REPRODUCTION AND DIET OF RED SNAPPER *LUTJANUS CAMPECHANUS* ON NATURAL AND ARTIFICIAL REEFS IN THE NORTHWESTERN GULF OF MEXICO

A Thesis

by

CHARLES H. DOWNEY

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

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December 2016

ABSTRACT

Energy exploration in the Gulf of Mexico (Gulf) has resulted in the addition of numerous oil and gas production platforms adding structurally complex habitat to an area otherwise comprised of primarily barren mud/sand bottom. The impact of these artificial structures on fish populations is generally unknown, and there is ongoing debate regarding their performance in comparison to natural reefs. Thus, the purpose of this study was to characterize trends in Red Snapper reproduction and diet in the northwestern Gulf at oil and gas platforms relative to natural reefs. Red Snapper were collected from standing and reefed platforms and natural hard-bottom. Fecundity parameters (sex, total weight, gonad weight, total length) were measured, and these data showed Red Snapper fecundity and spawning behavior were similar among natural, standing, and reefed habitats. These results suggest that artificial reefs are functionally similar to natural reefs in terms of reproductive output. I also examined the composition of prey items present in the stomachs of Red Snapper at each of these areas. I found that prey composition among habitats was similar, and there was a temporal influence on the composition of fish diets. In addition, I created feeding strategy diagrams for each habitat type which showed that Red Snapper exhibit similar strategies of prey selection at all habitats. Therefore, artificial reefs appear to be providing a similar means of prey selection as natural banks for Red Snapper in the northwestern Gulf. Furthermore, based on comparative studies, apparent differences exist in the Gulf indicating there may be regional differences in these life history characteristics that could influence the management of this species. Future studies should consider site specific characteristics to further clarify the question of habitat influence on reproduction and diet which would improve reefing strategies in the northwestern Gulf of Mexico. Collectively, this study

suggests that artificial reefs are a valid tool for creating additional habitat for Red Snapper in the northwestern Gulf in terms of feeding and reproduction.

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GENERAL INTRODUCTION AND RATIONALE

Red Snapper *Lutjanus campechanus* is an economically and ecologically important reef fish ranging from North Carolina throughout the Gulf of Mexico (Gulf) to the Yucatan Peninsula (Bradley and Bryan 1975; White and Palmer 2004). This species has been fished commercially and recreationally in the Gulf of Mexico since the 1840s (Hood et al. 2007), but management of Red Snapper did not begin until 1976 under the Magnuson-Stevens Fisheries Management and Conservation Act. In 1981 the reef fish fisheries management plan reported that the population was in decline and in 1984 regulations were put in place in an attempt to rebuild the stock (Hood et al. 2007). Since 1994 Red Snapper has been considered overfished (Gallaway et al. 2009) although no longer undergoing overfishing, and the populations have been in a state of strong recovery, particularly in the western Gulf of Mexico (GMFMC 2010, 2012). However, management of Red Snapper remains extremely controversial in that allocation of the catch between the commercial and recreational sectors as well as among groups within the recreational sector is highly contested. This creates a need for accurate data regarding basic biological parameters that can improve our understanding of this population and allay these conflicts.

Red Snapper are a long-lived species, reaching 50+ years (Szedlmayer and Shipp 1994; Wilson and Nieland 2001). They mature by age 2 and a single individual is capable of producing 55.5 million eggs over its lifespan (Szedlmayer and Shipp 1994; Wilson and Nieland 2001; SEDAR 2005). After spawning, there is an approximate 1-day egg duration (20-27 hours) followed by a 26 to 30-day planktonic stage after which the larvae settle out at about 16-18 mm total length (TL; Gallaway et al. 2009). Larvae are initially attracted to low relief habitat then shift to larger, high relief structures as they grow, then enter the directed fishery at about age 2 or 200 mm total length (Gallaway et al. 2009; Szedlmayer and Lee 2004; Wells 2004). Bottom longline surveys indicate that Red Snapper are most abundant between 55-92m depth. As a demersal fish they are associated with hard substrates, often occupying natural banks, ridges, and reefs throughout their range and show an affinity for vertical structures (Patterson et al. 2001; Walter and Ingram 2009). Furthermore, early studies suggest long term residence of Red Snapper around natural hard-bottom structure (Beaumariage and Bullock 1976).

The Gulf of Mexico is largely bare, mud/sand bottom with relatively few areas of natural hard substrate, potentially limiting natural habitat for red snapper. There is 2,571 km^2 of natural reef habitat between 18 and 91m depth from Pensacola, FL to Pass Cavallo, TX, about 3.3% of the total area, and only 1.6% of this is greater than 1 m relief (Parker 1983). From Pass Cavallo, TX to the Rio Grande only 1.3% of the shelf area was estimated to be reef habitat. On the western Gulf shelf total reef area is 1,578 km^2 including natural and artificial reefs, which amounts to less than 2% of the total shelf area (Gallaway 2009). Therefore, availability of structure may be a limiting factor to Red Snapper productivity and may be an important factor for population control in the Gulf of Mexico (Gallaway et al. 2009; Shipp and Bortone 2009). However, the addition of numerous oil and gas platforms to the western Gulf has inadvertently created a relatively large amount of artificial reef habitat, and may have contributed to stock recovery (Shipp and Bortone 2009). Additionally, intentional artificial reef development has increased during the last few decades for habitat restoration or mitigation, recreation, and fisheries enhancement (Pitcher and Seaman 2000; Baine 2001; Baine and Side 2003; Dupont 2008).

There are an estimated 3.1 million Red Snapper located on oil and gas platforms in the western Gulf (Gallaway et al. 2009). There is evidence that a high proportion of Red Snapper populations found at artificial reefs are age 2 and after age 8 are less abundant, likely caused by a decrease in dependence on structure due to size refugia (Gallaway et al. 2009). However, several mark and recapture studies show that Red Snapper have high site fidelity to structure (Beaumariage 1969; Beaumariage and Bullock 1976; Gallaway 1981; Szedmayer and Ship 1994); individuals stay within an average of 22.3 m away from reef sites over a 24-h period and a maximum reported distance of 66 m (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011). Additional acoustic tagging studies found similar results with 94% of individuals showing no movement between receivers within a study area of about 12 km^2 (Peabody and Wilson 2006). These findings suggest that artificial reefs may be an important habitat for Red Snapper in the Gulf of Mexico.

In Texas artificial reefs are created using several methods; nearshore reefs are often constructed of concrete culverts, pyramids and ships, while offshore reefs are generally constructed of modified decommissioned oil and gas platforms. To manage this habitat, the Texas Artificial Reef Plan, created by Texas Legislature and implemented in 1990 by Texas Parks and Wildlife, resulted in one of the largest artificial reef programs in the United States with over 16,000 km^2 of reef structure within Texas Gulf waters. Recently, a federal directive, known as “Idle Iron Policy”, mandated the speedy removal of inactive platforms. The high decommissioning and removal rate due to Idle Iron raised concern for the loss of habitat and diversity associated with these structures. From this concern several pieces of legislation have been proposed, such as the “Rigs to Reefs” Habitat Protection Act (re-introduced 2013), to preserve these structures in standing form. Under the Texas Rigs to Reefs plan, decommissioned oil and gas platforms can be turned into reefs by cutting off the rig 85 ft. below the surface or by placing explosives in the base of the rig below the subsurface and laying the entire structure on its side. However, the ideal reefing strategy is not known and the function of artificial reefs compared to natural reefs is largely unknown, and is much debated (Cowan et al. 2011).

Given the economic importance and controversial nature of the management of Red Snapper, there is a need for a comprehensive assessment of life history characteristics such as reproduction and diet of Red Snapper to determine the relative importance of natural and artificial reefs for the fish stock. This information will serve to determine the value of offshore habitats to Red Snapper and fill knowledge gaps for successful management of the species in the western Gulf of Mexico. This study will also directly address recommendations in the last South East Data Assessment and Review (SEDAR) requesting histology analysis and fecundity data for all areas of the Gulf of Mexico to improve the management of these populations, especially the western Gulf (SEDAR 2013).

CHAPTER 1

RED SNAPPER *LUTJANUS CAMPECHANUS* ARE REPRODUCTIVELY SIMILAR ON NATURAL AND ARTIFICIAL HABITATS IN THE NORTHWESTERN GULF OF MEXICO

Introduction

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

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

The relative value of these artificial reefs in comparison to natural habitat is still widely debated. Several studies argue that artificial reefs do not provide suitable habitat and also increase fishing pressure, which act together to create a sink in the population (Jackson et al. 2007; Walters et al. 2008; Cowan et al. 2011). However, others have argued that artificial reefs do provide suitable habitat and have significantly contributed to the recovery of Red Snapper in the Gulf (Szedlmayer 2007; Gallway et al. 2009; Shipp and Bortone 2009; Streich et al. in review). As many platforms are mandated for removal due to federal regulations such as "Idle Iron" (United States Department of the Interior 2010), it is important to understand how artificial structures function in comparison to natural reefs to provide key data to determine if these structure and enhancing the population.

