampled significantly smaller Red Snapper at artificial reefs (mean = 462 mm TL; SE = 9.8) than natural banks (mean = 522 mm TL; SE = 12.5), while the 11/0 hook sampled larger individuals at natural banks (mean = 556 mm TL; SE = 10.5) than either artificial reefs (mean = 510 mm TL; SE = 8.4) or standing platforms (mean = 515 mm TL; SE = 9.6; Figure 3-2).

Table 3-1. Species composition of vertical line catch by habitat type for surveys conducted off the Texas coast from 2012-2015. Total catch is sorted in decreasing order of abundance. Bold numbers below column headings denote number of sets (i.e., effort).

Species	Artificial	Standing	Natural	Total catch
	76	**59**	**57**	**192**
Red Snapper *Lutjanus campechanus*	904	621	508	2033
Vermilion Snapper *Rhomboplites aurorubens*	33	13	33	79
Almaco Jack *Seriola rivoliana*	5	14	2	21
Gray Triggerfish *Balistes capriscus*	15	3	−	18
Greater Amberjack *Seriola dumerili*	4	1	3	8
Blue Runner *Caranx crysos*	1	−	5	6
Warsaw Grouper *Hyporthodus nigritus*	1	3	−	4
African Pompano *Alectis ciliaris*	1	2	−	3
Gray Snapper *Lutjanus griseus*	2	−	−	2
Scamp *Mycteroperca phenax*	−	2	−	2
Cobia *Rachycentron canadum*	1	−	−	1
Gag *Mycteroperca microlepis*	−	1	−	1
Graysby *Cephalopholis cruentata*	−	1	−	1
Lane Snapper *Lutjanus synagris*	1	−	−	1
Pinfish *Lagodon rhomboides*	−	1	−	1
Red Hind *Epinephelus guttatus*	−	1	−	1
Rock Hind *Epinephelus adscensionis*	1	−	−	1
Silky Shark *Carcharhinus falciformis*	−	1	−	1

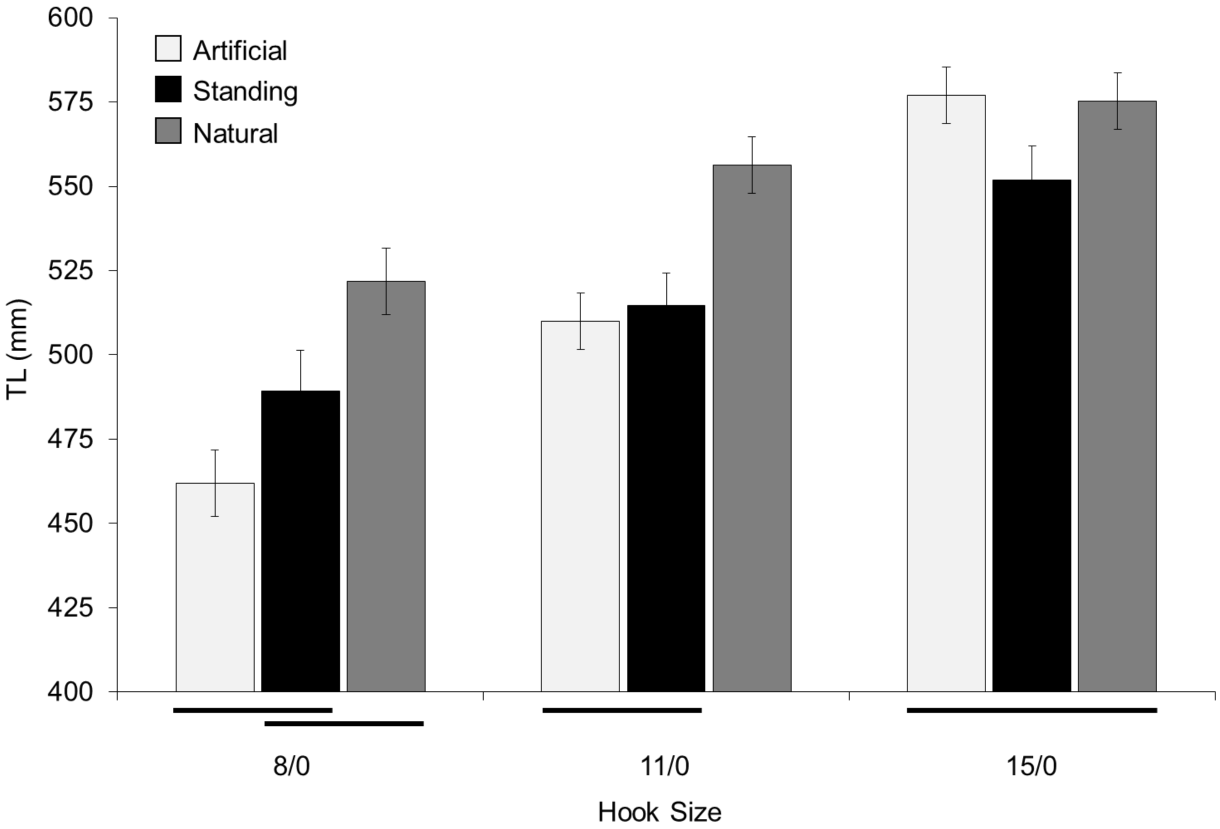

Figure 3-2. Mean TL (mm) ± 1 SE of Red Snapper captured with vertical lines in the western GOM from 2012-2015. Means are plotted by hook size and habitat type. Within each hook size, means that do not share a black horizontal bar are significantly different ($\alpha = 0.05$).

Analysis of mean Red Snapper CPUE by hook position suggested marginal evidence of different efficiencies by habitat type (ANCOVA slopes: $F_{2, 24} = 3.05$, $P = 0.066$). There was no relationship between CPUE and hook position at artificial reefs ($t = 0.63$, df = 8, $P = 0.547$) or standing platforms ($t = 0.37$, df = 8, $P = 0.719$); however, a significant relationship was evident at natural habitat ($R^2 = 0.62$, $t = 3.62$, df = 8, $P = 0.007$), with CPUE increasing from the top to bottom hook position (i.e., shallow to deep along the backbone; Figure 3-3A). Red Snapper mean TL by hook position also varied by habitat type (ANCOVA slopes: $F_{2, 24} = 5.20$, $P = 0.013$). At all three habitat types, mean TL was greatest at the shallowest hook positions and declined towards the deeper hook positions along the backbone (Figure 3-3B). This relationship was not significant at natural habitats (*t* = -1.92, df = 8, *P* = 0.091); however, mean TL significantly decreased from shallow to deep hook positions at artificial reefs (R^2 = 0.91, *t* = -9.09, df = 8, *P* < 0.001) and standing platforms (R^2 = 0.92, *t* = -9.26, df = 8, *P* < 0.001).

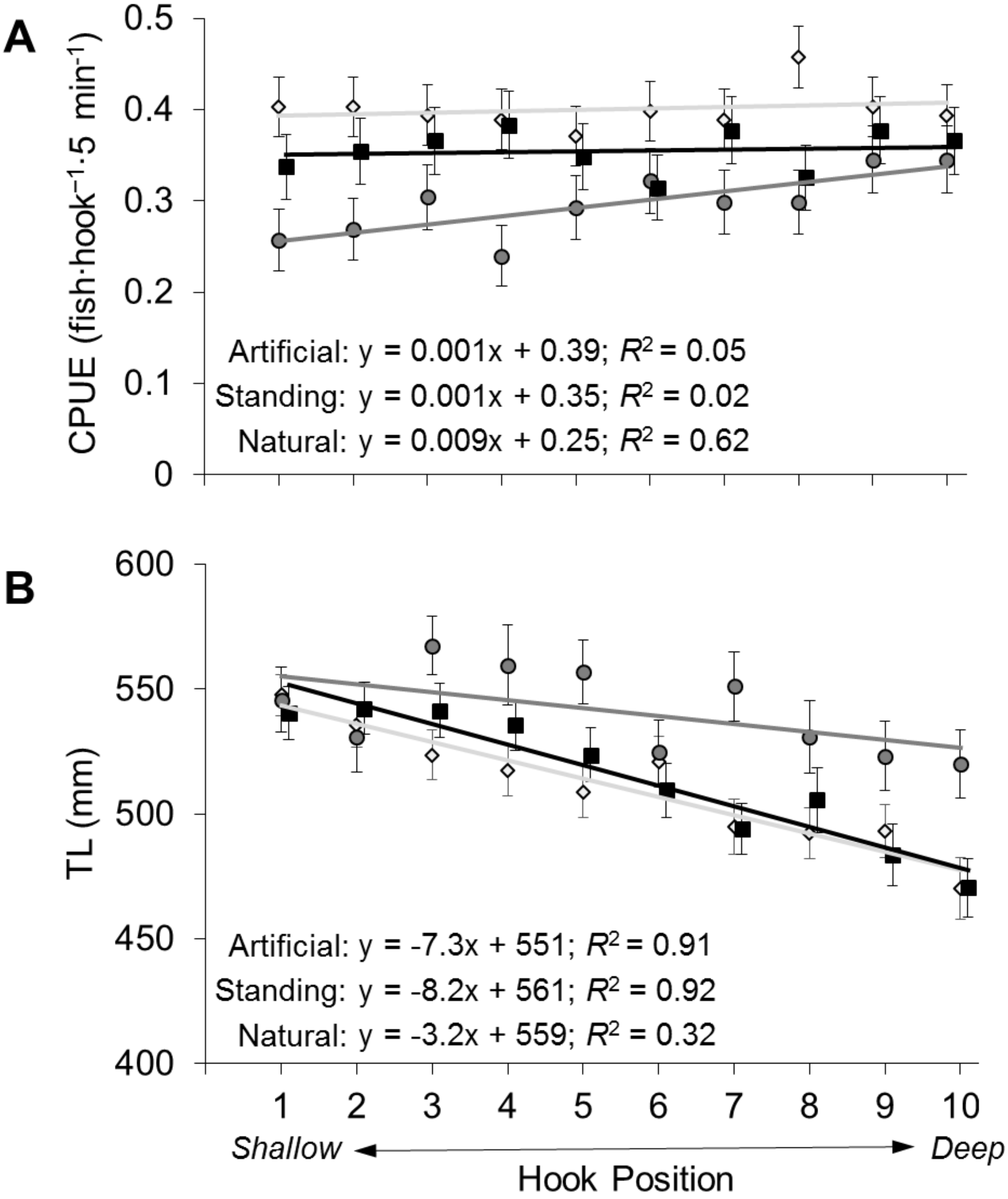

Figure 3-3. Plots of (A) mean Red Snapper CPUE (fish·hook^{-1}·5 min^{-1}) and (B) TL (mm) by hook position along the backbone of vertical lines fished in the western GOM. Data are plotted separately for artificial reefs (light diamonds), standing platforms (black squares), and natural banks (gray circles). Error bars represent ± 1 SE.

Paired vertical line-video deployments.—Of the 166 paired vertical line-video deployments, 108 (65%) were not useable primarily due to high turbidity. Only five useable vertical line-video deployments were available from standing platforms, and I included these samples in the artificial reef group after determining there was no difference in Red Snapper mean CPUE or MinCount between these two habitats (Welch's *t*-test, $P < 0.05$). Thus, useable vertical line-video deployments were divided fairly evenly between natural (n = 31) and artificial habitats (n = 27). The use of paired video permitted identification of 21 species on artificial reefs and 12 species at natural banks (Table 3-2). Of these, only Red Snapper, Vermilion Snapper, and Greater Amberjack (*Seriola dumerili*), and Gray Triggerfish (*Balistes capriscus*) were captured on vertical lines. Video identified 22 additional species that were not captured on vertical lines. With the exception of Red Snapper on artificial reefs, which were seen and captured on all 27 deployments, species frequency of occurrence was greater on video. For example, Vermilion Snapper were observed on 74% of the vertical line deployments at artificial habitats and 52% of the deployments at natural banks, but were only captured on 11% and 16% of these deployments, respectively. The Red Snapper video index of abundance was significantly greater on artificial reefs than natural banks ($t = 2.45$, df = 40.9, $P = 0.018$). MinCounts averaged 22.4 (SE = 3.7) at artificial reefs and 11.9 (SE = 2.1) at natural banks. MinCounts as high as 89 on artificial and 52 on natural habitats were recorded.

Table 3-2. Frequency of occurrence (FO) for species either captured on vertical lines or seen on video at artificial reefs and natural banks off the Texas coast, 2012-2015. Species are sorted in order of decreasing video FO. Sample sizes for each habitat indicate the number of paired vertical line-video deployments.