Generally, reproductive characteristics of Red Snapper have been well-studied in the Gulf. Red Snapper have been shown to be sexually mature by age 2 and are asynchronous batch spawners that develop oocytes continuously, but at different rates within a single individual (Porch et al. 2007; Lowerre-Barbieri et al. 2011). Fecundity has been shown to increase with age, and individuals spawn multiple times throughout the season with diel periodicity (Winemiller and Rose 1992, 1993; Collins et al. 2001; Jackson et al. 2006). Red Snapper are long-lived, capable of reaching 50 years in age, and potentially producing 55.5 million eggs over their lifespan (Szedlmayer and Shipp 1994; Wilson and Nieland 2001; SEDAR 2005). Generally, spawning in the Gulf is thought to occur from April through September (Bradley and Bryan 1975; Gallaway et al. 2009), with peak spawning occurring along the Texas coast during June, July and August (Collins et al. 2001).

Previous studies of Red Snapper reproduction in the Gulf of Mexico have focused on the northern Gulf near Louisiana and Alabama (Collins et al. 2001; Woods et al. 2003; Jackson et al. 2006, 2007; Kulaw 2012), Florida (Brown-Peterson et al. 2008), and the southern Gulf (Brulé et al. 2010). Offshore of Louisiana, differences in GSI, maturity, and spawning frequency were found among natural shelf-edge banks, standing platform sites, and toppled platform sites (Kulaw 2012). Additionally, differences in reproduction, including gonadosomatic index (GSI), spawning frequency, and batch fecundity were found among six sites including differences among Red Snapper collected offshore of Galveston and South Padre Island, TX (Kulaw 2012).

Variation in size at maturity has been found between fish collected offshore of Louisiana and Alabama, with Alabama Red Snapper reaching maturity at smaller sizes but similar ages (Woods et al. 2003). In Florida, east and west coast Red Snapper appear to exhibit reproductive differences in spawning seasonality, batch fecundity, and spawning frequency (Brown-Peterson et al. 2008). Red Snapper from Florida (Brown-Peterson et al. 2008) and the northern Gulf (Woods et al. 2003) show differences in spawning seasonality from the southern Gulf near the Yucatan Peninsula, with Red Snapper in the southern Gulf exhibiting protracted spawning seasons, possibly due to the warmer waters (Brulé et al. 2010).These studies suggest there may be regional differences in reproduction throughout the Gulf; specifically that there could be differences in the western Gulf compared to previously studied regions as well as localized differences among habitat types. Thus, these differences in region and habitat type warrant further research.

Few studies have investigated differences in Red Snapper reproduction among habitat types, particularly in the western Gulf. To date, the focus has been on large spatial and regional differences, on the order of 1000s of km (Brown-Peterson et al. 2008; Kulaw 2012). Population-level effects of artificial structures on Red Snapper reproduction are sparse; yet, there is the potential for enhancement of fish production by providing additional habitat (Powers et al. 2003). In addition, there is growing evidence that subpopulations of Red Snapper exist throughout the Gulf that could drive important differences in life history parameters such as reproduction (Gold and Saillant 2007). To address this debate, it is essential to understand if Red Snapper are using these habitats similarly by identifying reproductive parameters at different habitat types. Given the lack of information on life history differences between natural reefs and artificial habitat in the Gulf of Mexico, the purpose of this study is to further characterize regional trends in Red Snapper reproduction in the western Gulf of Mexico with particular interest in the influence of oil and gas platforms on Red Snapper reproductive parameters relative to natural reefs. This study is particularly relevant to management in that a recent report of the Southeast Data Assessment and Review - SEDAR 31 specifically requested reproduction data from the western Gulf (SEDAR 2013). Specifically, this study had the following objectives:

1. Evaluate reproductive parameters such as fecundity and maturity of Red Snapper and compare them among offshore habitats in the northwestern Gulf of Mexico.

   H_a: Habitat type influences reproductive parameters in the northwestern Gulf of Mexico.

2. Use reproduction data to make recommendations about habitat types in relation to reefing, fisheries enhancement, and restoration strategies in the northwestern Gulf of Mexico.

Methods

Study Area

The study area was located in the western Gulf of Mexico approximately 45-60 nautical miles east of Port Aransas, Texas (Figure 1). Three habitat types with three replicate sites each were sampled (n=9 total sites): natural banks (natural: Aransas Bank, Baker Bank, and South Baker), standing oil and gas platforms (standing: MU-A-111-A, MU-A-85-A, and BA-133-A), and "reefed" oil and gas platforms (reefed: MU-A-85, MI-A-7, and BA-A-132) that were decommissioned oil and gas platforms converted to artificial reefs. The sites were selected within a 30 nautical mile area, and were restricted to 60-90 m of water to control for bottom depth.

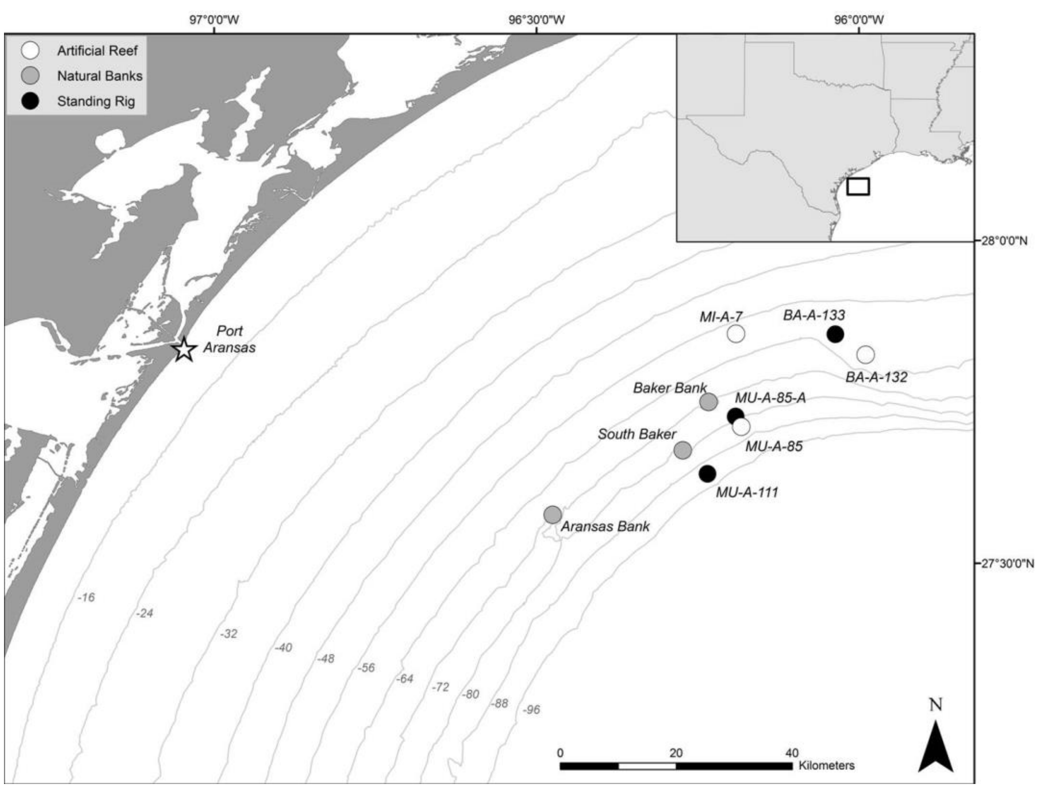

Figure 1.1: The study area was comprised of nine sites located in the northwestern Gulf of Mexico offshore of Port Aransas, Texas. Each habitat type was represented by three sites. Natural bank sites are: Baker, South Baker, and Aransas Bank. Standing rig sites are: BA-A-133, MU-A-85A, and MU-A-111. Artificial reef sites are: MI-A-7, BA-A-132, and MU-A-85.

Collection and Sample Processing

Red Snapper were collected from 2013-2015 during April through October, in an effort to capture the extent of the spawning season, (Woods 2003; Fitzhugh et al. 2004; Jackson et al. 2007) using Gulf-wide standardized vertical longline sampling following the Southeast Area Monitoring and Assessment Program (SEAMAP) protocol (Gregalis et al. 2012). Individuals were tagged with an identifying label in the field and kept on ice and brought to the laboratory for processing. Total weight (TW, kg) and total length (TL, mm) were recorded. Fish were dissected to collect biological samples, including gonad weight (g) and otoliths. Sex was determined by macroscopic examination of gonads. I calculated a condition index for female fish (relative weight, *Wr* = measured weight (lbs)/predicted weight (lbs)* 100; Anderson and Neumann 1996) using the TL (in) to weight (lbs) conversion formula for Red Snapper from SEDAR 31 to obtain the predicted weight of the fish based on its length (*W* = 0.00047 * TL ^2.994, SEDAR 2013). A *Wr* value of 100 is interpreted as a healthy individual and is used as a benchmark for comparison among samples and populations (Murphy et al. 1990). A value well below 100 means the individual is in relatively poor condition compared to the population mean while a value above 100 means the individual is in better condition relative to the population mean (Murphy et al. 1990).

Red Snapper otoliths were weighed and processed following VanderKooy (2009). Thin sections containing the core of the left sagittal otolith were mounted to slides and viewed under a dissecting microscope. Two independent readers made blind counts of opaque annuli and assigned an edge code according to the development of the marginal edge following VanderKooy (2009). When counts of annuli differed between the two readers, the section was jointly examined and a consensus was reached. Age was determined based on the annuli count and edge code assigned (Allman et al. 2005).

Reproduction status was determined by using well-established methods (Erickson et al. 1985; Fitzhugh et al. 2004; Kulaw 2012). Briefly, Ovaries were fixed in 10% formalin for a minimum of two weeks. Ovary subsamples (2mm) were randomly taken from tissue post-fixation and secured in labeled histology cassettes. The subsamples were encased in paraffin wax, cut into 4 μm sections and stained using hematoxylin and eosin. Red Snapper oocytes develop continuously and asynchronously throughout the spawning season, and progresses through stages starting with primary growth (PG) followed by cortical alveoli (CA), vitellogenic (V), and hydrated (H; Wallace and Selman 1981; Glenn 2014). Thus, a reproductive stage was assigned and maturity was determined through microscopic examination (Olympus BX51, 40-100x) based on the most advanced oocyte stage present. An individual was considered spawning capable if the ovary exhibited vitellogenic stage oocytes (Hunter and Goldberg 1980; Jackson et al. 2007; Brown-Peterson et al. 2011). Two other oocyte spawning markers were also considered: atresia (ATR), the breakdown and resorption of oocytes into the body, and post ovulatory follicles (POF), the remains of hydrated cells after spawning which indicate recent spawning activity.

Reproductive Biology Analysis

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

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

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

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

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

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

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

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

Statistical Analyses

Differences in TL, age, *Wr*, GSI, BFE, and AFE among habitat types and season were assessed using nested ANOVA (Site within Habitat). GSI values were arcsine square root transformed to correct for ratio data (Gotelli and Ellison 2004). ANCOVA was used to test for differences in BFE and AFE at age among habitat types. ANCOVAs were restricted to the ages 4 through 8, where at least one individual per age exhibited hydrated oocytes for BFE and AFE to be determined. Chi-square tests were performed to examine differences in male:female ratios, spawning frequency, and number of spawning capable individuals. Univariate statistics were performed using R Statistical Software v3.3.1. Individuals classified by the most advanced oocyte stages were grouped by sample site and date to create a sampling event containing the count of oocyte stage classifications identified for a particular site on a particular date. These sampling events were square root transformed, and then a Bray-Curtis index of similarity was calculated. A multidimensional scaling (MDS) plot of reproductive stage by habitat was created to visualize differences in oocyte composition. A permutational analysis of variance (PERMANOVA) was conducted to examine the statistical differences in oocyte stage distribution among habitat and month, with site nested in habitat (Clarke et al. 2014). Multivariate statistical analyses were conducted in PRIMER-E. Results were considered significant at $\alpha \leq 0.05$.

Results

A total of 1585 Red Snapper were collected. Of these, 863 were male, 717 were female, and 5 had indeterminate sex. There were significantly more males collected across all habitat types in this study (χ^2 = 13.49, df = 1, P = 0.0002; Figure 1.2). There were fewer females than males collected on artificial reefed habitats (χ^2 = 16.45, df = 1, P = 5e-16; Figure 2), however, male:female ratios were not significantly different on natural and artificial standing habitats (natural: χ^2 = 0.33, df = 1, P = 0.56; standing: χ^2 = 2.49, df = 1, P = 0.11; Figure 1.2).

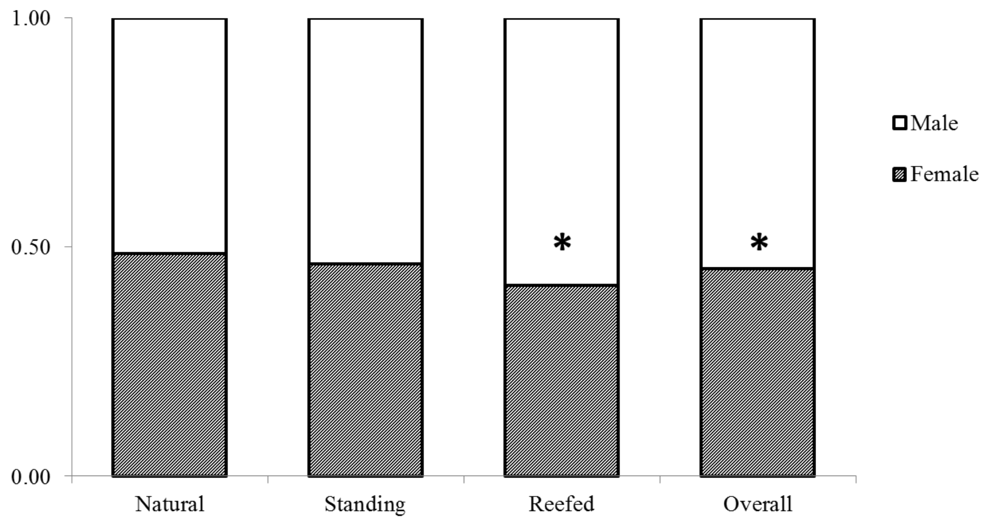

Figure 1.2: Male:Female ratio of Red Snapper *Lutjanus campechanus* collected in the northwestern Gulf of Mexico by habitat type (natural = 505, standing = 491, reefed = 584 and overall = 1580). Chi-square analysis was used to test Male:Female ratios on each habitat, an asterisk (*) denotes significance at $p < 0.05$.

Out of the 717 total female Red Snapper, 544 were collected during the spawning season from natural (n =175), standing (n = 177), and reefed (n = 192) habitats and were included in spawning season analyses. Ages of females collected during the spawning season ranged from 2 to 14 years with TLs of 276 to 767 mm and were generally similar among habitat types. Red Snapper from natural habitats were 2 to 10 years old with TLs ranging from 294 to 739 mm, individuals from standing habitats were 2 to 14 years old with TLs of 300 to 694 mm, and individuals collected from reefed habitats were 2 to 14 years old with TLs ranging from 276 to 767 mm. The mean age (natural = 6.2, standing = 5.0, reefed = 5.8) and TLs (natural = 549, standing = 503, reefed = 545) of female Red Snapper collected during the spawning season was similar among habitats (ANOVA (age): $F = 0.39$, df = 2, $P = 0.19$; ANOVA (TL): $F = 0.23$, df = 2, $P = 0.28$).

Since condition can affect reproductive output of fish I used *Wr* to assess the condition of female Red Snapper from each habitat type. The *Wr* on natural (104±8), standing (107±16), and reefed (105±10) habitats was not significantly different (ANOVA: F = 1.73, df = 2, P = 0.25; Figure 1.3). The similarity in *Wr* indicates the fish on each habitat are in similar condition.

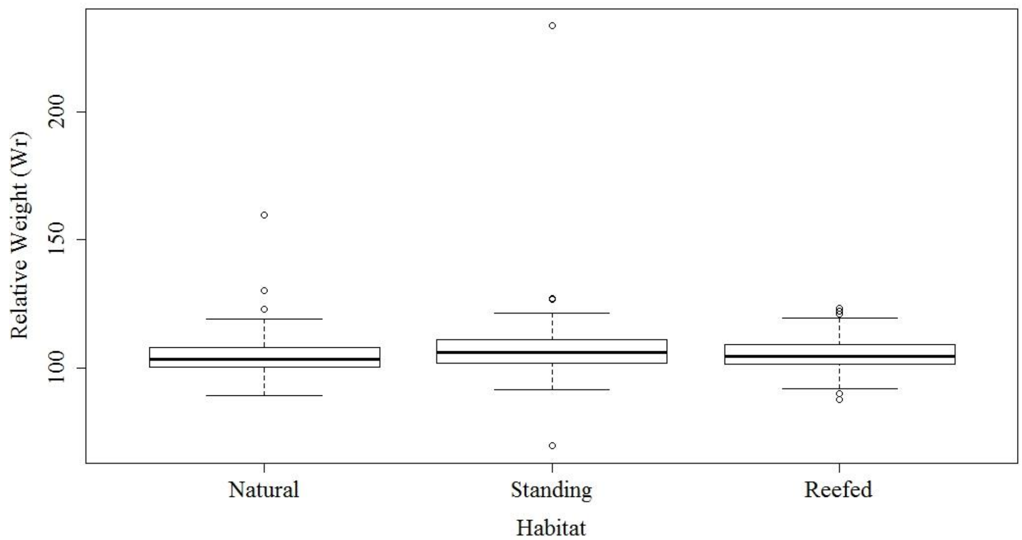

Figure 1.3: Boxplot of the condition index, relative weight (Wr), for Red Snapper *Lutjanus campechanus* collected on natural, standing and reefed habitats in the northwestern Gulf of Mexico. The median, 25-75% inner-quartile range, and 95% confidence interval along with outliers are shown. Wr among habitats was tested using nested ANOVA (Site within Habitat) and no statistical differences were found (F = 1.73, df = 2, P = 0.25).