Species	Video FO (FO %)	Vertical line FO (FO %)
Artificial (n = 27)		
Red Snapper *Lutjanus campechanus*	27 (100)	27 (100)
Vermilion Snapper *Rhomboplites aurorubens*	20 (74)	3 (11)
Greater Amberjack *Seriola dumerili*	16 (59)	
Almaco Jack *Seriola rivoliana*	13 (48)	
Gray Triggerfish *Balistes capriscus*	9 (33)	1 (4)
Great Barracuda *Sphyraena barracuda*	6 (22)	
Lookdown *Selene vomer*	3 (11)	
Sandbar Shark *Carcharhinus plumbeus*	3 (11)	
Spotfin Hogfish *Bodianus pulchellus*	3 (11)	
Blue Runner *Caranx crysos*	2 (7)	
Crevalle Jack *Caranx hippos*	2 (7)	
Gray Snapper *Lutjanus griseus*	2 (7)	
Rainbow Runner *Elagatis bipinnulata*	2 (7)	
Scamp *Mycteroperca phenax*	2 (7)	
Spanish Hogish *Bodianus rufus*	2 (7)	
Spinner Shark *Carcharhinus brevipinna*	2 (7)	
Warsaw Grouper *Hyporthodus nigritus*	2 (7)	
African Pompano *Alectis ciliaris*	1 (4)	
Bermuda Chub *Kyphosus saltatrix*	1 (4)	
Blacktip Shark *Carcharhinus limbatus*	1 (4)	
Cobia *Rachycentron canadum*	1 (4)	
Natural (n = 31)		
Red Snapper *Lutjanus campechanus*	29 (94)	21 (68)
Greater Amberjack *Seriola dumerili*	18 (58)	1 (3)
Vermilion Snapper *Rhomboplites aurorubens*	16 (52)	5 (16)
Sandbar Shark *Carcharhinus plumbeus*	9 (29)	
Black Grouper *Mycteroperca bonaci*	8 (26)	
Almaco Jack *Seriola rivoliana*	3 (10)	
Scamp *Mycteroperca phenax*	2 (6)	
Sharksucker *Echeneis naucrates*	2 (6)	
Bar Jack *Caranx ruber*	1 (3)	
Blue Angelfish *Holacanthus bermudensis*	1 (3)	
Cobia *Rachycentron canadum*	1 (3)	
Crevalle Jack *Caranx hippos*	1 (3)	

Several species interactions with the vertical line were observed on video including bait removal, depredation events, and hooked fish escaping after initial capture. Video observations suggested that large groups of Vermilion Snapper (MinCounts up to 76) and Gray Triggerfish (to a lesser extent due to their lower frequency of occurrence) were effective at removing bait from hooks while avoiding capture. When Vermilion Snapper were observed on video (n = 36), there was moderate, but significant ($r = -0.51$, $P = 0.002$), negative correlation between Vermilion Snapper MinCount and Red Snapper CPUE (Figure 3-4A). There was also a weak negative correlation ($r = -0.35$, $P = 0.036$) between the Vermilion Snapper MinCount and Red Snapper MinCount during these deployments (Figure 3-4B). Of all hooks fished during this study (5,730 hooks), 40% returned without bait, and no bait was observed falling off the hook during the paired video deployments. Depredation of captured individuals was observed on 19% (11 of 58) of all paired video deployments, with 19 individual depredation events observed (i.e., multiple depredation events occurred during some deployments). Predators of the vertical line catch included Great Barracuda (*Sphyraena barracuda*; 2 events), Greater Amberjack (8 events), Sandbar Shark (*Carcharhinus plumbeus*; 8 events), and Warsaw Grouper (*Hyporthodus nigritus*; 1 event). Depredation of the catch occurred more frequently at artificial habitats (33% [9 of 27] of deployments) than natural habitats (6% [2 of 31] of deployments). Greater Amberjack most commonly preyed upon Vermilion Snapper (7 of 8 events), while Sandbar Sharks exclusively preyed upon Red Snapper (8 of 8 events). In total, depredation of captured Red Snapper was observed on 10% (6 of 58) gear deployments and more frequently at artificial habitats (19% [5 of 27] of deployments) than natural habitats (3% [1 of 31] of deployments). Generally, predators removed the entire fish from the gangion. Only four Red Snapper were observed escaping from hooks after initially being captured, indicating escapement from the vertical line was minimal.

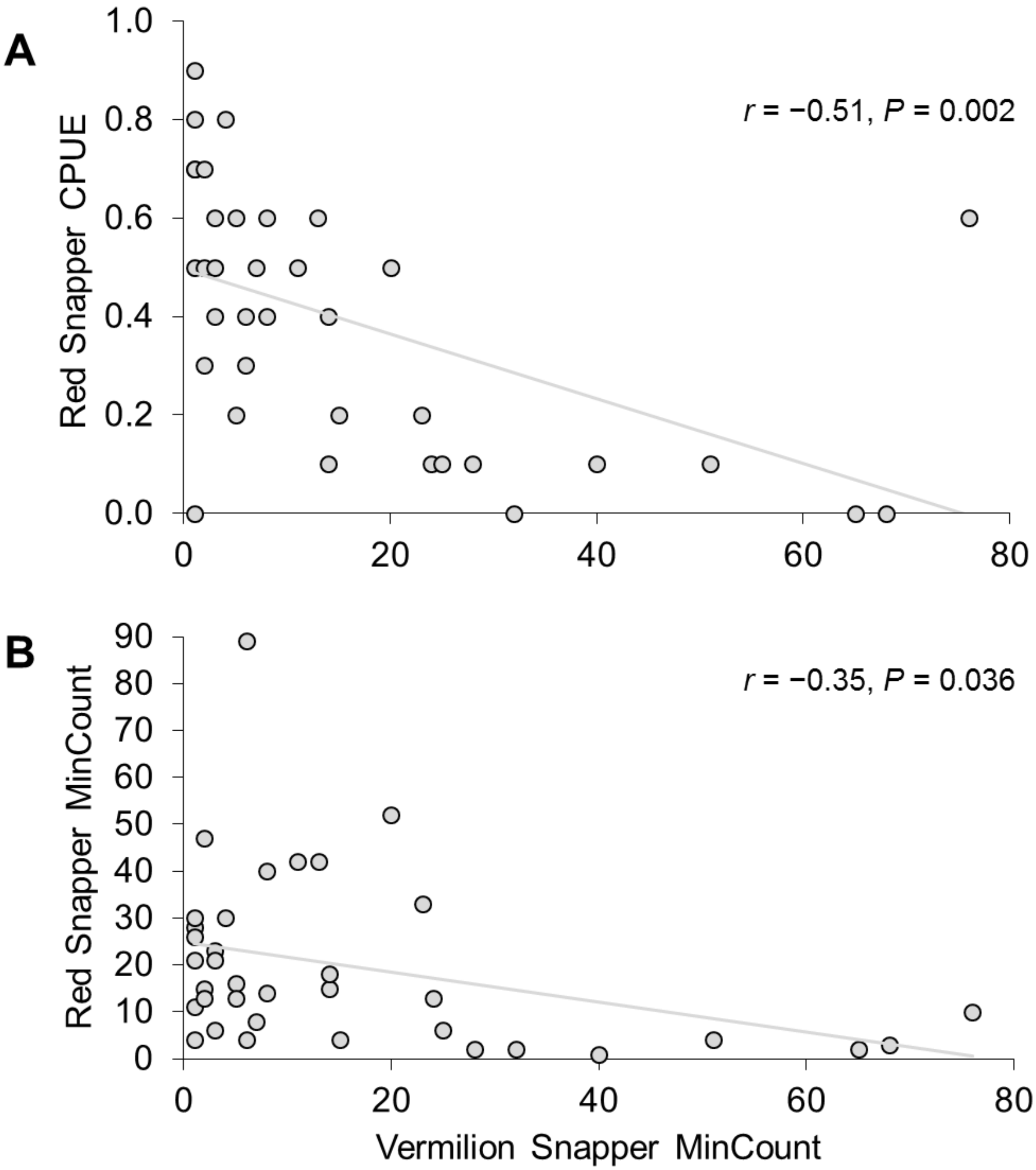

Figure 3-4. Scatterplots depicting the negative correlation between (A) Vermilion Snapper MinCount and Red Snapper CPUE (fish·hook^{-1}·5 min^{-1}) and (B) Vermilion Snapper MinCount and Red Snapper MinCount. Best-fit line depicting negative association between variables is shown in gray.

Comparison of the Red Snapper log-transformed video index of abundance and log-transformed vertical line index of abundance indicated a positive relationship. The linear model best fit the data for artificial reefs ($t = 18.11$, df = 26, $P < 0.001$), although evidence for the Beverton-Holt model was strong as well (Table 3-3). Similarly, a linear model best fit the data for natural banks. While the slope for artificial reefs ($b = 0.54$) was greater than the estimate for natural banks ($b = 0.47$), 95% confidence intervals for these estimates overlapped (Figure 3-5). The likelihood ratio test confirmed the slope estimates were not significantly different ($\chi^2 = 1.80$, df = 1, $P = 0.179$).

Table 3-3. Models fit to assess relationship of Red Snapper log-transformed video index of abundance and log-transformed vertical line index of abundance. K = number of estimated parameters; AICc = Akaike's information criterion with small sample bias adjustment; ΔAICc = AICc difference; w_i = Akaike weight.

Model	Log likelihood	K	AICc	ΔAICc	w_i
Artificial					
Linear	-16.8	2	38.1	0.0	0.62
Beverton-Holt	-16.0	3	39.1	1.0	0.38
Exponential	-22.0	2	48.4	10.3	0.00
Natural					
Linear	-26.6	2	57.7	0.0	0.60
Exponential	-27.6	2	59.7	1.9	0.23
Beverton-Holt	-26.6	3	60.2	2.5	0.18

Paired vertical line-video deployments suggested that gear saturation was prevalent at both habitats. In total, vertical lines became saturated on 70% (41 of 58) of the deployments. Saturation occurred as quickly as 15 s at artificial reefs and 18 s at natural banks, and time to saturation was similar between habitats (1.3 and 1.6 min, respectively). Frequency of gear saturation differed between habitats (Fisher's exact test, *P* = 0.041), with saturation estimated to occur more often at artificial reefs (85% [23 of 27] of deployments) than natural banks (58% [18 of 31] of deployments). Effective time fished also differed between habitats (*t* = -2.5385, df = 56, *P* = 0.014), averaging 1.9 min (SE = 0.33) at artificial reefs and 3.1 min (SE = 0.36) at natural banks. Red Snapper MinCounts were observed at similar times into the soak (*t* = 0.88, df = 52.7, *P* = 0.384), averaging 2.5 min into the soak at artificial reefs and 2.2 min at natural banks.

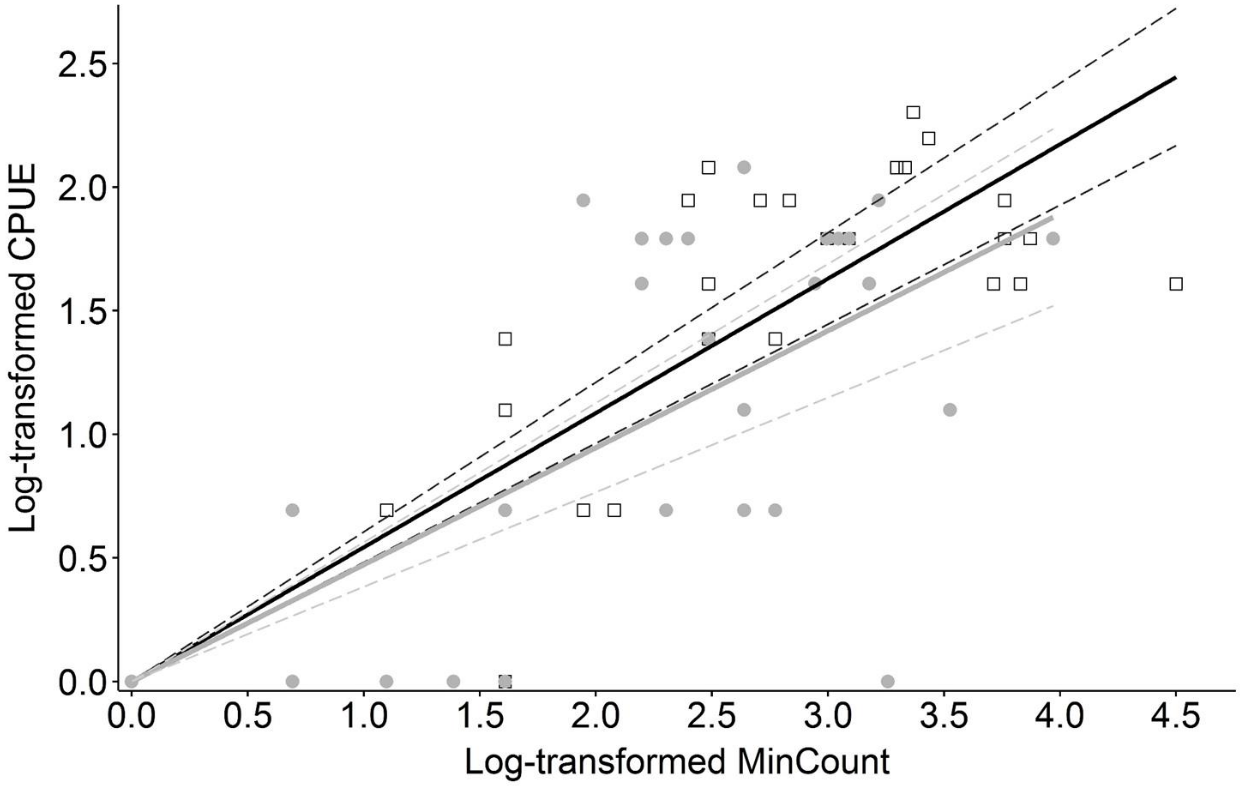

Figure 3-5. Log-transformed CPUE (fish·10 hooks^{-1}·5 min^{-1}) versus log-transformed MinCount for Red Snapper at artificial (black line and open squares) and natural habitats (gray line and circles). The corresponding dashed lines for each habitat indicate 95% confidence limits for the slope estimate.

Discussion

Gear efficiency usually varies among habitat types (Rozas and Minello 1997; Wells et al. 2008); therefore, comparisons of gear performance among various habitats a survey is likely to encounter are essential for understanding the habitat-specific biases of a gear to make accurate assessments. Knowledge of these biases is necessary for interpreting observed trends and making accurate inferences regarding the population of interest. In this study, I evaluated the performance of standardized SEAMAP vertical line gear to sample Red Snapper at artificial reefs, standing platforms, and natural banks through traditional catch-based comparisons and via the use of a paired camera survey. My results indicate several differences in gear performance that could affect inferences regarding relative abundance and size structure of Red Snapper inhabiting these habitats. Most notably, the use of paired video showed that gear saturation was prevalent on most (70%) of the vertical line deployments. Thus, caution should be applied when using vertical line CPUE to compare relative abundance of Red Snapper among the habitats sampled in this study, and especially with those where fish occur in lower abundance.