To examine the overall effort put into reproduction by Red Snapper among habitats, I calculated GSI to compare among habitats. There was no difference found among habitats for male or female Red Snapper. The mean GSI of Females collected from natural (0.956±0.084), standing (0.901±0.080), and reefed (0.752±0.058) habitats were not significantly different (ANOVA: F = 0.46, df = 2, P = 0.65; Figure 4). The differences in the GSI of males collected from natural (0.783±0.070), standing (0.848±0.071), and reefed (0.500±0.051) habitats were also not significant (ANOVA: F = 1.84, df = 2, P = 0.12; Figure 1.4).

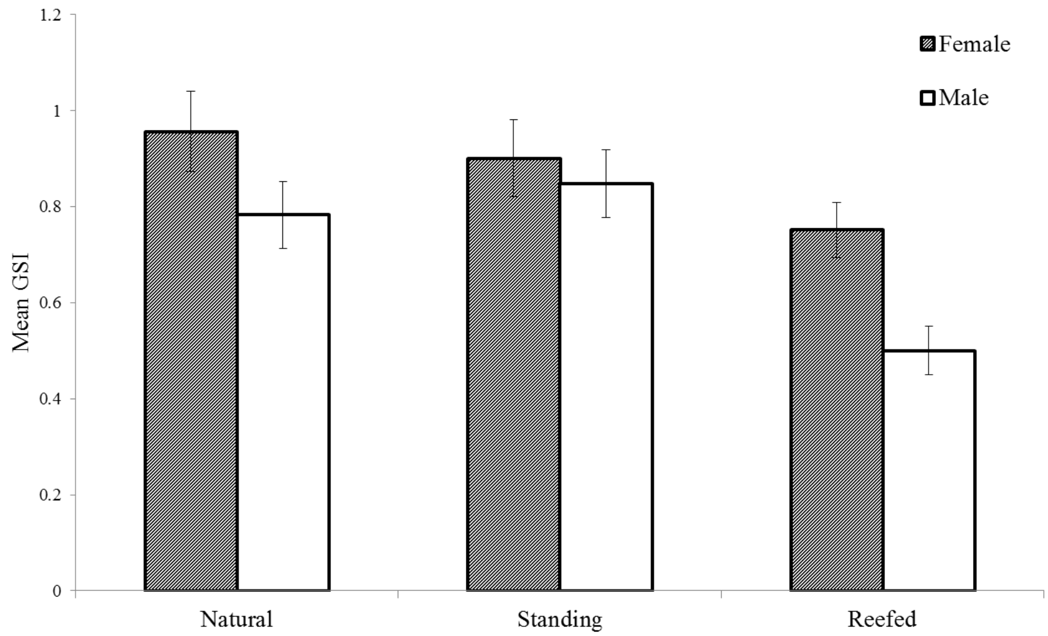

Figure 1.4: Mean gonadosomatic index (GSI) and standard error of male and female Red Snapper *Lutjanus campechanus* collected during the spawning season (May – August) from natural, standing, and reefed habitats in the northwestern Gulf of Mexico. Mean GSI was tested for each sex among habitats using nested ANOVA (Site within Habitat) and no statistical differences were found (females: F = 0.46, df = 2, P = 0.65; males: F = 1.84, df = 2, P = 0.12).

Female GSI values at all habitats were low in May (natural = 0.578, standing = 0.790, reefed = 0.700), increased to a peak in June (natural = 1.284, standing = 1.469, reefed = 1.097), before decreasing in July (natural = 0.701, standing = 0.498, reefed = 0.707) and in August (natural = 0.745, standing = 0.408, reefed = 0.406). In July, female GSI values on standing reefs were lower than on both natural and reefed habitats, while in August both standing and reefed GSI values appeared lower than natural areas. However, these differences were not significant and overall there were no significant differences in female GSI among habitats within each month of the spawning season (ANOVA habitat*month: $F = 0.94$, df = 6, $P = 0.47$; Figure 1.5) although month was significant overall (ANOVA: $F = 28.73$, df = 3, $p < 0.0001$; Figure 1.5).

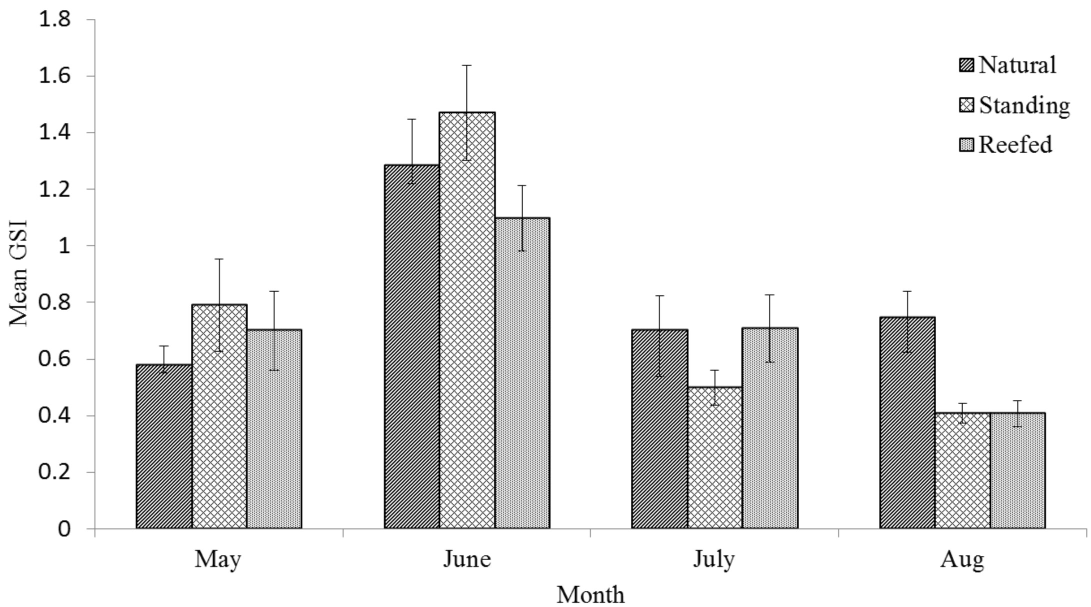

Figure 1.5: Mean GSI and standard error per month and habitat of female Red Snapper *Lutjanus campechanus* collected during the spawning season in the northwestern Gulf of Mexico. The effects of habitat within each month on mean GSI was tested using nested ANOVA (Site within Habitat) and there were no significant differences among habitats within each month ($F = 0.94$, df = 6, $P = 0.47$). The effect of month on mean GSI was also tested and was found to be significant ($F = 28.73$, df = 3, $p < 0.0001$).

A total of 526 females were assigned a reproductive stage and percent spawning capability was determined by habitat type to be: 87% at natural banks, 79% at standing platforms, and 73% at reefed platforms (Figure 1.6). The percentage of spawning capable individuals among habitat types was not significantly different from one another ($\chi^2 = 1.24$; $P = 0.53$).

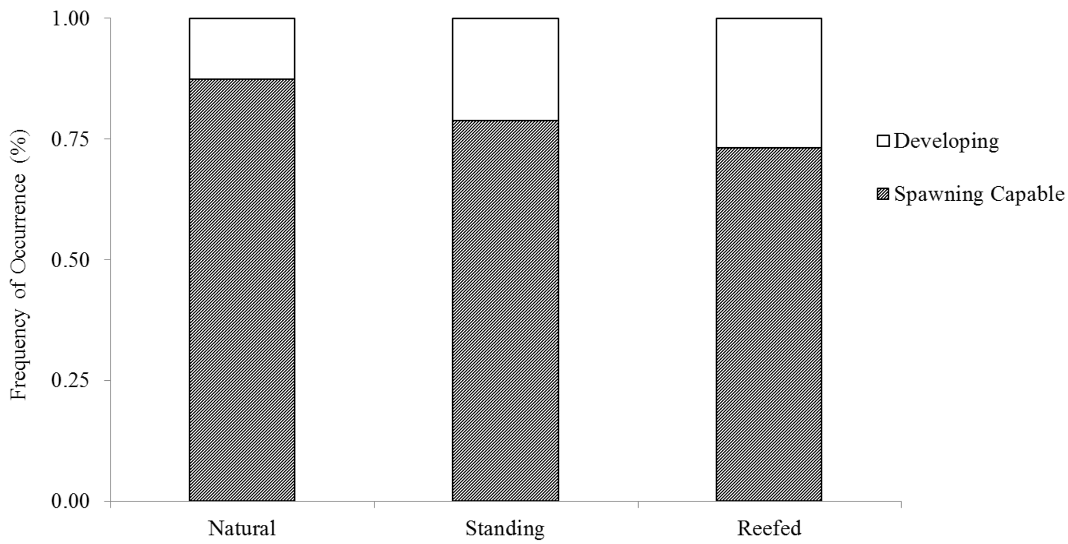

Figure 1.6: The percent Frequency of Occurrence (%FO) of spawning capable female Red Snapper *Lutjanus campechanus* collected in the northwestern Gulf of Mexico on natural, standing, and reefed habitats. Spawning capable refers to individuals exhibiting vitellogenic or more advanced oocytes. The %FO among habitats was compared using chi-square and there were no significant differences identified ($\chi 2 = 1.24$, $P = 0.53$).