Catch based comparisons suggested no interactive effects of hook size and habitat on Red Snapper CPUE, suggesting similar catch efficiencies for each hook size regardless of habitat type. In contrast, the effect of habitat type on Red Snapper size differed depending on the hook size fished. Specifically, mean Red Snapper TL was significantly lower at artificial reefs than natural banks for the 8/0 hook and 11/0 hook but not for the 15/0 hook. Circle hook size does influence size selectivity; however, selectivity curves are broad, and small hooks can sample the large fish (Patterson et al. 2012; Campbell et al. 2014). This was particularly evident for the 8/0 hook, which sampled fish at natural banks that were on average 60 mm larger than fish at artificial reefs. Furthermore, the 8/0 hook sampled larger fish at natural banks than the 11/0 hook sampled at either of the artificial habitats. Given a similar size distribution of fish at two theoretical habitats, one would expect that the same size hook would sample the same size fish. Thus, a plausible explanation for the differences in this study is that natural banks support greater proportions of large fish than artificial habitats in the region (Chapter 2), which serves to increase the mean TL sampled by 8/0 and 11/0 hooks. This also implies that studies examining hook size selectivity could be biased depending on the number of fish collected among various habitat types.

My observation of differing trends in mean CPUE and TL by hook position (i.e., height along backbone) suggest differences is gear efficiency and potentially selectivity among habitats. No trends in CPUE by hook position should be evident if each hook fished on a backbone has similar efficiency (i.e., equal CPUE per hook position). This pattern was observed at artificial reefs and standing platforms; however, at natural banks CPUE tended to be lower for the shallower hooks. This implies that these hooks were less efficient at capturing Red Snapper than hooks near the bottom of the backbone. An assumption of any survey gear is equal or constant efficiency among survey conditions (Hilborn and Walters 1992); therefore, the observed trend at natural habitats, but not at artificial habitats, may invalidate this assumption and would likely result in underestimation of relative abundance at natural habitats. Understanding why these patterns in catch rates and size exist was beyond the scope of this study; however, given that numerous studies have demonstrated the importance of predation and the availability of refuges in structuring fish habitat use (e.g., Werner et al. 1983; Lima and Dill 1990; Hixon and Beets 1993), I hypothesize that differences in the immediate vertical relief at each habitat and relative predation risk may have played a role. For example, while natural banks in this study had relief up to 17 m, this relief was spread over a much larger area than the relief at artificial reefs. As a result, the immediate relief in the vicinity of a backbone fished at a natural bank was quite low (<2 m) compared to a backbone that was fished at an artificial reef or standing platform (with relief spanning the entire length of backbone). Thus, the lower CPUE at natural banks may be function of fish tending to avoid the more open water where the shallow hooks fished and instead stay toward the structure provided near the bottom. A similar mechanism may explain the increase in TL towards the top of the backbone (i.e., larger fish more likely to forage away from benthic substrate) at all habitats. Regardless, future investigations into trends in catchability and selectivity by habitat type and depth are warranted.

While previous studies have suggested that Red Snapper densities are greater at artificial habitats than either bare substrate or natural reef habitats (Wilson et al. 2006; Patterson et al. 2014; Streich et al., in press), vertical line CPUE from this study suggested no differences in relative abundance among habitats. Although this could indicate that true densities are not different among the habitats sampled here, the use of paired video indicated that saturation occurred more frequently at artificial habitats. Gear saturation often occurs when the true density of fish is so high that the number of effective hooks (i.e., baited and unoccupied) approaches zero before the gear is retrieved. At such high abundances, CPUE becomes an insensitive indicator of true abundance (Ricker 1975; Robinson et al. 2015). In addition to a higher frequency of saturation at artificial habitats, the effective time fished was less at artificial habitats, suggesting that effort (5 min) was overestimated more often at artificial habitats. Furthermore, the Red Snapper video index of abundance was greater at artificial reefs and MinCounts up to 89 were observed around a single backbone. While vertical line saturation also occurred at natural banks, these data suggest that CPUE was underestimated more frequently (and more severely given the differences in time fished) at artificial habitats. As such, the ability to detect differences in relative abundance among habitat types using vertical line CPUE was severely impaired.

The addition of cameras to a subset of vertical line deployments in this study provided a better characterization of the fish community attracted to vertical lines as well as information on species selectivity that would not have been possible based on vertical line catch alone. While only three species were captured on vertical lines at each habitat type, video data showed that many additional species were attracted to the gear. Frequency of occurrence for all species was higher on video, consistent with previous studies employing paired video techniques (Harvey et al. 2012; Bacheler et al. 2013a). While Red Snapper were frequently observed on video and also captured, other species like Vermilion Snapper were captured far less frequently than they were observed—a likely artifact of hook size selectivity (Campbell et al. 2014) or gear avoidance. In addition, other important species groups such as groupers were never captured on the vertical line-video deployments despite being observed on video. Gears that reduce the frequency of zero catches generally allow for an index of abundance with reduced variability, which is more desirable for stock assessment purposes (Maunder and Punt 2004). Thus, while vertical lines can generate a useful index of abundance for Red Snapper (Gregalis et al. 2012), a video-based index, or at least one calibrated with similar video-based methods may be more suitable when determining indices of abundance for these other important species that are often present, but not sampled with vertical line gear.

Other aspects of gear performance such as bait loss and interspecific interactions with the gear would also have gone overlooked without the use of video. The negative correlation between Vermilion Snapper MinCount and Red Snapper CPUE is a concern if the goal of the vertical line survey is to generate an index of abundance for Red Snapper. Hook competition occurs when several species attack the gear such that the CPUE of one species is reduced by the catch of the other (Rothschild 1967; Rodgveller et al. 2008). While not hook competition per se, given that Vermilion Snapper were rarely captured, Vermilion Snapper had a relatively high frequency of occurrence (52-74% depending on habitat), and video documented their effectiveness in removing bait from hooks. Thus, vertical line efficiency may be substantially reduced in areas with high Vermilion Snapper abundance. The negative correlation between Vermilion Snapper MinCount and Red Snapper MinCount suggests that fewer Red Snapper are present when Vermilion Snapper are abundant, which could also contribute to lower Red Snapper CPUE. Nevertheless, the observation of no bait falling off hooks supports the notion that bait removal by Red Snapper and other species like Vermilion Snapper is an important contributor to depressed Red Snapper CPUE. Depredation of longline catch may also substantially affect CPUE estimates (Ward et al. 2004). In this study, vertical-line video data revealed depredation occurred on nearly 20% of the deployments and showed prey selectivity of some predators (e.g., Greater Amberjack on Vermilion Snapper; Sandbar Shark on Red Snapper). Sandbar Sharks were identified as a primary predator of captured Red Snapper and usually removed the entire fish from the gangion, suggesting that depredation may be underestimated on deck. Depredation was also likely underestimated on video because of the visibility constraints imposed by the nepheloid layer on some deployments. Importantly, video data suggested that depredation of captured Red Snapper was more common at artificial reefs (19% of deployments) than natural banks (3% of deployments), providing another potential driver of habitat-specific vertical line efficiency. Collectively, these two gear interactions represent important sources of variability in Red Snapper CPUE estimates, and I recommend the use of paired vertical line-video deployments to estimate their prevalence.

An index of abundance is commonly assumed to be proportional to true abundance (Maunder and Starr 2003; Rodgveller et al. 2011). True abundance data were unavailable for this study, so the vertical line index (i.e., CPUE) was compared with the video index (i.e., MinCount), finding a positive linear relationship for both artificial and natural habitats. The finding of a linear relationship suggests that both methods may index true abundance equally well and are comparable across the habitats sampled here; however, it does not necessarily indicate they index true abundance linearly (Bacheler 2013a). In fact, it is likely that both the vertical line index and video index true abundance in a nonlinear fashion, especially given the high prevalence of vertical line saturation observed on video. This inference is also supported by several studies that have demonstrated a non-linear relationship of the MinCount index with true abundance (also known as MaxN; Schobernd et al. 2014; Campbell et al. 2015). Specifically, the MinCount is hyperstable at high abundances, a trait Campbell et al. (2015) attributed to the inability of the MinCount to account for the increasing number of individuals outside the camera field-of-view as true abundance increases. This was almost certainly the case with the vertical line-video derived MinCount, thus future comparisons of this index with vertical line CPUE at locations that may have lower abundances of Red Snapper are needed to assess the stability of this relationship.

The increasing call for fishery-independent monitoring data in modern fisheries management requires the identification of efficient and accurate methods of data collection. My results indicate that several factors affect vertical line CPUE for Red Snapper and these factors may affect the efficiency of vertical lines at artificial and natural habitats differently. While catch data alone did not suggest differences in relative abundance among habitats, several lines of evidence including the higher prevalence of gear saturation and the shorter time to saturation at artificial habitats point to higher relative abundance at these habitats compared to the natural banks in this study. Given the prevalence of gear saturation at both habitats and the linear relationship with the video-based MinCount, vertical line CPUE in the region is most likely not proportional to true abundance. Thus, while vertical lines are effective in obtaining a large number of Red Snapper for life-history studies of age, growth, and reproduction (Gregalis et al. 2012; this study), vertical line estimates of Red Snapper CPUE should be used with caution when attempting to discriminate relative abundance at the scale (i.e., habitat) assessed in this study. Vertical line CPUE may be useful for identifying differences in relative abundance at larger spatial scales or when large gradients or shifts in true abundance are expected, such as during the colonization of new artificial reefs (Chapter 4). Gear saturation, especially long before the gear is retrieved (as was the case in this study), results in severely biased CPUE estimates, and many have advocated the use of time-to-capture data rather than CPUE to correct for this problem (Somerton and Kikkawa 1995; Hovgård and Lassen 2000; Kaimmer 2004). Acquiring such data requires information on the fate of each hook over time, which can be obtained using hook timers. While the use of hook timers may be unfeasible over the large-scale SEAMAP vertical line survey, experimental trials could shed additional light on the dynamics of vertical line gear saturation and provide an alternative index of abundance for comparison (Somerton and Kikkawa 1995). The frequency of vertical line saturation is likely to increase given the Gulf of Mexico Red Snapper stock is recovering (SEDAR 2013); therefore, at the very least, paired cameras should be used to assess the prevalence of saturation. Finally, numerous calibration methods are available to standardize catch or CPUE by modeling the effects of explanatory variables that influence gear efficiency (Maunder and Punt 2004; Bacheler 2013b). These approaches seem suitable for standardizing vertical line CPUE and could employ data generated from the paired camera (e.g., depredation, interspecific MinCount [Vermilion Snapper]) to increase the usefulness of a vertical line index of abundance for assessment purposes.

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CHAPTER IV:

IMPACTS OF A NEWLY CONSTRUCTED ARTIFICIAL REEF ON RED SNAPPER AND THE ASSOCIATED FISH COMMUNITY: COLONIZATION OF THE CORPUS CHRISTI NEARSHORE REEF, TEXAS, USA

Abstract

Artificial reefs are commonly created with the goal of enhancing marine fish populations; however, many studies evaluating their effects on these populations have been hindered by a lack of pre-construction data from existing natural habitats and temporal comparison to control versus reefed area. Here, I present findings from a before-after control-impact study designed to assess the impacts of a new artificial reef on reef fish populations in the western Gulf of Mexico. I used vertical lines and fish traps to sample the planned reef site and a paired control site with soft bottom substrates typical of the region for one year prior to and two years after reef construction. Prior to reef construction, which occurred in October 2013, and over bare substrates in general, infrequent catches of sea catfish (Ariidae) and small coastal shark species (Carcharhinidae) were observed. With the exception of the rare occurrence of early juvenile Gray Triggerfish (*Balistes capriscus*) and Red Snapper (*Lutjanus campechanus*), which were observed during the summer season, the control site displayed a distinct lack of reef fish species. In contrast, the frequency of occurrence and abundance of several reef species increased at the reef site following addition of structured habitat. Most notably, I documented dramatic increases in Red Snapper and Gray Triggerfish abundance. Red Snapper were in good condition and growing quickly while at the reef site. Distinct cohorts of Red Snapper could be followed through time suggesting site fidelity; however, few fish older than 2 years of age were captured. Given that the new artificial reef

hosted high densities of juvenile Red Snapper that appeared to be in good condition and growing quickly and were no longer exposed to shrimp trawl mortality, the new reef likely enhanced the export of juveniles (i.e., production) to the adult population. My study highlights the potential benefits of nearshore artificial reefs to species like Red Snapper; however, future studies should investigate the relative roles of emigration and fishing mortality to better understand the effects of nearshore artificial reefs on reef fish population dynamics.

Introduction

Artificial reefs are commonly created with the goal of enhancing populations of commercially or recreationally exploited marine fishes (Bohnsack and Sutherland 1985; Seaman 2000; Baine 2001; Baine and Side 2003; Broughton 2012). In the northern Gulf of Mexico (GOM), large and active artificial reef programs have resulted in the deployment of thousands of artificial reefs (Minton and Heath 1998; Kaiser and Pulsipher 2005; Gallaway et al. 2009). These man-made structures may benefit reef fish populations as they provide additional hard-bottom "reef" habitat on a shelf dominated by mud and sand substrates (Parker et al. 1983; Dufrene 2005). Several important reef fish species in the GOM including Red Snapper (*Lutjanus campechanus*) and Gray Triggerfish (*Balistes capriscus*) commonly reside at artificial reefs where they are taken in directed fisheries, and both stocks are currently considered to be overfished (Gallaway et al. 2009; Simmons and Szedlmayer 2011; SEDAR 2013, 2015). As such, understanding the influence artificial reefs may have on the population dynamics of these species is essential to their sustainable management.

Artificial reefs may confer benefits such as increased recruitment, growth, or survival if they provide additional limiting habitat, increased prey resources, or shelter from predation

(Alevizon and Gorham 1989; Bohnsack 1989). The ability of an artificial reef to benefit reef fish populations may also depend on a variety of species- or life stage-specific behaviors and life-history traits, associated fishing mortality, and several aspects of artificial reef design such as reef density, location, and spacing (Bohnsack 1989; Pickering and Whitmarsh 1997; Strelcheck et al. 2005; Brandt and Jackson 2013; Addis et al. 2013, 2016). For example, off the coast of Mississippi, Brandt and Jackson (2013) found that larger Red Snapper were associated with artificial reefs with intermediate spacing and proposed that this reefing configuration may have provided foraging benefits leading to increased growth. Similarly, in recent work off south Texas, Froehlich and Kline (2015) observed larger Red Snapper were associated with lower reef density. Mudrak and Szedlmayer (2012) showed that densities of age-0 Red Snapper were significantly greater on small reefs deployed far (500 m) from large reefs than those deployed near (15 m) large reefs. They suggested the increased density on the far small reefs resulted from reduced predation as large, potential predators were observed on the large reefs. In contrast, another study off north Florida determined that unreported artificial reefs were unlikely to provide a refuge from fishing mortality for adult Red Snapper and Gray Triggerfish due to the high degree of movement among nearby structures that can occur for these species (Addis et al. 2013, 2016). Clearly, myriad factors influence artificial reef function; nevertheless, continued effort to identify artificial reefs that best support enhancement of exploited reef fish populations and which species and life-stage(s) is necessary for effective future deployments and assessment of these habitats as a management tool.

Evaluating the ecological performance of fishes inhabiting artificial reefs compared to those inhabiting adjacent natural habitats may promote a more comprehensive understanding of the value and function of artificial reefs in supporting marine fish populations (Carr and Hixon

1997; Love et al. 2006; Broughton 2012). Unfortunately, many evaluations of artificial reefs are hindered by a lack of background pre-deployment data (Brickhill et al. 2005; Cenci et al. 2011). Furthermore, studies that quantify the impact of these structures on fish communities from the onset of construction and those that monitor the recruitment of younger fishes to these habitats are sparse, leaving significant knowledge gaps regarding which artificial reefs best support fisheries production. These monitoring-based approaches are especially absent from the northwestern GOM, where the succession of fish communities following artificial reef construction remains unknown. Given the overfished status of multiple fisheries in the GOM and the expectation of future artificial reef deployments, habitat monitoring studies of this nature are particularly warranted, as such approaches can identify artificial reefs that may disproportionately contribute to the recovery and maintenance of these stocks.

In October 2013, under the guidance of the Texas Parks and Wildlife Department Artificial Reef Program, approximately 200 concrete box culverts and 470 prefabricated reef pyramids were deployed off the Texas coast in the western GOM to create the Corpus Christi Nearshore Reef (CCNR). The construction of the CCNR represents a unique opportunity to better understand artificial reef colonization and recruitment processes. The primary goal of this study was to characterize the reef fish community at nearby natural bottom habitats and the CCNR both prior to and following reef construction. I specifically evaluated: (1) relative abundance, (2) size structure, and (3) age of fishes recruiting to the CCNR. My comparisons focused on Red Snapper and (to a lesser extent) Gray Triggerfish given their importance to fisheries in the region.

Study Area

This study occurred within the coastal waters of the Texas continental shelf in the western GOM. The region is characterized by a gently sloping shelf covered in terrigenous sediments consisting of silt and clay muds and a low availability of natural hard substrates with vertical relief ≥1 m (Parker et al. 1983; Rezak et al. 1985). The CCNR site (officially known as MU-775) and a nearby control site were located approximately 15 km offshore near Port Aransas, Texas (Figure 4-1). The control site was approximately 3.5 km northeast of the CCNR site and was selected to mimic environmental conditions at the CCNR site prior to reef construction (i.e., both sites had water depths of 22 m; ambient bare substrates of sandy and silty muds). Both sites are influenced by turbidity stemming from coastal runoff and a persistent but variable nepheloid layer of resuspended sediment (Shideler 1981). Artificial structures consisting of 470 prefabricated limestone pyramids (3 m base x 2.4 m height) and 200 concrete box culverts (various sizes; 1.2 m x 1.2 m to 3 m x 3 m) were deployed across an approximately 11-ha area at the CCNR site in October 2013. Though not a focus of this study, the 47-m M/V *Kinta S* was also scuttled in this reefing block approximately 330 m southeast of the existing structure at the CCNR site in September 2014.

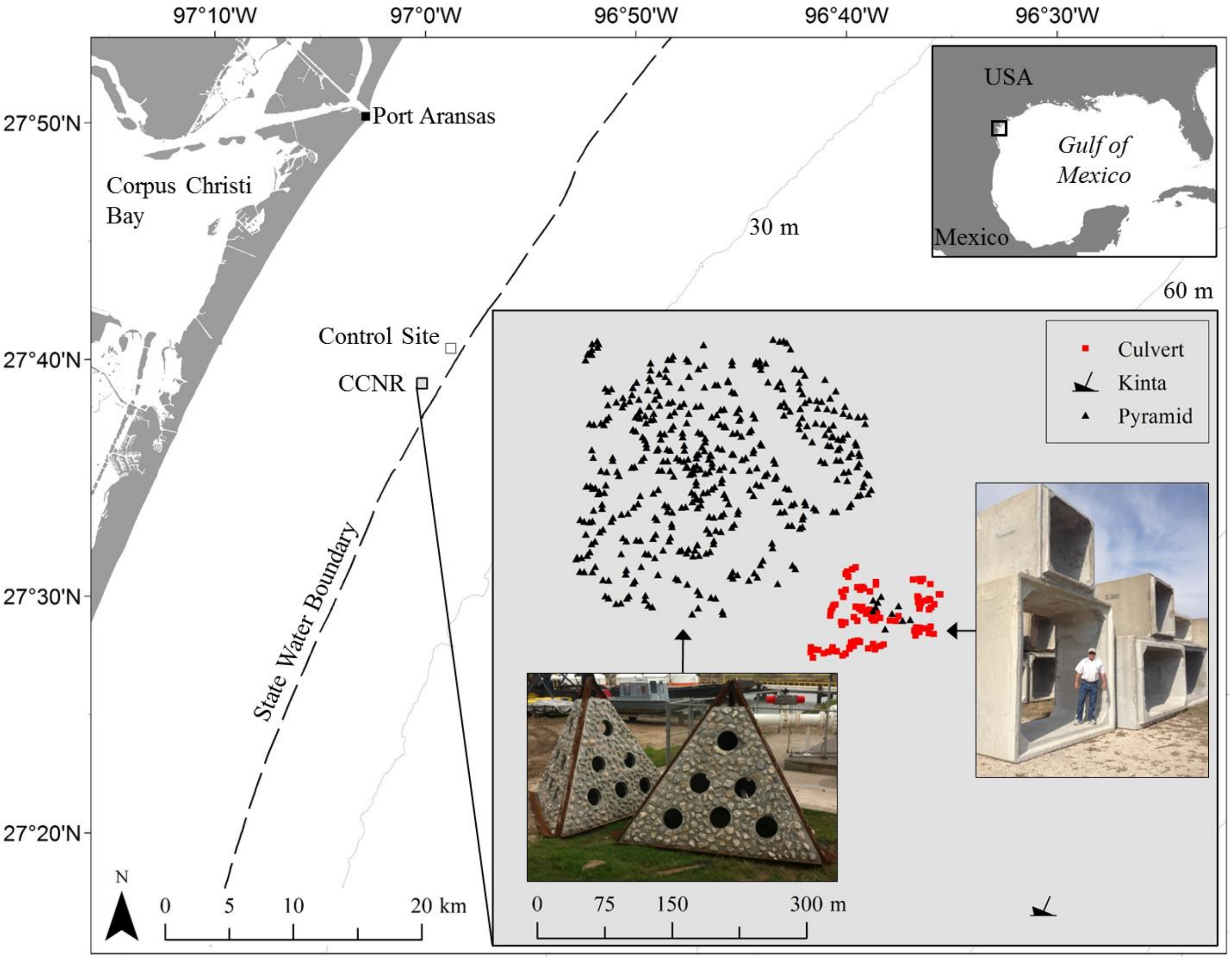

Figure 4-1. Map of the study area showing the CCNR site and the bare control site which were monitored with vertical lines and fish traps for 1 year prior to reef construction and 2 years after (i.e., summer 2012 through summer 2015). Inset map (top right) displays the location of the study area relative to the Gulf of Mexico, while the enlarged reef site displays the configuration of structures deployed at the CCNR site.

Methods

Study Design and Sampling Procedure.—This study used a before-after control-impact (BACI) framework to assess the effect of an environmental impact, such as the construction of the CCNR (e.g., Stewart-Oaten et al. 1986; Underwood 1994). The relative abundance of reef fish at the CCNR site and the bare control site was quantified for one year prior to reef construction and two years after (i.e., summer 2012 – summer 2015; reefing occurred October 2013) using vertical line surveys and small fish traps. Sampling at both sites was generally conducted once per season (fall: Oct.-Dec.; winter: Jan.-Mar.; spring: Apr.-Jun.; summer: Jul.-Sept.); however, for the first 6 months following reef construction, sampling occurred monthly to better monitor colonization rates. At each site, a combination of either random or stratified random sampling was used. Prior to reef construction, 9 locations for fish trap deployments and 3 locations for vertical line sets were randomly selected within each site. After reef construction, sampling locations at the CCNR site were selected using stratified random sampling (i.e., stratified by area of structure types). Using this protocol, 6 pyramids and 3 culverts were randomly selected for fish trap deployments, while 2 pyramids and 1 culvert were randomly selected for vertical line sets. Sampling locations were selected using the 'Create Random Points' tool in ArcMap 10.3.1 (ESRI 2015). On a given sampling day, a trap was deployed at the nine pre-selected sampling locations at each site (i.e., 9 replicate traps at control site; 9 replicate traps at CCNR site), while one vertical line set (see below for description) was conducted at each of the pre-selected sampling locations at each site (i.e., 3 replicate sets at control site; 3 replicate sets at CCNR site). Water mass characteristics including temperature (°C), dissolved oxygen ($mg \cdot L^{-1}$), and salinity (‰) were measured at each site with a Hydrolab® DS5 data sonde.

I used both small fish traps and vertical lines to help ensure representative samples as both gears may have differing species or size selectivity (e.g., Wells et al. 2008a; Gregalis et al. 2012). Small fish traps (0.97 m long x 0.67 m wide x 0.64 m high), identical to those used by Brandt and Jackson (2013), were used to sample fish inhabiting the study sites. Small mesh size (6 cm; stretch measure) and funnel mouth openings (17.5 x 11.5 cm) likely increased selectivity of juvenile fishes. Fish traps were baited with 0.5 kg of cut Atlantic Mackerel (*Scomber scombrus*) and were allowed to soak for approximately two hours before retrieval. Vertical lines followed Southeast Area Monitoring and Assessment Program (SEAMAP) protocol with gear consisting of 136-kg-test (300 lb) monofilament mainline connected to 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. 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 deployment, the backbone containing the third (unused) hook size was fished. Hook sizes were rotated such that each hook size was fished on the first, second, and third drop at a site on a given sampling day.

Fishes were identified to species and retained for further processing. In the laboratory, fish were measured (SL, FL, stretched TL; mm), weighed (kg), sexed, and sagittal otoliths of Red Snapper were extracted. Otoliths were processed following the guidelines of VanderKooy (2009). Briefly, the left otolith of each individual was weighed (g) and then thin-sectioned in the transverse plane (0.5 mm thickness) using an IsoMet® 1000 Precision Sectioning Saw. Sections containing the core region were mounted to microscope slides with thermoplastic cement and then viewed under a dissecting microscope with reflected light. Two readers independently counted all opaque annuli on a random subsample of Red Snapper otoliths (n=50), and ages were assigned based on the count of annuli and the degree of marginal edge completion (Allman et al.

2005). Because Red Snapper generally form an annulus sometime between January and June in the northern GOM, fish captured on or before June 30th had their age advanced one year if the otolith displayed a large translucent edge. For fish captured after June 30th, age was equal to the annulus count. Following this standard convention for aging Red Snapper, an annual age cohort was based on calendar year rather than time since spawning (Jerald 1983; Allman et al. 2002, 2005; VanderKooy 2009). Agreement and precision of age assignments between readers was evaluated using linear regression, the coefficient of variation (CV), and average percent error (APE).

Data Analyses.—Species accumulation curves were used to qualitatively assess the presence of different fish species over time at both the control site and the CCNR site. Catch per unit effort (CPUE) from vertical line ($\text{fish}\cdot\text{set}^{-1}$) and fish trap ($\text{fish}\cdot\text{trap-hr}^{-1}$) surveys was calculated for each species at the control site and the CCNR site before and after reef construction. Relative abundance (RA; %) was estimated for each species captured at the CCNR site and was calculated as the proportion of the total fish catch before and after reef construction. Subsequently, the change in relative abundance (Δ RA; %) was calculated by subtracting the before-reefing RA from the after-reefing RA. A positive Δ RA value was interpreted as an increase in relative abundance, while a negative value suggested a decrease in relative abundance (Reese et al. 2008; Hall et al. 2016).