The MDS plot did not reveal a discernable pattern among habitat types where any single habitat grouped out separately from the others (Figure 1.7). Further analysis by PERMANOVA statistically confirmed that there was not a significant difference among the three habitat types in terms of the distribution of most advanced oocyte stages (*Pseudo-F* = 1.35, df = 2, $P = 0.33$).

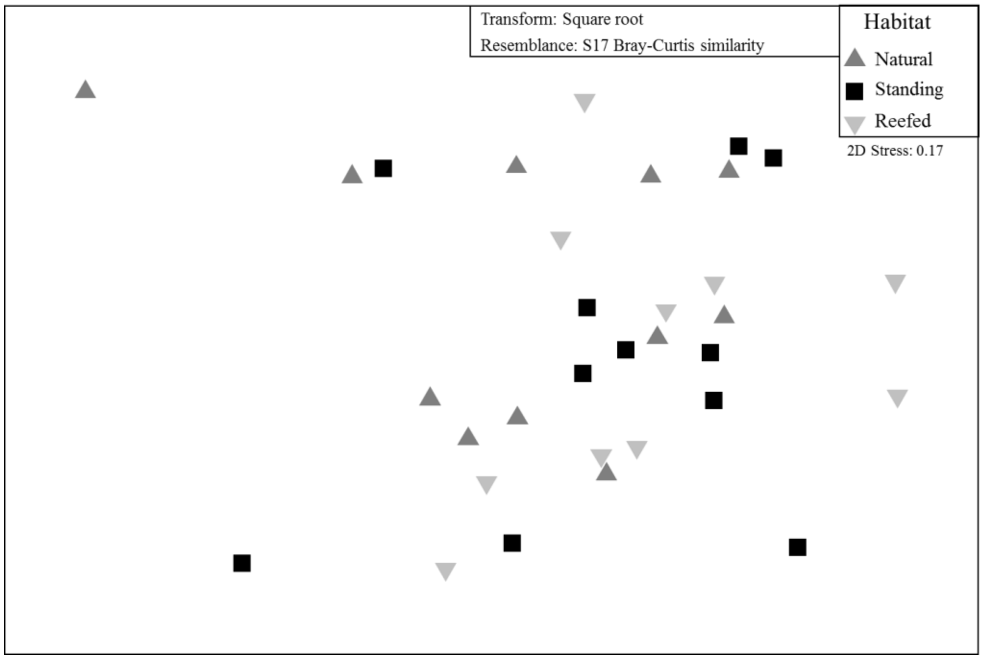

Figure 1.7: A multidimensional scaling (MDS) ordination of oocyte stage distribution by habitat type of female Red Snapper *Lutjanus campechanus* collected in the northwestern Gulf of Mexico. Oocyte stages were grouped by sample site and date, square root transformed, and a Bray-Curtis similarity calculated on the resulting oocyte composition per sampling event.

Batch fecundity estimates and annual fecundity estimates were calculated for all hydrated females (n = 71; natural = 21, standing = 27, reefed = 23), and time-calibrated spawning frequency was calculated for fish exhibiting spawning markers (V, H, & POF; n = 421). The largest mean BFE was calculated for natural habitats which also exhibited the largest mean AFE. Standing habitats exhibited the next largest mean BFE and mean AFE values while reefed habitats exhibited the lowest of both mean BFE and mean AFE. However, standing habitats exhibited the fastest spawning frequency which resulted in the most spawning events per season followed by natural habitats, then reefed habitats. Although apparent differences in mean BFE and AFE existed, standard error for each habitat type was large; therefore, BFE (ANOVA: F =

0.50, df = 2, *P* = 0.64), SFE (χ^2 = 0.539, p = 0.76), and AFE (ANOVA: *F* = 1.20, df = 2, *P* = 0.39) were not significantly different among habitat types (Table 1.1).

Table 1.1: Overview of female reproductive characteristics from Red Snapper *Lutjanus campechanus* collected in the northwestern Gulf of Mexico on natural, standing, and reefed habitats from May – August in the years 2013-2015 combined. Spawning frequency (SFE) is reported in days. Batch fecundity (BFE) and annual fecundity (AFE) are reported as mean ± standard error (SE).

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

Both BFE and AFE showed an increasing trend with age for Red Snapper between 4 and 8 years (Figure 1.8a and b). Age was significant in predicting BFE (ANCOVA: *F* = 20.14, df = 1, *P* = $3.19\text{x}10^{-5}$), while habitat type was not (ANCOVA: *F* = 0.75, df = 2, *P* = 0.48; Figure 1.8a). A similar trend was apparent for AFE where age was a significant predictor (ANCOVA: *F* = 16.69, df = 1, *P* = 0.0001; Figure 1.8b) but not habitat (ANCOVA: *F* = 1.59, df = 2, *P* = 0.21; Figure 1.8b).

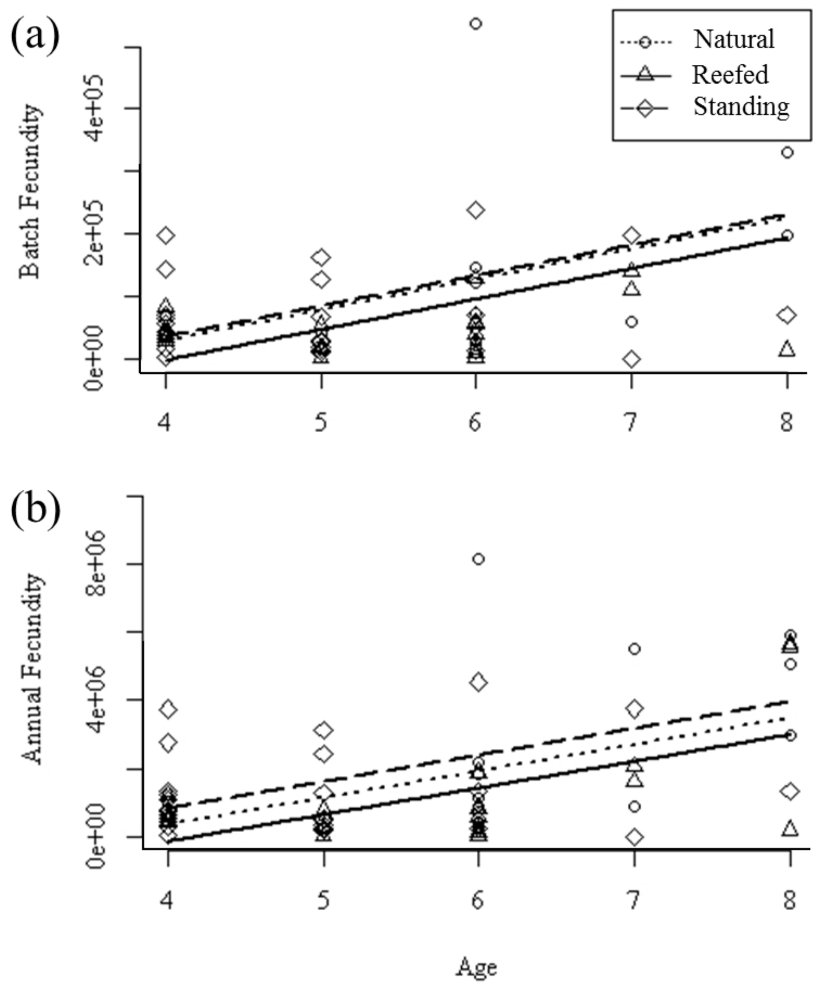

Figure 1.8: Batch fecundity (a) and annual fecundity (b) by age and habitat of female Red Snapper *Lutjanus campechanus* collected in the northwestern Gulf of Mexico. Differences in BFE and AFE per age were tested among habitats using ANCOVA. There were no statistical differences in BFE (F = 0.75, df = 2, P = 0.48) or AFE (F = 1.59, df = 2, P = 0.21) among habitat types by age; while age was significant in predicting BFE (F = 20.14, df = 1, P = $3.19\text{x}10^{-5}$) and AFE (F = 16.69, df = 1, P = 0.0001).