Catch per unit effort data were analyzed in a BACI design using a partially-nested hierarchical ANOVA. The model included before-after (BA), control-impact (CI), and their interaction (BA x CI) as main effects. Sampling date was nested within BA and was treated as a random effect. Using this model, changes in CPUE attributable to the construction of the CCNR were evaluated for total fish (i.e., all species included) and several reef fish species of interest (e.g., Red Snapper; Gray Triggerfish). Tests for significant main effects were carried out in R 3.2.3 (R Core Team 2015) using functions from the ‘nlme’ package (Pinheiro et al. 2016). Separate analyses were conducted for traps and vertical line surveys because of their differing CPUE metrics. Prior to testing, CPUE data were assessed for homogeneity of variance and normality of residuals and log transformed. If the main effects ANOVA detected a significant BA x CI interaction, Welch’s *t*-test was used to examine potential differences in mean CPUE at the control site and CCNR before versus after reef construction. All tests of significance were conducted using $\alpha = 0.05$.

Changes in size structure over time were examined for Red Snapper and Gray Triggerfish using length frequency histograms. Length frequencies were plotted by season and included pooled data from vertical lines and fish traps as both gears were used during each season. Because age data was available for Red Snapper, otolith-derived ages were overlain for each fish represented in the length frequency. This allowed confirmation that modal length classes were indeed representing distinct age groups and facilitated visual tracking of a cohort through time. If it was possible to follow a particular cohort through time, I interpreted this as evidence of site fidelity and continued use of the CCNR over time.

Change in size and age over time was further evaluated using Pearson’s correlation coefficient. I specifically tested for changes in Red Snapper mean total length, weight, and age, and Gray Triggerfish fork length and weight with reef age. Reef age was calculated as the time in years since reef construction. Linear regression was used to estimate Red Snapper growth at the CCNR. Only size-at-age data for fish captured in the two years following reef construction were included to help ensure that estimated growth was representative of fish inhabiting CCNR. To assess the condition of Red Snapper at CCNR, relative weight (W_r) was calculated following the equation of Wege and Anderson (1978):

$$W_r = (W / W_s) \times 100$$

where W is the measured weight of a fish and W_s is the predicted weight for a fish of the same length estimated from a weight-length regression for the species. Predicted weights (W_s) were calculated from the weight-length regression reported for Red Snapper in the latest benchmark stock assessment (SEDAR 2013). Fish were considered in good condition if their W_r was ≥ 100. To assess any changes in condition over time, Pearson's correlation coefficient was used to test for a significant relationship of mean W_r and reef age.

Results

Over the course of our study, 504 fish representing 17 species and 11 families were collected (Table 4-1). Vertical line surveys captured 124 of these fish (24.6%), representing 7 species and 5 families, and fish traps captured the remaining 380 fish (75.4%), which represented 14 species from 11 families. Prior to reef construction, few fish were captured at the control site or the planned CCNR site. For example, vertical lines captured only 3 Ariid catfish (e.g., *Bagre marinus* and *Ariopsis felis*), while traps captured 28 fish, 21 (75%) of which were Gray Triggerfish. After construction of the CCNR, vertical lines captured 121 fish, while fish traps captured 352 fish. Approximately 94% of these fish were captured at the CCNR site; accordingly, large increases in CPUE of Red Snapper and Gray Triggerfish were observed with both sampling gears after the construction of CCNR (Table 4-1).

Table 4-1. Fish species captured at the CCNR site and control site before and after reef construction. Catch per unit effort (fish·set^{-1} or fish·trap-hr^{-1}), standard error (SE), and sample size (n), are presented separately for vertical lines and fish traps. Sample size (n) represents the number of vertical line sets or fish trap deployments used in calculations.

		CONTROL						CCNR					
		Before-reefing			After-reefing			Before-reefing			After-reefing		
		Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Vertical Lines (fish·set^{-1})													
Total Fish		0.182	0.122	11	0.030	0.030	33	0.083	0.083	12	3.636	0.762	33
Atlantic Sharpnose Shark	*Rhizoprionodon terraenovae*	0	0	11	0.030	0.009	33	0	0	12	0	0	33
Gafftopsail Catfish	*Bagre marinus*	0.091	0.091	11	0	0	33	0	0	12	0	0	33
Hardhead Catfish	*Ariopsis felis*	0.091	0.091	11	0	0	33	0.083	0.083	12	0	0	33
Lane Snapper	*Lutjanus synagris*	0	0	11	0	0	33	0	0	12	0.030	0.030	33
Red Snapper	*Lutjanus campechanus*	0	0	11	0	0	33	0	0	12	3.424	0.753	33
Sand Seatrout	*Cynoscion arenarius*	0	0	11	0	0	33	0	0	12	0.152	0.098	33
Warsaw Grouper	*Hyporthodus nigritus*	0	0	11	0	0	33	0	0	12	0.030	0.030	33
Traps (fish·trap-hr^{-1})													
Total Fish		0.126	0.053	27	0.053	0.022	99	0.090	0.031	27	1.077	0.148	99
Atlantic Bumper	*Chloroscombrus chrysurus*	0	0	27	0.003	0.003	99	0	0	27	0	0	99
Atlantic Croaker	*Micropogonias undulatus*	0	0	27	0	0	99	0	0	27	0.004	0.004	99
Blue Runner	*Caranx crysos*	0	0	27	0.002	0.002	99	0.007	0.007	27	0	0	99
Cobia	*Rachycentron canadum*	0	0	27	0	0	99	0	0	27	0.002	0.002	99
Conger Eel	*Conger oceanicus*	0	0	27	0	0	99	0	0	27	0.004	0.004	99
Gray Triggerfish	*Balistes capriscus*	0.094	0.043	27	0.004	0.003	99	0.060	0.024	27	0.420	0.092	99
Hardhead Catfish	*Ariopsis felis*	0.017	0.017	27	0.037	0.021	99	0	0	27	0.005	0.003	99
Lane Snapper	*Lutjanus synagris*	0	0	27	0	0	99	0	0	27	0.005	0.004	99
Pigfish	*Orthopristis chrysoptera*	0	0	27	0	0	99	0	0	27	0.164	0.043	99
Pinfish	*Lagodon rhomboides*	0	0	27	0	0	99	0.008	0.008	27	0	0	99
Red Snapper	*Lutjanus campechanus*	0.014	0.010	27	0.002	0.002	99	0.015	0.010	27	0.455	0.091	99
Southern Kingfish	*Menticirrhus americanus*	0	0	27	0	0	99	0	0	27	0.002	0.002	99
Spinner Shark	*Carcharhinus brevipinna*	0	0	27	0.005	0.003	99	0	0	27	0	0	99
Warsaw Grouper	*Hyporthodus nigritus*	0	0	27	0	0	99	0	0	27	0.015	0.007	99

Water quality varied seasonally but was similar at the CCNR at the nearby control site over time. Benthic water temperatures ranged from 13.9 °C in winter to 28.7 °C in the summer. Evidence of thermal stratification was generally present in the summer months with thermoclines present around the 10-15 m depths. An exception was summer 2015 when no thermocline was present. Benthic dissolved oxygen levels were generally highest in winter (Mean = 7.83 $mg \cdot L^{-1}$) and lowest in fall (Mean = 5.6 $mg \cdot L^{-1}$). Hypoxia (i.e., DO <2 $mg \cdot L^{-1}$) was absent during most of the study but was observed on one occasion in late spring 2015 (1.7 $mg \cdot L^{-1}$) over both the control and reef sites. Benthic salinity levels ranged from 31.8 ‰ in the fall to 36.4 ‰ in the summer months.

Assessment of species accumulation curves for both sites revealed the number of species observed following reef construction increased more rapidly at the CCNR site. Prior to reef construction, 5 species were observed at the planned CCNR site, while 4 were observed at the bare control site. Notably, Red Snapper and Gray Triggerfish were observed at each site prior to reef construction. In the first fall and winter following reef construction, only one additional species (Spinner Shark; *Carcharhinus brevipinna*) was observed at the control site, while six additional species were observed at the CCNR site. These included several species of Sciaenids such as Sand Seatrout (*Cynoscion arenarius*), Atlantic Croaker (*Micropogonias undulatus*), and Southern Kingfish (*Menticirrhus americanus*), reef fish including Warsaw Grouper (*Hyporthodus nigritus*) and Pigfish (*Orthopristis chysoptera*), and the migratory Cobia (*Rachycentron canadum*). Interestingly, the Sciaenids were not observed in samples after the first fall and winter following reef construction. Maximum observed species richness at both the CCNR site (13 species) and control site (8 species) was observed by the first summer following reef construction with no additional species observed at either site for the remainder of the study.

Changes in the RA of many species were most pronounced at the CCNR site following reef construction. Vertical lines failed to capture a single Red Snapper prior to reef construction, but RA increased dramatically to 94.2% in post-reefing samples (Table 4-2). Although less apparent, several other species including Sand Seatrout, Lane Snapper (*Lutjanus synagris*), and Warsaw Grouper also displayed increased RA in vertical line samples after being absent or undetected prior to reef construction (i.e., 0% RA). Among trap samples, the greatest changes in RA occurred for Gray Triggerfish (− 24% Δ RA), Red Snapper (+ 23.1% Δ RA), and Pigfish (+ 13.9% Δ RA). Despite the decline in Gray Triggerfish RA, they accounted for the greatest RA in trap samples following reef construction (42.3%). Red Snapper RA increased from 16.7% before reef construction to 39.8% after reef construction, while Pigfish RA increased from 0% to 13.9% following reef construction (Table 4-2). Similar to vertical line samples, other species of recreational or commercial importance also showed increased RA in trap samples after being absent in pre-reef samples.

Table 4-2. Total catch, catch per unit effort (CPUE; fish·set^{-1} or fish·trap-hr^{-1}), relative abundance (RA; %), and change in relative abundance (Δ RA; %) of fish at the CCNR site before and after reef construction.

	Before-reefing			After-reefing			
	Catch	CPUE	RA	Catch	CPUE	RA	Δ RA
Vertical Lines							
Hardhead Catfish	1	0.083	100	0	0	0	-100
Lane Snapper	0	0	0	1	0.030	0.8	0.8
Red Snapper	0	0	0	113	3.424	94.2	94.2
Sand Seatrout	0	0	0	5	0.152	4.2	4.2
Warsaw Grouper	0	0	0	1	0.030	0.8	0.8
Total Fish	1	0.083		120	3.636		
Traps							
Atlantic Croaker	0	0	0	1	0.004	0.3	0.3
Blue Runner	1	0.007	8.3	0	0	0	-8.3
Cobia	0	0	0	1	0.002	0.3	0.3
Conger Eel	0	0	0	1	0.004	0.3	0.3
Gray Triggerfish	8	0.060	66.7	137	0.420	42.3	-24.4
Hardhead Catfish	0	0	0	2	0.005	0.6	0.6
Lane Snapper	0	0	0	2	0.005	0.6	0.6
Pigfish	0	0	0	45	0.164	13.9	13.9
Pinfish	1	0.008	8.3	0	0	0	-8.3
Red Snapper	2	0.015	16.7	129	0.455	39.8	23.1
Southern Kingfish	0	0	0	1	0.002	0.3	0.3
Warsaw Grouper	0	0	0	5	0.015	1.5	1.5
Total Fish	12	0.090		324	1.077		

Abundance of fish at the control site generally remained low and similar to pre-reefing levels following reef construction, but large increases in CPUE were observed for several groups at the CCNR site. The construction of CCNR had a significant effect on vertical line total fish CPUE (BA x CI: $F_{1,73} = 16.82$, $P < 0.001$) and trap total fish CPUE (BA x CI: $F_{1,236} = 31.02$, $P < 0.001$; Table 4-3). Post-hoc testing suggested that no differences in CPUE existed at the control site before versus after reefing for vertical line ($t = 1.21$, $df = 11$, $P = 0.253$) or fish trap data ($t =$

1.57, $df = 32$, $P = 0.126$). In contrast, vertical line and fish trap CPUE increased at the CCNR site following reef construction ($t = 4.99$, $df = 41$, $P < 0.001$ and $t = 5.40$, $df = 60$, $P < 0.001$, respectively; Table 4-1). There was a significant effect of the CCNR on Gray Triggerfish abundance (BA x CI: $F_{1,236} = 17.33$, $P < 0.001$; Table 4-3). At the control site, CPUE declined from 0.094 to 0.004 fish·trap-hr^{-1} after reef construction ($t = 2.45$, $df = 27$, $P = 0.021$; Table 4-1), while CPUE increased at the CCNR site from 0.060 fish·trap-hr^{-1} before reefing to 0.420 fish·trap-hr^{-1} after reef construction ($t = 2.71$, $df = 63$, $P = 0.008$; Figure 4-2). Red Snapper abundance estimated from vertical lines and fish traps was also significantly affected by the construction of the CCNR (BA x CI: $F_{1,73} = 17.99$, $P < 0.001$ and BA x CI: $F_{1,236} = 14.21$, $P < 0.001$, respectively; Table 4-3). Vertical line CPUE was significantly greater at the CCNR site following reef construction, increasing from 0 to 3.42 fish·set^{-1} ($t = 6.44$, $df = 32$, $P < 0.001$; Figure 4-2A). Red Snapper trap CPUE did not change at the control site before versus after reef construction ($t = 1.23$, $df = 27$, $P = 0.228$), but increased at the CCNR from 0.02 fish·trap-hr^{-1} prior to reef construction to 0.46 fish·trap-hr^{-1} after ($t = 5.14$, $df = 114$, $P < 0.001$; Figure 4-2B). Although Lane Snapper and Warsaw Grouper were not captured prior to reefing, the construction of the CCNR did not significantly increase their abundance estimated from vertical lines (BA x CI: $F_{1,73} = 0.35$, $P = 0.558$) or fish traps (BA x CI: $F_{1,236} = 0.58$, $P = 0.447$ and BA x CI: $F_{1,236} = 1.41$, $P = 0.237$, respectively; Figure 4-2; Table 4-3).