Discussion

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

While our study showed that reproductive characteristics were similar among habitat types, other studies have shown differences in Red Snapper reproductive characteristics between natural and artificial habitats. Kulaw (2012) found that natural banks yielded the highest GSI out of the habitats, although SFE was not found to be significant; however, this study was characterized by low sample size of hydrated females (n = 8), and their numbers did not allow for statistical comparisons of BFE and AFE between habitats. Glenn (2014) also found the reproductive potential of Red Snapper at artificial reefs to differ significantly from natural reefs located on the Louisiana shelf edge. A GSI value greater than 1 are generally associated with spawning, and Glenn (2014) observed these “spawning” values only in June on artificial reefs (Grimes 1987; Collins et al. 1996). This was interpreted as a truncated spawning season for fish found on artificial habitat. However, in this study similar GSI patterns were observed for all habitat types. Additionally, spawning capable and hydrated females were identified during all months of the spawning season, at times with GSI values < 1, which correlates with GSI values above 0.5 indicating the onset of vitellogenesis as found by Fitzhugh et al. (2004). Glenn (2014) also found mean BFE to be lower on the artificial reef site than on the natural sites; however, these results were based on a relatively small sample size (only nine hydrated females were identified; two from natural reefs and seven from the artificial site), and an unequal size distribution of hydrated fish; one of the two fish from natural sites was the largest fish sampled and exhibited the highest fecundity. These results here with a much larger representation of fish showed similar spawning characteristics using increased sample size (71 vs 8 hydrated fish), fish of similar lengths, and an equal distribution among habitat types (natural = 21, standing = 27, reefed = 23). Additionally, during site location and fish collection, a directed effort was made in our study to control for depth and proximity of habitat types, and these geographic differences may have confounded some of the previous findings, artificially inflating habitat differences. For example, site selection in these previous studies was limited due to the distribution of natural habitat along the Louisiana shelf edge which resulted in site depths ranging from 55–160 m (Kulaw 2012; Glenn 2014). In contrast, depth of the sites selected for this study ranged from 60-90 m. Therefore, reproductive differences identified between habitats may also be related to physical differences of sample location rather than habitat type and large differences in reproductive potential have been observed across the Gulf (Porch et al. 2015).

I found no statistical differences in fish condition, TL, and age among habitats during the spawning season which suggests the similarities in reproductive characteristics among habitats did not have differing influences from age and length. In previous studies, the differences between Red Snapper reproduction found on artificial and natural reefs were attributed to several factors including fish size and age, as well as nutritional condition, but that was not what was observed here. For example, Kulaw (2012) found differences in fish size and age among habitats. In addition, natural banks had a larger slope on length-weight regressions than artificial habitats, which can be interpreted as the fish being in better condition. However, it was acknowledged that bias was possible due to seasonal fluctuation and significant differences in TL among habitats (Kulaw 2012). Reproductive differences were also attributed to poor nutritional condition of the fish located on the artificial reef site based on a concurrent diet study (Glenn 2014; Schwartzkopf 2014) and previous literature stating reduced fecundity can be linked to poor diet and condition (Marteinsdottir and Begg 2002; Rideout et al. 2006). Nevertheless, for this study fish condition was similar among natural vs. artificial reefs. The differences between this study and other Gulf studies are not simply an artifact of demographic differences among samples analyzed because fish ages and sizes were similar between studies. For example, the size range of this study (276 to 767 mm) was similar to the ranges reported by Kulaw (2012; 235-864 mm) and Glenn (2014; 327 – 793 mm). Additionally, the age range of female Red Snapper (2-14 years) was also similar to the age range reported by Kulaw (2012; 1 – 12 years) and Glenn (2014; 3 – 17 years). This reinforces the speculation that Red Snapper in the western Gulf may have more varied reproductive capacities than fish from the northern Gulf (Lyczkowski-Shultz and Hanisko 2007; Porch et al. 2015).

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

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

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

Certainly, this work refining reproductive characteristics of Red Snapper in the northwestern GOM has several management implications. Red Snapper reproduction appears to be similar on natural and artificial habitats in the northwestern Gulf of Mexico. With thousands of platforms off the Texas coast that are scheduled for decommissioning and removal or donation to the TPWD Rigs-to-Reefs program, the identification of an artificial reef's value should be an important component of the decision making process. Minimally, the use of platforms as artificial reefs does not appear to negatively affect the population, in terms of reproduction, and removing platforms may be detrimental to Red Snapper populations by removing scarce habitat (Peabody and Wilson 2006; Gallaway et al. 2009, Streich et al. in review). If the influence of habitat on other factors like age, growth, and feeding habits can be determined to be equal to natural reefs, then creating or preserving artificial reefs may be a good way to create additional habitat for Red Snapper populations in the western Gulf. Furthermore, there is evidence from this study as well as others throughout the Gulf that indicate there are demographic and genetic differences (Puritz et al. 2016) in Red Snapper populations located in separate areas of the Gulf. This suggests that fishery managers should consider regional differences in Red Snapper populations when making management decisions.

CHAPTER 2

FEEDING HABITS OF RED SNAPPER *LUTJANUS CAMPECHANUS* ARE SIMILAR AMONG ARTIFICIAL AND NATURAL REEFS IN THE NORTHWESTERN GULF OF MEXICO

Introduction

Understanding the relationship between artificial reefs and associated fish has important implications for whether these structures are beneficial to the population or merely aggregate fish. To understand this relationship more clearly, evidence is needed for whether artificial reefs provide additional food or increase feeding efficiency of fish associated with these structures in comparison to natural reefs (Bohnsack 1989; Baine and Side 2003). Red Snapper are an ideal species to investigate this relationship due to their importance and abundance on both natural and artificial reefs (Tarnecki and Patterson 2015). However, most available data on Red Snapper feeding habits is from Alabama and Louisiana in the northern Gulf of Mexico ("Gulf") with very little data investigating the influence of habitat type on feeding habits. In addition, at least one study has indicated possible dietary differences between Louisiana and Texas populations through stable isotope analysis (Zapp Sluis et al. 2013). In light of these finding and lack of information from a regional perspective, more accurate estimates of the relative proportions of prey in the diet of Red Snapper from different habitats (Gallaway et al. 2009) as well as overall dietary data from the northwestern Gulf of Mexico are needed.

Early diet studies showed that Red Snapper are polyphagous at all life stages, with adults consuming mainly fish and crabs (Moseley 1966; Siegel 1983). Juvenile Red Snapper have been shown to consume amphipods, squid, and shrimp (Beaumariage and Bullock 1976; Wells et al. 2008); while age 3+ fish consume greater amounts of fish and crabs which is supported by data showing that fish comprise the highest proportion of the diet along the Texas coast (Bradley and

Bryan 1975). More recent studies corroborate the early studies, finding nearly half of Red Snapper diet is made up of fish; decapods contribute a large portion at 17.6%, while other invertebrates, such as stomatopods, squid, and others, contribute a small portion (Tarnecki and Patterson 2015).

Previous studies in the Gulf have been inconclusive regarding the influence of habitat on the diet of Red Snapper. Ouzts and Szedlmayer (2003) collected Red Snapper from artificial reefs, and assigned a habitat type to each prey item. Small Red Snapper (200-299 mm SL) fed mostly on reef and sand prey items, medium Red Snapper (300-399 mm SL) fed on reef, sand, and mixed habitat items, and large Red Snapper (400-499 mm SL) fed on prey associated with a variety of habitats. In a separate study Red Snapper within the 200 – 250 mm SL range fed on both reef and open habitat prey with reef prey making up a substantial, if not major proportion (Szedlmayer and Lee 2004). It has also been shown that with increasing growth, the diet of Red Snapper is increasingly similar among habitat types (Wells et al. 2008). Conversely, other studies show that adult Red Snapper are almost entirely trophically independent from the reefs on which they live with only 1.3% to 2% of their diet containing reef associated organisms (McCawley and Cowan 2006, 2007). Wells et al. (2008) detected habitat-specific differences, but fish were eating prey associated with sand and mud substrates. Gallaway (1981) suggested that Red Snapper at oil and gas platforms move away from the platforms and feed over soft bottoms at night or early in the morning. In addition, sand and mud habitats appear to be the source of prey items while more structured habitats may act as a refuge (Wells et al. 2008). All of these studies were conducted in various geographic areas, and each exhibited differing effects of natural and artificial reefs on the diet of Red Snapper. Clearly, information regarding the feeding habits of

Red Snapper on different habitat types in the western Gulf of Mexico is needed. Thus, the objectives of this study were:

1. Evaluate and compare feeding habits of Red Snapper among different offshore habitat types in the northwestern Gulf of Mexico.

H_a: Habitat type influences the feeding habits of Red Snapper in the northwestern Gulf of Mexico.

2. Use the dietary data to make predictions about habitat types in relation to reefing, fisheries enhancement, and restoration strategies in the northwestern Gulf of Mexico.

Methods

<u>Study Area</u>

Red Snapper were collected from natural banks, standing oil and gas platforms, and reefed platforms in the northwestern Gulf of Mexico approximately 45-60 nautical miles east of Port Aransas, Texas. At each habitat type three replicate sites were sampled: natural bank (natural) sites included: Aransas Bank, Baker Bank, and South Baker Bank; standing platform (standing) sites included MU-A-111-A, MU-A-85-A, and BA-133-A; reefed platform (reefed) sites included MU-A-85, MI-A-7, and BA-A-132 (Figure 2.1). All sites were selected within a 30 nautical mile area, 60-90 m deep, to control for as much variation as possible.

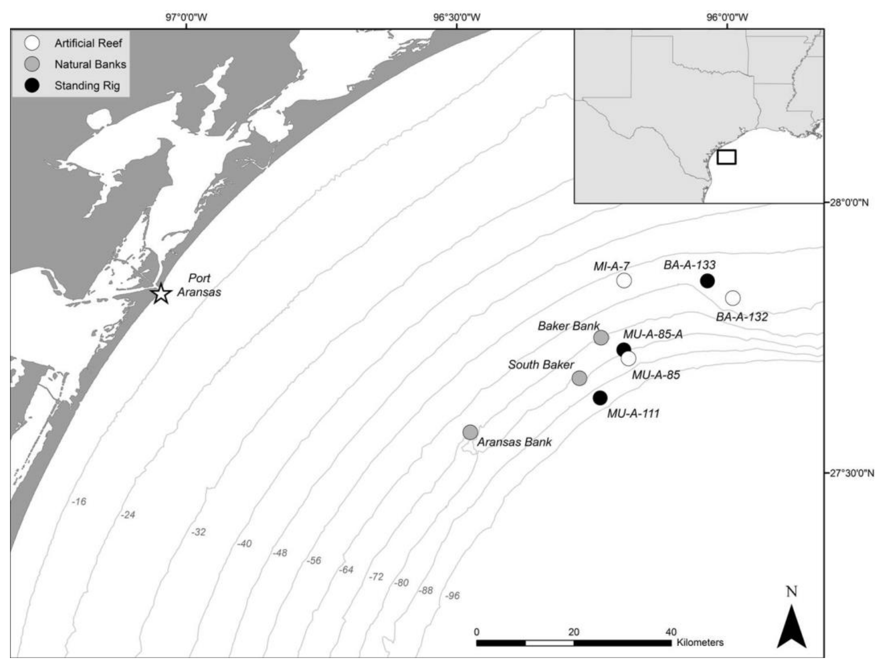

Figure 2.1: The study area was comprised of nine sites located in the northwestern Gulf of Mexico offshore of Port Aransas, Texas, which represented three habitat types. Natural banks (Baker, South Baker, and Aransas Bank), standing oil and gas platforms (BA-A-133, MU-A-85A, and MU-A-111), and reefed platforms (MI-A-7, BA-A-132, and MU-A-85).

Collection and Processing

Red Snapper were collected using vertical longline following the Southeast Area Monitoring and Assessment Program (SEAMAP) protocol (Gregalis et al. 2012). Following collection, fish were stored on ice and returned to the lab for processing. Fish were weighed (kg), and measured (mm) for total length (TL). Fish were dissected for otoliths, muscle plugs, and stomachs, which were classified as distended, empty, or containing prey. Stomachs collected from 2013-2014 were initially placed whole into 10% formalin for at least a month of preservation after which the contents were removed and transferred to 70% ethanol. Red Snapper were aged via sagittal otoliths. Otoliths were weighed, sectioned, and polished then annular rings were counted by two independent readers to determine age class. A relative weight (*Wr* = actual weight (lbs)/predicted weight (lbs)* 100; Anderson and Neumann 1996) condition index was calculated based on a species specific TL to weight conversion formula (0.00047 * TL in ^2.994, SEDAR 2013).

Stomach Content Analysis

Following fixation, stomach contents were enumerated and identified to the lowest possible taxon and individual prey items were weighed (g). Frequency of occurrence (*FO*), percent frequency of occurrence (*%FO*), percent by number (*%N*), and percent composition by weight (*%W*) were calculated for each prey type. Using these parameters, the Index of Relative Importance (*IRI* = (*%N* + *%W*) x *FO*; Liao et al. 2001) and percent *IRI* (*%IRI*) were calculated. However, percent weight has been identified as a useful representation of fish diet and was used for analysis and will be the only parameter discussed for statistical analyses. Prey weight was converted to standardized prey weight by dividing each taxon by individual body weight of the fish to control for fish size in all multivariate analyses (Ajemian and Powers 2012). Additionally, feeding strategy diagrams were created, using frequency of occurrence and prey specific aweight of prey items grouped by family or the next highest taxon identifiable, to further investigate dietary patterns of Red Snapper among the three habitat types. Prey specific weight was determined by dividing the total weight of prey items by the total content weight of stomachs containing that prey item (Amundsen et al. 1996; Ajemian and Powers 2011).

Statistics

Mean TL, age, and *Wr* were compared among sites and habitats with a nested ANOVA (site nested within habitat). Prey taxa were grouped according Class for all multivariate analyses and ease of interpretation. Differences in prey composition by habitat were visualized with multidimensional scaling (MDS; Clarke et al. 1993). A Bray-Curtis similarity index was created using square-root transformed standardized weight. A cluster analysis was also performed on prey weight that was averaged by site, square-root transformed and used to create a Bray Curtis similarity index. The cluster analysis was overlaid on an MDS ordination of the site averaged standardized weight data. Then a permutational multivariate analysis of variance (PERMANOVA) was conducted to identify differences among habitat, site (nested within habitat), and month (Clarke et al. 2014). Dispersion of prey within each habitat was assessed with permutational dispersion (PERMDISP) analysis. Univariate statistical analyses were conducted in R Statistical Software v3.3.1 and multivariate analyses were conducted in PRIMER-E. Results were considered significant at $\alpha \leq 0.05$.

Results

Overview

A total of 1585 Red Snapper were collected from natural (505), standing (494), and reefed (586) habitat ranging in TL from 275-767 mm TL and aged 2-13 years. The mean age (natural = 5.3, standing = 5.1, reefed = 5.1) and TL (natural = 517, standing = 502, reefed = 513) for collected fish were not significantly different among habitat types (TL: F = 0.10, df = 2, P = 0.91; Age: F = 3.59, df = 2, P = 0.09). There were 333 empty stomachs, 558 distended stomachs, and 694 containing prey. On natural banks 40% of fish stomachs were classified as distended, 16% were empty, and 44% contained prey. On standing platforms stomachs were classified as 31% distended, 21% empty, and 48% with prey. For fish from reefed platforms 34% of stomachs were distended, 26% were empty, and 40% contained prey. The ratios of stomachs that were distended, empty, or contained prey were not significantly different among habitat types (distended: X^2=1.26, P = 0.53; empty: X^2=2.55, P = 0.28; prey: X^2=0.77, P = 0.68). Identifiable prey was obtained from 560 stomachs and only these fish were included in the statistical analysis of diet composition among habitat types. The *Wr* for fish collected on natural (104±0.34), standing (107±0.70), and reefed (105±0.40) *Wr* was not significantly different among habitat types (F = 1.26, df = 6, P = 0.35; Figure 2.2).

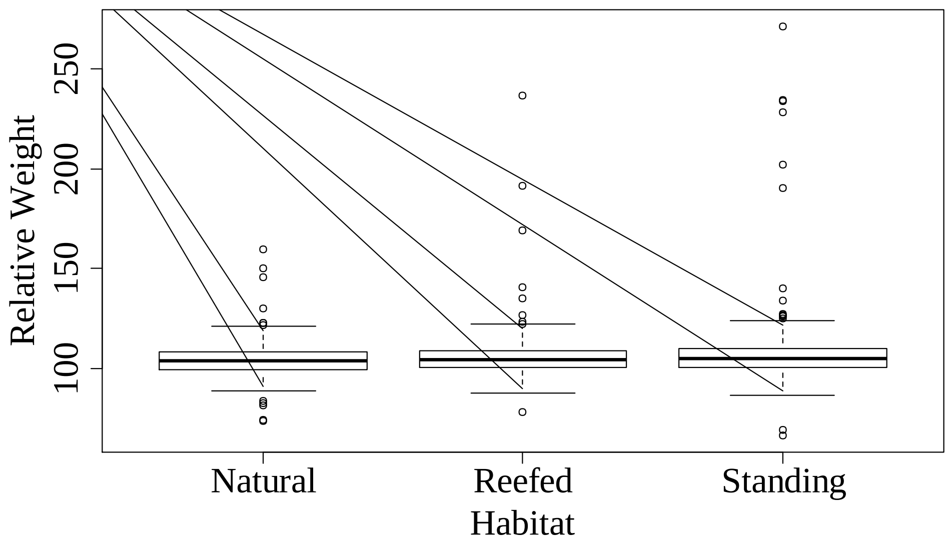

Figure 2.2: Boxplot of the condition index, relative weight (*Wr*), for Red Snapper *Lutjanus campechanus* collected on natural, standing and reefed habitats in the northwestern Gulf of Mexico. The median, 25-75% inner-quartile range, and 95% confidence interval along with outliers are shown. *Wr* among habitats was tested using nested ANOVA (Site within Habitat) and no statistical differences were found (F = 1.26, df = 6, P = 0.35).