Table 4-3. Results of partially-nested hierarchical two-way ANOVA testing for the effect of constructing the CCNR on overall abundance of fish and several species of economically important reef fish species. Type III tests for the main effects of before vs. after (BA), control vs. impact (CI), and their interaction (BA x CI) are displayed for both vertical line (fish·set^{-1}) and fish trap data (fish·trap-hr^{-1}). No Gray Triggerfish were captured with vertical lines in this study. * denotes statistical significance ($P < 0.05$).

	Vertical Line				**Trap**			
	df	*F*	*P*		*df*	*F*	*P*	
Total Fish								
Source								
BA	12	3.78	0.076		12	1.17	0.301	
CI	73	10.02	0.002	*	236	32.68	<0.001	*
BA x CI	73	16.82	<0.001	*	236	31.02	<0.001	*
Gray Triggerfish								
Source								
BA	-	-	-		12	0.03	0.870	
CI	-	-	-		236	14.68	<0.001	*
BA x CI	-	-	-		236	17.33	<0.001	*
Red Snapper								
Source								
BA	12	5.54	0.037	*	12	2.37	0.150	
CI	73	17.99	<0.001	*	236	14.32	<0.001	*
BA x CI	73	17.99	<0.001	*	236	14.21	<0.001	*
Lane Snapper								
Source								
BA	12	0.32	0.583		12	0.26	0.621	
CI	73	0.35	0.558		236	0.58	0.447	
BA x CI	73	0.35	0.558		236	0.58	0.447	
Warsaw Grouper								
Source								
BA	12	0.32	0.583		12	1.32	0.274	
CI	73	0.35	0.558		236	1.41	0.237	
BA x CI	73	0.35	0.558		236	1.41	0.237	

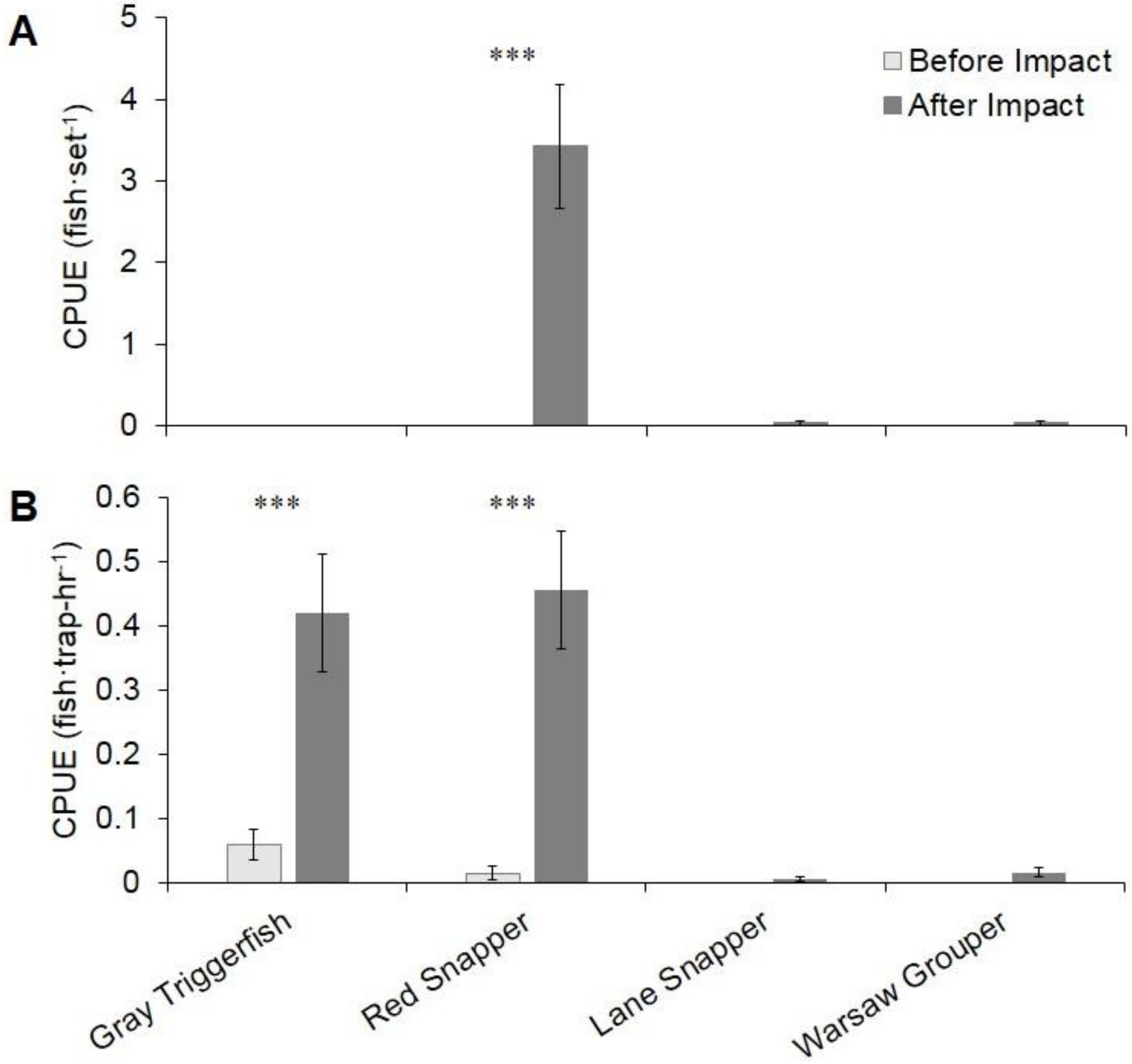

Figure 4-2. Mean CPUE of select reef fish at the CCNR site before and after reef construction. Data are displayed separately for vertical lines (A; fish·set^{-1}) and fish traps (B; fish·trap-hr^{-1}). Error bars represent ±1 SE. Significant differences ($P < 0.05$) are denoted with ***.

Red Snapper and Gray Triggerfish abundance increased over time following the construction of the CCNR; (Figure 4-3). Vertical line sampling suggested Red Snapper CPUE increased slowly following reef construction, but CPUE increased to approximately 9 to 11 times greater than CPUE immediately after reefing by the first summer following reef construction

(Figure 4-3A). No Red Snapper were captured at the control site with vertical lines over the course of the study. Red Snapper trap CPUE was more variable than vertical line CPUE, but also showed increases in CPUE following reef construction (Figure 4-3B). Similar to vertical line CPUE, Red Snapper trap CPUE reached the greatest observed levels by the first summer following reef construction—approximately 32 times greater than the highest CPUE observed before reef construction (maximum CPUE before = 0.04 fish·trap-hr^{-1}; maximum CPUE after = 1.31 fish·trap-hr^{-1}). Both gears showed a decline in CPUE the second winter after reef construction followed by an increase to pre-winter levels by summer. Hypoxia was observed during this period of lower abundance. Low Red Snapper CPUE (e.g., 0.02-0.04 fish·trap-hr^{-1}) was observed at the control site but only during the summer season.

Gray Triggerfish were only captured in fish traps, and CPUE increased at the CCNR site following reef construction (Figure 4-3C). Gray Triggerfish CPUE also displayed a potential seasonal trend in CPUE with declines observed during the first two winters after reef construction followed by increases the following summer and fall. Peak CPUE was observed by the second summer following reef construction, reaching levels approximately 9 times greater the maximum observed the at the CCNR site prior to reef construction (maximum CPUE before = 0.18 fish·trap-hr^{-1}; maximum CPUE after = 1.63 fish·trap-hr^{-1}). Low abundances of Gray Triggerfish were observed at the control site, but only during the summer season (Figure 4-3C).

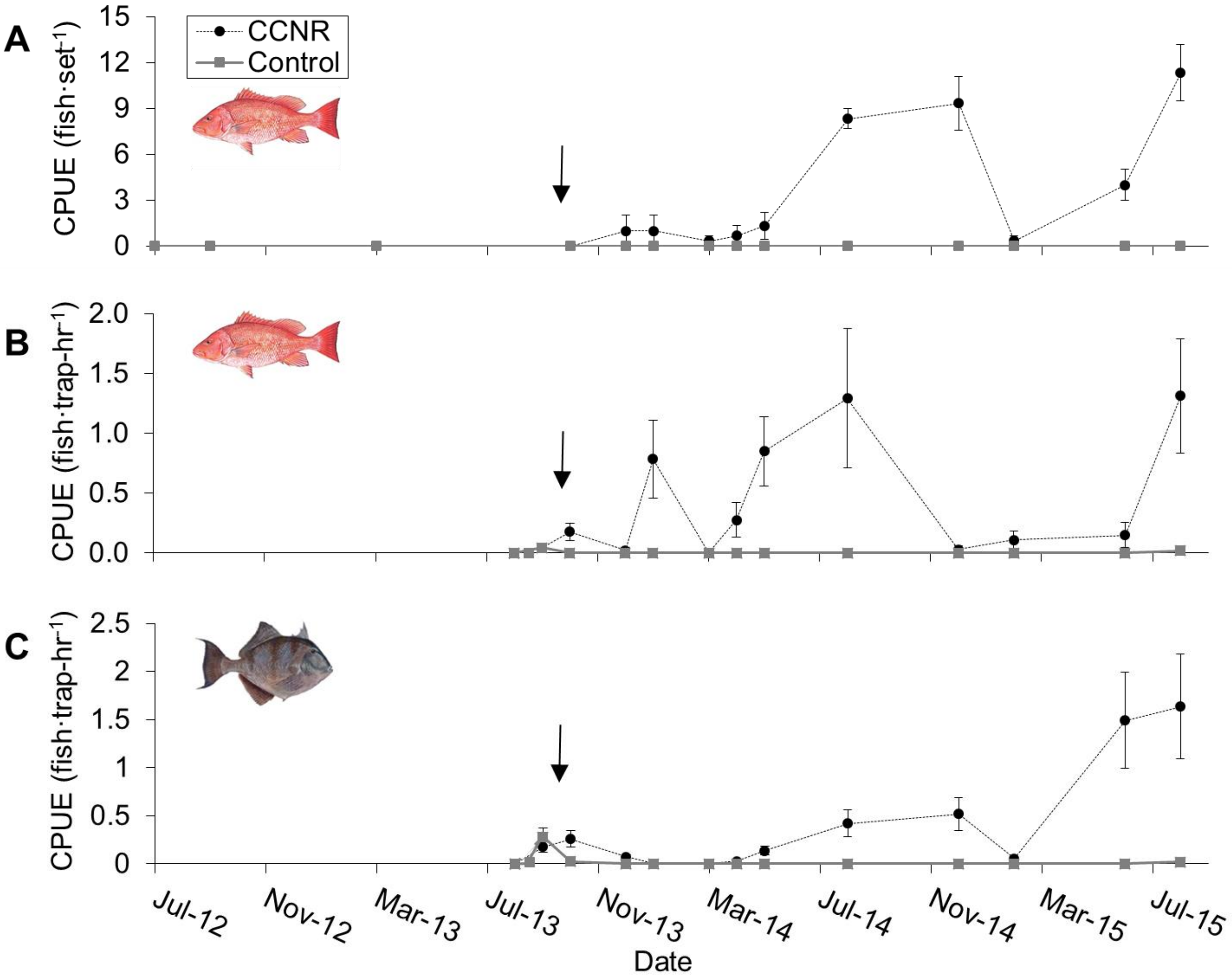

Figure 4-3. Mean CPUE for Red Snapper captured at the CCNR (black circles) and bare control site (gray squares) with vertical lines (A; fish·set^{-1}) and fish traps (B; fish·trap-hr^{-1}) over time from summer 2012 through summer 2015. Mean Gray Triggerfish CPUE (C; fish·trap-hr^{-1}) at the CCNR (black circles) and control site (gray squares) is also displayed for comparison. The black arrow on each panel represents the time of reef construction. Error bars represent ±1 SE.

Annual age estimates were obtained for 247 Red Snapper captured during this study. Agreement between readers was high (reader 1 age = 1.01 × reader 2 age + 0.01, $R^2 = 0.94$), and variability between age assignments was low (CV = 1.35; APE = 0.95%). Ages ranged from 0 to 4 years and consisted primarily of age-2 fish (59.9%) followed by age-1 fish (31.5%). Age-0 Red Snapper (mean TL = 112.8 mm) were first captured in traps during the summer (i.e., August) at the bare control and CCNR site prior to reef construction (Figure 4-4A). It was possible to identify three cohorts of Red Snapper inhabiting the CCNR over time when assigned ages were overlain onto the seasonal length frequency histograms (Figure 4-4A). The first cohort consisted of age-0 fish that recruited to the CCNR the first fall after reef construction (i.e., fall 2013). By late fall, more age-0 fish were captured along with several age-1 fish. No age-0 fish were captured at the CCNR after the first fall after reef construction. This cohort was classified as age-1 fish in winter 2014 and then age-2 fish in winter 2015, although length frequency data were limited that winter. Nevertheless, this cohort was visible again by spring and displayed a modal size of approximately 325-350 mm TL by summer 2015. The second Red Snapper cohort recruited to the CCNR as age-1 fish in fall 2013. This cohort was well represented in the length frequency histograms until fall 2014. Few fish from this cohort remained after fall 2014, with few age-3 fish represented through summer 2015. The third Red Snapper cohort was apparent in summer 2015 and was represented by a strong supply of new age-1 recruits (Figure 4-4A). Gray Triggerfish seasonal length frequencies were similar to Red Snapper in that the smallest fish were sampled in the summer prior to reef construction and the first fall following reef construction (Figure 4-4B). Gray triggerfish appeared to be absent from the CCNR during the winter months as only 1 fish was captured in the two winters that sampling occurred. Gray

Triggerfish had weak representation in the seasonal length frequencies until summer 2015, the second summer following reef construction.

Red Snapper mean age increased from < 1 year immediately following reef construction to nearly 2 years by the end of this study (r = 0.76, P = 0.004). Red Snapper mean length (r = 0.71, P = 0.010) and weight (r = 0.78, P = 0.003) also increased as the age of the CCNR increased. Positive relationships with reef age were also observed for Gray Triggerfish mean fork length (r = 0.69, P = 0.060) and weight (r = 0.60, P = 0.116), but these relationships were not significant. A linear regression of Red Snapper size-at-age data suggested that fish were growing approximately 124 mm·year^{-1} (TL = 124.1 × age (years) + 80.3; R^2 = 0.81; P < 0.001), aligning well with modal sizes from the seasonal length frequency histograms. Evaluation of Red Snapper relative weights suggested that fish were in good health while inhabiting the CCNR (mean W_r = 126.17; SE = 0.74). There was no evidence of a relationship between Red Snapper condition (i.e., W_r) and reef age (r = -0.24, P = 0.510).

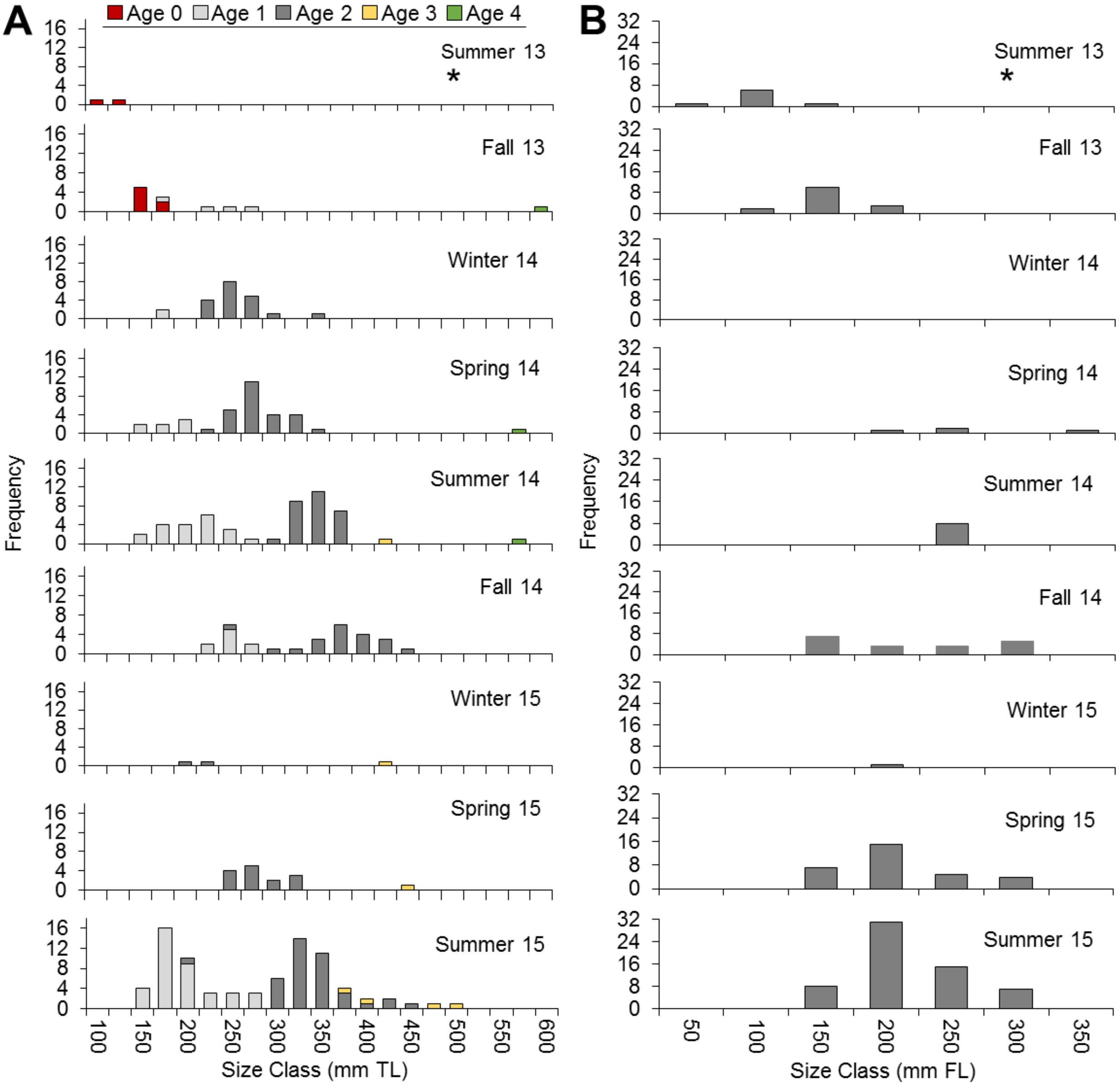

Figure 4-4. Length frequency histograms by season for Red Snapper (A) and Gray Triggerfish (B) captured at the CCNR site from summer 2013 (* prior to reef construction) through summer 2015. Red Snapper length frequencies include pooled data from vertical lines and fish traps, while Gray Triggerfish length frequencies include only trap-caught fish as no fish were captured with vertical lines during the study. Red Snapper age data have been overlain onto the length frequencies and confirm the presence of distinct cohorts through time.

Discussion

Understanding the effects artificial reefs have on marine ecosystems and their role in maintaining marine fish populations remains an important issue in modern fisheries management. Results from this study suggest that the construction of the CCNR had significant positive impacts on the fish community by increasing the abundance of several key species. For example, after reef construction, I observed increased frequency of occurrence for several economically important species at the CCNR, while the catch at the control site remained characterized by infrequent catches of sea catfish (Ariidae) and several small shark species (Carcharhinidae). Gray Triggerfish and Red Snapper were the dominant members of the fish community following construction of the CCNR. Although individuals of both of these fisheries species were also captured over bare substrates at the control site and the CCNR site prior to reef construction, they were representative of young-of-the-year based on the sizes at capture and presence only during the summer months—the peak spawning and recruitment season for these species (Gallaway et al. 2009; Simmons and Szedlmayer 2011, 2012). Perhaps most notably, Red Snapper and Gray Triggerfish abundances increased substantially at the CCNR following reef construction, while both species remained undetected or occurred infrequently in low abundances at the bare control site. As these changes did not occur at the bare control site, they can almost certainly be attributed directly to the addition of artificial hard substrates at the newly reefed CCNR site.

Increased abundance of economically important reef fish following the construction of an artificial reef is not uncommon as colonization rates are often rapid (Bohnsack et al. 1991; Bohnsack et al. 1994; Grossman et al. 1997). For example, Bohnsack et al. (1994) observed peak species richness, number of individuals, and biomass within two months of reef construction. In contrast, although rapid colonization was observed, I did not observe peak abundance of Red Snapper until the first summer and fall following reef construction (i.e., $\geq$ 11 months following reef construction), and Gray Triggerfish peak abundance was not observed until the second summer following reef construction (i.e., $\geq$ 23 months following reef construction). The slower colonization pattern observed for Gray Triggerfish may be due to the species preference for encrusting and reef dwelling invertebrates (Vose and Nelson 1994) that take time to colonize the ‘clean’ structure. Given that the CCNR was constructed in October, cooler water temperatures associated with the fall and winter seasons likely slowed or delayed growth of Gray Triggerfish prey, which may explain the seasonal decrease in abundance observed for Gray Triggerfish during the winter months. Prey availability on the CCNR structures may have had a lesser impact on Red Snapper as the species relies on prey sources from reef structures as well as open sand or mud bottom habitats (Moseley 1966; Ouzts and Szedlmayer 2003; Szedlmayer and Lee 2004; McCawley and Cowan 2007; Wells et al. 2008b). The slower rates of colonization observed in this study may also stem from the size of the artificial reefs studied as the largest artificial reefs examined by Bohnsack et al. (1994) were approximately 14 m^2, while the CCNR was a much larger complex of artificial structures spanning 11 ha. Consequently, the greater habitat area provided by the CCNR may have contributed to the longer colonization times I observed. Thus, more research is warranted to examine the influence of reef sized on the population dynamics of these reef fishes.

Patterns in abundance that were observed may also be an effect of environmental conditions or other biological processes like competition. For example, the presence of a relatively rare hypoxia event that occurred in spring 2015 is likely responsible for lower Red Snapper trap CPUE. Previous studies have also observed depressed catches of juvenile Red Snapper when hypoxia is present (Gallaway et al. 1999). The lone occurrence of hypoxia in our study may have been driven by heavy rainfall totals and subsequent runoff observed in spring 2015 (http://www.srh.noaa.gov). The occurrence of several Sciaenid species (*C. arenarius*, *Micropogonias undulatus*, and *Menticirrhus americanus*) during the first fall and winter following reef construction may be a function of their broad presence over sand and mud bottoms of the inner shelf (Hoese and Moore 1998). Likewise, their absence in samples after this period may be a result of competition with more reef associated species like Red Snapper and Gray Triggerfish for space or other resources at the CCNR; however, gears with less species selectivity (e.g., cameras or visual census) could help to better evaluate this inference.

Age-0 and age-1 Red Snapper cohorts first recruited to the CCNR during the first fall (2013) and winter (e.g., for 2014 classified as age-1 and age-2 fish) following reef construction. Interestingly, no age-0 fish were captured after the first fall when reef construction occurred, which may be explained in part by gear selectivity and Red Snapper behavior. For example, age frequencies indicated Red Snapper were not fully recruited to trap gear until age-1; therefore, age-0 fish were likely under-sampled in my study. In fact, most studies of age-0 snapper have required the use of trawl gear to successfully sample early juvenile Red Snapper (Holt and Arnold 1982; Gallaway and Cole 1999; Rooker et al. 2004; Wells et al. 2008c). Another explanation for the lack of age-0 snapper in these samples may be behavioral exclusion of these fish from the immediate reef structures or at least the traps by older Red Snapper (Bailey et al. 2001; Mudrak and Szedlmayer 2012). For example, Bailey et al. (2001) showed older Red Snapper actively excluded age-0 conspecifics from occupying experimental reef stuctures. These hypotheses are further supported by ancillary trap-camera deployments at the CCNR that show the presence of age-0 Red Snapper, especially during the summer and fall recruitment seasons (M. K. Streich, unpublished data). Several previous studies have also reported recruitment of early juvenile Red Snapper to artificial reefs during this time (Mudrak and Szedlmayer 2012; Syc and Szedlmayer 2012). Thus, it is likely that the CCNR still provided habitat to age-0 fish despite their absence in samples following the first fall recruitment season.

Changes in Red Snapper seasonal size structure indicated that a majority of the Red Snapper remained at the CCNR after recruiting to the reef. Furthermore, the ability to track distinct cohorts through time can be interpreted as indirect evidence of site fidelity. Despite the high susceptibility of older Red Snapper (i.e., ≥ age 3) to vertical line gear (e.g., Gregalis et al. 2012), there was little evidence of movement of older fish to the CCNR as only four individuals ≥ age 3 were captured during the first year following reef construction. This finding was somewhat unexpected as age-frequencies from this study suggested Red Snapper were fully recruited to the vertical line gear by age 2. In addition, Addis et al. (2013) reported that Red Snapper tagged at small concrete artificial reefs in the northeastern GOM displayed a relatively high degree of movement; therefore, if immigration of older individuals was a significant component of the Red Snapper abundance at the CCNR, one would expect these fish to be better represented in the age structure observed here. Although age-3 Red Snapper were rare throughout this study, seasonal age-length frequencies showed they were most represented in late summer 2015. Assuming the degree of site fidelity suggested above, some of these fish would have recruited to CCNR as age-1 individuals the first fall after reef construction. We also observed increases in Red Snapper mean length, weight, and age with the age of CCNR, further supporting the hypothesis that most fish remained at the CCNR after arrival. Perhaps most striking was the change in mean age from less than 1 year just after reef construction to approximately 2 years by the end of summer 2015—approximately two years after reef construction. Thus, it appears that a majority of Red Snapper at CCNR recruited as age-1 individuals (or age 0, but under-sampled) and remained at the CCNR for up to two years following reef construction. Similarly, Syc and Szedlmayer (2012), working in the northern GOM, observed increases in mean length, weight, and age of Red Snapper as the age of the artificial reefs they sampled increased and implied that these positive correlations would not occur if at least some fish did not remain at these habitats for several years. Nevertheless, future studies, similar to that of Workman et al. (2002), using acoustic tagging of small individuals could be used to provide direct estimates of the site fidelity suggested in this study.

This study suggests that Red Snapper inhabiting CCNR were in good condition, which indicates they were able to obtain adequate prey resources from the CCNR and surrounding mud bottom. The growth rate observed for Red Snapper in this study (~124 $\text{mm}\cdot\text{year}^{-1}$) was faster than previously reported growth rates for similar aged fish off the Texas coast of 60-90 $\text{mm}\cdot\text{year}^{-1}$ (Bradley and Bryan 1975), 90 $\text{mm}\cdot\text{year}^{-1}$ (Moseley 1966), and 110 $\text{mm}\cdot\text{year}^{-1}$ (Holt and Arnold 1982), supporting the assertion that Red Snapper at the CCNR were healthy and growing quickly. Although I did not quantify prey abundance at CCNR, artificial reefs can promote increased growth by providing additional reef-associated prey resources or increasing access to or efficiency of obtaining these resources (Bohnsack 1989; Peterson et al. 2003). Because Red Snapper may obtain significant portions of their prey from surrounding mud or sand bottom (McCawley and Cowan 2007; Wells et al. 2008b), other factors such as reef spacing could have played a role in the availability of prey resources at CCNR. For example, previous studies have observed that species foraging over open bottoms surrounding reefs can create foraging halos of intense prey depletion surrounding the reefs in which they reside, and the degree of prey depletion may become more severe as reef spacing decreases due to increased foraging overlap (Ogden et al. 1973; Lindberg et al. 1990; Frazer and Lindberg 1994). Spacing of artificial structures at the CCNR was variable with some structures as close as 3 m apart while farther spacing of at least 75 m was also present between “patches” of structure (Figure 4-1). Therefore, the spatial configuration of structures or the larger overall footprint (11 ha) at CCNR may not have resulted in severe foraging halos that could have limited Red Snapper growth. Previous studies have investigated the effects of reef density on Red Snapper size and abundance and have generally found increased abundances and larger fish associated with low to intermediate reef densities (e.g., Strelcheck et al. 2005; Froehlich and Kline 2015). Due to the haphazard deployment of structures at the CCNR, the effect of structure density on Red Snapper growth was not assessed here, but such studies would be beneficial in determining optimal configurations for future artificial reef deployments.

The increased habitat complexity associated with the addition of artificial structure at CCNR likely resulted in differences in survivorship of fishes that recruited to the reef site versus those that remained over the bare mud and sand substrates typical of the area prior to reef construction. This inference is supported by several previous studies that demonstrate greater survival of juvenile fish in high complexity habitats (Connell and Jones 1991; Sale 1991; Wells et al. 2008c). Typically, high survival in high complexity habitats is attributed to decreased predation, which can be a significant factor affecting fish densities at reefs (Connell and Jones 1991; Hixon and Beets 1993). For example, Lindberg et al. (2006) demonstrated that Gag (*Mycteroperca microlepis*) selected reef shelters at the expense of maximizing growth. The reef pyramids and box culverts deployed at CCNR have numerous holes and crevices, and thus may benefit reef fish by providing refuges from predation. The habitat complexity associated with the CCNR also resulted in the creation of a de facto no-trawl zone. This aspect of habitat alteration should not be overlooked as Red Snapper suffer significant mortality as bycatch in the shrimp-trawl fishery in the GOM (Goodyear 1995; Gallaway and Cole 1999). A study by Wells et al.

(2008c) observed that early juvenile Red Snapper had truncated size distributions, increased mortality, and decreased growth over trawled habitats compared to non-trawled habitats. Accordingly, the elimination of trawling following the construction of the CCNR likely provided increased survival for Red Snapper—and other species including Gray Triggerfish—as juveniles were especially vulnerable to trawling over the soft bottom prior to reef construction.

Based on the ages of Red Snapper collected in this study and the reported age-at-maturity for Red Snapper in the GOM (Gallaway et al. 2009; Kulaw 2012), a vast majority of individuals inhabiting CCNR were juveniles. An ontogenetic habitat shift has been suggested for Red Snapper, with juveniles moving from low-relief shell rubble habitats to intermediate-relief structures within the first year (Wells et al. 2008c; Gallaway et al. 2009). These juveniles appear to remain at these reefs for about a year at which time (~ age-2 fish) they begin to recruit to high-relief structures such as oil and gas platforms, ship wrecks, and natural hard rock outcroppings. My findings suggest Red Snapper recruited to CCNR as age-1 fish and moved from the reef at around 2-3 years of age. The lack of older fish at the CCNR may in part be due to a combination of emigration and fishing mortality. For example, the oldest fish may be emigrating from CCNR to larger structured habitat as the resources and space at CCNR is reduced with the advent of age-0 and age-1 recruits each summer and fall season. An alternative but not mutually exclusive explanation is that fishing mortality is largely responsible for the disappearance of fish after age-2, especially considering that the CCNR is located near shore and also open to fishing year round. Moreover, the minimum size limit in state waters is 381 mm (15 in)—the upper size range of age-2 fish in our length frequency histograms—thus it is likely that fishing removal of these size classes also plays some role in the lack of older Red Snapper at CCNR. Certainly, future studies should be developed to determine the relative rates of emigration and fishing mortality to better understand the apparent decline of individuals over age-2.

Collectively, my results suggest that the construction of CCNR provided several benefits to reef fish that recruited to the reef. It was evident that CCNR provided valuable habitat for juvenile Red Snapper, potentially serving a nursery role for the species. Beck et al. (2001) defined a nursery habitat as one that contributes—on a per unit area basis—greater production and export of juveniles to the adult population than production occurring from other habitats where juveniles occur. Greater contribution to the adult population may occur through any combination of increased density, growth, survival of juveniles, and movement to adult habitats (Beck et al. 2001). Much higher densities of juveniles were observed at CCNR than surrounding soft bottom habitats following reef construction. Despite increased densities of Red Snapper at the CCNR, growth rates appeared to be at least as fast as those previously reported for the species, and condition of individual fish was high. Although I did not directly estimate survival, mortality from shrimp trawl bycatch was effectively eliminated at the reef site following reef construction, and age-0 and age-1 fish residing at the CCNR likely experienced high survival compared to similar-aged conspecifics over the open soft bottom that is typical on much of the inner shelf (Parker et al. 1983). Based on the length frequencies observed following reef construction, the aforementioned benefits likely apply to Red Snapper for up to two years after they recruit to CCNR. Finally, though it was apparent that recruitment of new individuals to CCNR was an important process acting at the reef site, export (i.e., production) of juveniles to the adult (fishable) population was also evident and likely greater on a per unit area basis than surrounding bare habitats. Thus, while our findings clearly indicate that artificial reefs like the CCNR can benefit reef fish such as Red Snapper and possibly Gray Triggerfish, we recommend future studies directly evaluate the relative roles of emigration and fishing mortality in structuring reef fish populations at nearshore artificial reefs in the GOM.

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SUMMARY

The goal of my dissertation was to provide new information necessary to evaluate the relative value of artificial reefs to Red Snapper (*Lutjanus campechanus*) in the western Gulf of Mexico (GOM). Although numerous studies have addressed Red Snapper life history in this region, few have directly compared abundance and other demographic variables between artificial and natural habitat types. In my studies, the use of concurrent comparisons between artificial and natural habitats was essential and key for revealing patterns in Red Snapper relative abundance and vital rates (e.g., growth) that would have remained unknown had these studies focused only on artificial habitats alone. Accurate evaluation of stock status requires an understanding of stock dynamics at regional or even sub-regional levels such as among habitats as these finer scale dynamics ultimately influence overall stock productivity (Pulliam 1988; Pulliam and Danielson 1991; Cadrin and Secor 2009; Kerr et al. 2010). My findings contribute to our understanding of Red Snapper population dynamics at the habitat scale and provide insight into the value of artificial reefs in supporting the GOM Red Snapper stock.

In Chapter 1, I compared fish communities inhabiting Rigs-to-Reefs (RTR) artificial reef structures and natural banks and estimated Red Snapper density using remotely operated vehicle (ROV) transects. While both habitats support several important fisheries species, community structure differs, and Red Snapper density is greater at artificial habitats. Despite higher densities on RTR structures, extrapolated total abundance and biomass were much greater on natural banks given their larger habitat area. Estimated Red Snapper biomass at the five natural banks surveyed was 278,530 kg, equivalent to 7.6% of the 2012 GOM annual catch limit. These results suggest that natural habitats likely support a larger portion of the Red Snapper biomass than artificial reefs in the western GOM. Because fishermen, both commercial (Nieland et al. 2007) and recreational (Garner and Patterson 2015), commonly target artificial habitats, artificial reefs have the potential to divert fishing effort away from natural habitats and the large Red Snapper biomass they support. While similar studies with increased spatial and temporal replication should be conducted to improve the estimates presented herein and determine abundance patterns in other areas, where artificial habitat is more common (e.g., Alabama and Florida panhandle), my results imply that strategically locating artificial reefs away from natural habitats may be a viable option to manage the distribution of fishing effort in the GOM Red Snapper fishery and potentially away from more sensitive areas.

In Chapter 2, I showed that differences in Red Snapper size and age structure and growth exist between RTR artificial reefs, standing platforms, and natural banks, corroborating several of the findings of Saari (2011) who compared these parameters over the Louisiana shelf. My results indicate that natural banks support a greater proportion of large and relatively old (≥ age-6) Red Snapper than artificial reefs or standing platforms. Fish from RTR artificial reefs tended to be larger-at-age and reach larger sizes than those from natural banks. Few older fish (i.e., > age-10) currently reside at the habitats sampled in this study. In contrast to my findings, Saari (2011) observed a greater proportion of larger individuals on artificial reefs than natural banks. This difference may have been driven by a single natural bank with a predominance of larger individuals, highlighting the sub-regional complexities of the GOM stock. Differences among habitats observed in this study are likely attributable to ontogenetic changes in habitat use and variation in habitat-specific fishing mortality. Because this study represents one of the first habitat-specific assessments (i.e., artificial vs. natural) of Red Snapper size structure, age, and growth, continued habitat-specific monitoring will be necessary to estimate how these parameters change as the stock recovers.

In Chapter 3, I evaluated the performance of SEAMAP vertical lines at artificial reefs and natural banks. In addition, I demonstrated the utility of a paired camera survey to compliment traditional catch data. My results indicate gear efficiency differs between habitat types, which is a concern if vertical lines are to be used for comparing relative abundance among habitats. Shallower hook positions have a lower efficiency than deeper hook positions at natural banks, while all hook positions have similar efficiencies at both artificial habitat types. The use of paired video is valuable in characterizing other aspects of gear performance such as bait removal, interspecific interactions with the gear, and gear saturation. Notably, video revealed vertical line saturation is a common issue, occurring on 70% of the paired deployments but more commonly at artificial habitats. The high prevalence of gear saturation observed in this study suggests vertical line CPUE is likely not proportional to true abundance and may be a poor indicator of differences in abundance at the habitats examined in this study. Thus, it is imperative that future studies evaluate the prevalence of saturation in the study area to determine if vertical line CPUE is a reliable indicator of relative abundance.

In Chapter 4, I conducted a before-after control-impact study to determine what effect a new artificial reef would have on Red Snapper and other reef-associated fishes. I specifically examined relative abundance, size structure, and age of fish colonizing the new reef. This study showed that the Corpus Christi Nearshore Reef (CCNR) provides valuable nursery habitat to juvenile Red Snapper and perhaps Gray Triggerfish (*Balistes capriscus*). Prior to reef construction, and in the absence of structured reef habitat, juvenile Red Snapper appear to occur in extremely low abundances over the ambient mud substrates that are common in our region. However, these results show that Red Snapper and other reef-associated fish increased in abundance following reef construction. Distinct cohorts of Red Snapper were followed through time, suggesting site fidelity; however, few fish older than 2 years of age appear to remain at the reef. It is unclear from my study how fishing mortality and emigration contribute to this lack of older individuals at CCNR; therefore, future studies are needed to unravel the importance of these processes. Nevertheless, given that juvenile Red Snapper are present in higher densities, appear to be in good condition and growing quickly, and are no longer exposed to shrimp trawl mortality, the CCNR likely enhances the export of juveniles (i.e., production) to the adult population.

Collectively, my results suggest that artificial reefs can be valuable habitat for enhancing the GOM Red Snapper stock. Given the comparatively large area of natural habitats in the GOM, artificial reefs may be an effective management option to divert fishing effort away from a large portion of the stock. Furthermore, fish at artificial habitats appear to grow as well as those on natural habitats, and based on a concurrent study (Downey 2016), similar aged fish appear to have similar reproductive potential. Finally, nearshore reefs like CCNR can provide nursery habitat to juveniles and may enhance production. To increase the effectiveness of artificial reefs in supporting GOM Red Snapper, future research should identify reef designs that maximize growth and survival. In addition, continued habitat-specific monitoring will be required to refine our understanding of how different habitat types contribute to the rebuilding and maintenance of the GOM Red Snapper stock.

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BIOGRAPHICAL SKETCH

Matthew (Matt) Karl Streich was born in July 1988, in Philadelphia, Pennsylvania. He grew up in Lilburn, Georgia, graduating from Parkview High School in 2006. Matt attended the University of Georgia and majored in Fisheries and Aquaculture at the Warnell School of Forestry and Natural Resources. During his undergraduate, he spent several field seasons assisting with research on endangered sturgeon populations in the Altamaha River Estuary near Darien, Georgia. Matt's undergraduate thesis research investigated the use of the estuary as a nursery for Bull Sharks. After graduating with a Bachelor of Science degree in May 2010, Matt continued at the University of Georgia where he earned a Master of Science degree under the supervision of Dr. Doug Peterson in August 2012. In collaboration with the Georgia Department of Natural Resources, Matt's thesis research focused on the seasonal residence and habitat use of Tripletail in the estuarine waters of Ossabaw Sound near Savannah, Georgia. Matt then moved to Texas, entering the doctoral program at Texas A&M University-Corpus Christi in fall 2012. There he joined the Fisheries and Ocean Health Laboratory of Dr. Greg Stunz at the Harte Research Institute for Gulf of Mexico Studies to begin his research of artificial reefs and Red Snapper. Matt is a member of the American Fisheries Society and has presented his research at various local, regional, and national conferences. He is also an avid sportsman and a member of the Coastal Conservation Association and Ducks Unlimited. Matt will earn a Doctor of Philosophy degree in Marine Biology from Texas A&M University in December 2016. Following graduation, he will begin a position as a post-doctoral research associate in the Center for Sportfish Science and Conservation at the Harte Research Institute for Gulf of Mexico Studies.