There were a total of 34 prey categories identified across all habitat types, including unidentified content (UIC), in the stomachs of Red Snapper sampled for this study. Unidentified content was excluded from the analysis. Species accumulation plots for natural (Figure 2.3a) and standing (Figure 2.3b) did not show an asymptotic trend; although, a slight decrease in slope near the end indicated a sufficient amount of the prey composition at these sites was obtained. The species accumulation plot for reefed habitats showed the fitted line approached an asymptote indicating the sample size captured most of the prey items consumed by fish on these habitats (Figure 2.3c). Overall, the majority of the stomach composition by *%W* was made up of Osteichthyes (63.51%) and Malacostraca (27.67%). The remaining prey categories made up less than 10% of the diet each (Table 2.1).

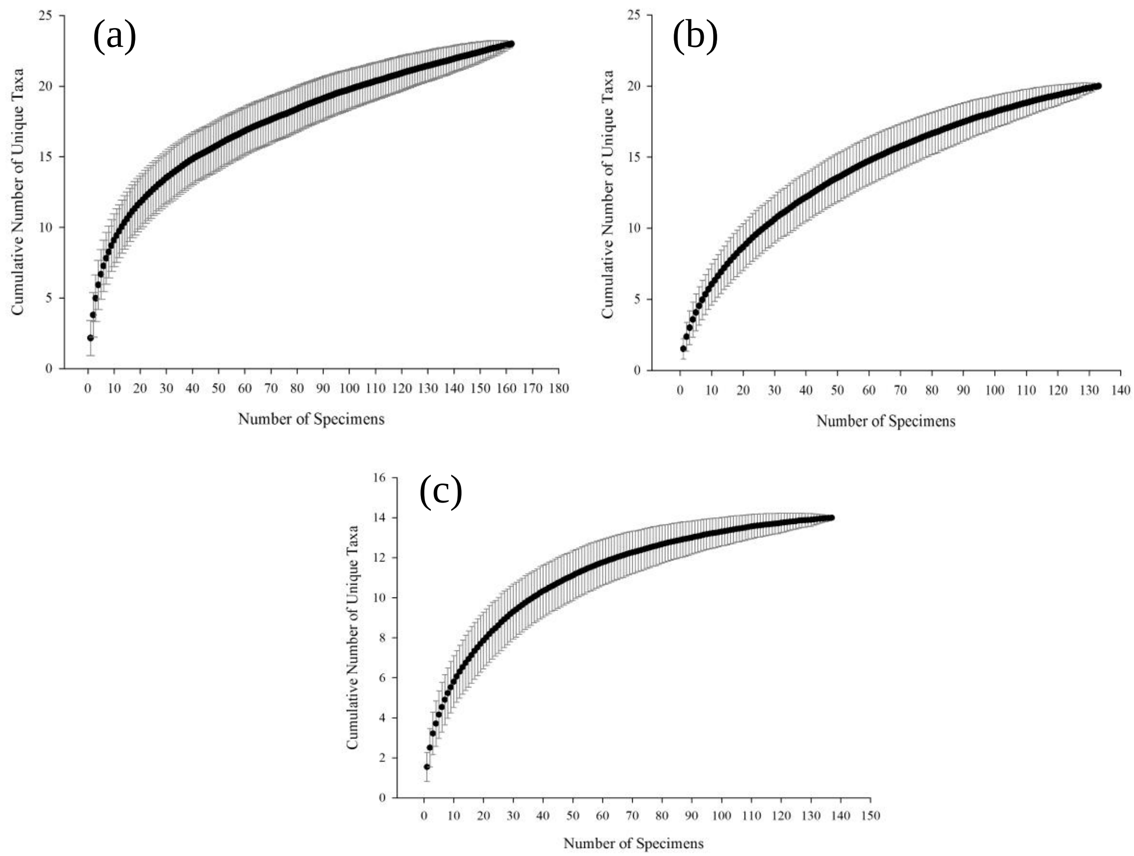

Figure 2.3: Cumulative prey curve plotting mean (±SE) of unique prey items and number of specimens sampled for Red Snapper *Lutjanus campechanus* (*n* = 560) collected from natural (a), standing (b), and reefed (c) habitats in the northwestern Gulf of Mexico. Collection occurred during 2013-2015.

<u>Diet per Habitat</u>

There were a total of 30 taxa identified from natural habitats. By Class, Osteichthyes (46.30%) made up the greatest percentage of Red Snapper diet by weight followed by Malacostraca (39.91%), and Hydrozoa (10.12%). Congridae, Ophichthidae, Carangidae, Anguilliformes, and unidentified fish (Osteichthyes) were the major prey items found in Class Osteichthyes. Within Malacostraca, the major taxa included *Portunus spp.*, *Portunus spinimamus*, unidentified crabs (Decapoda), and unidentified crustaceans (Malacostraca). The remaining classes made up less than 2% of the diet by weight. Six taxa were unique to natural habitats including Achelata, *Calamus leucosteus*, *Cavolinia tridentata,* Clupeidae, Holothuroidea, and Tanaidacea (Table 2.1).

On standing habitats, a total of 25 taxa were identified. By Class, Osteichthyes (79.80%) was the leading prey category in Red Snapper diets. Malacostraca (13.49%) is the next category followed by Cephalopoda (3.97%), and Hydrozoa (2.72%). Carangidae, *Hoplunnis spp.*, *Pristimoides aquilonaris,* and unidentified fish were identified within Osteichthyes. Unidentified crustaceans (Malacostraca) and crabs (Decapoda) were the major taxa identified in Class Malacostraca along with low amounts of Stomatopoda and *Portunus spinicarpus.* The cephalopods were made up of squid (Teuthida) and Hydrozoa was made up of Siphonophora. The remaining Classes made up less than 1% of the diet on standing habitats. Four taxa were unique to standing habitats including *Janthina janthina*, Ophidiidae, *Orthopristis chrysoptera*, and *Pristipomoides aquilonaris* (Table 2.1).

There were 22 taxa identified from the diet of Red Snapper on reefed habitats. By Class, Osteichthyes contributed the most (73.91%), followed by Malacostraca (23.50%), and Cephalopoda (2.09%). Prey items identified in Osteichthyes included mainly unidentified fish, and eel taxa (Angulliformes) including Ophichthidae and *Hoplunnis spp*. Within Malacostraca, *Farfantepenaeus spp.*, *Portunus spinicarpus,* Stomatopoda, and unidentified crustaceans were the most common prey identified. The remaining Classes made up less than 1% each of the diet on reefed habitats. Three unique taxa were identified on reefed habitats including *Speocarcinus lobatus*, *Portunus spinimanus*, and *Hippidae sp*. (Table 2.1).

Table 2.1: Diet composition of Red Snapper *Lutjanus campechanus* (n = 560) collected in the northwestern Gulf of Mexico by prey class, and lowest possible taxon showing percent frequency of occurrence (*%FO*), percent number (*%N*), and percent weight (*%W*) excluding unidentified content, and percent Index of Relative Importance (*%IRI*). Values are reported for overall totals, natural, standing and reefed habitats. Values in bold are totaled for prey class. Dashes represent absent taxon.

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

Visualization via multidimensional scaling revealed no discernable pattern by habitat type. Individual points did separate out from the main grouping which indicates individual fish that have differing stomach content. Two tight groupings of points were apparent though not related to habitat. These groupings were determined to be associated with the two most abundant prey taxa: Malacostraca and Osteichthyes (Figure 2.4a). When visualizing stomach content data averaged by site along with a cluster analysis six out of the nine sites, representing all three habitat types, were 80% similar. Eight of the sites were 60% similar and all nine sites were 40% similar (Figure 2.4b). Additional analysis using PERMANOVA revealed no statistical significance among habitat types (*Pseudo-F* = 1.52, df = 2, P = 0.184). There was no significant interaction between habitat and month (*Pseudo-F* = 0.62, df = 10, P = 0.889) while month was significant individually (*Pseudo-F* = 2.44, df = 5, P = 0.039; Table 2.2). Secondary testing by PERMDISP revealed significant differences among habitats (F = 6.21, df = 2, P =0.01) and pairwise comparisons revealed that natural banks exhibited a greater dispersion of data than artificial habitats (standing: t = 3.34, P= 0.004; reefed: t = 2.22, P = 0.039; df = 422).

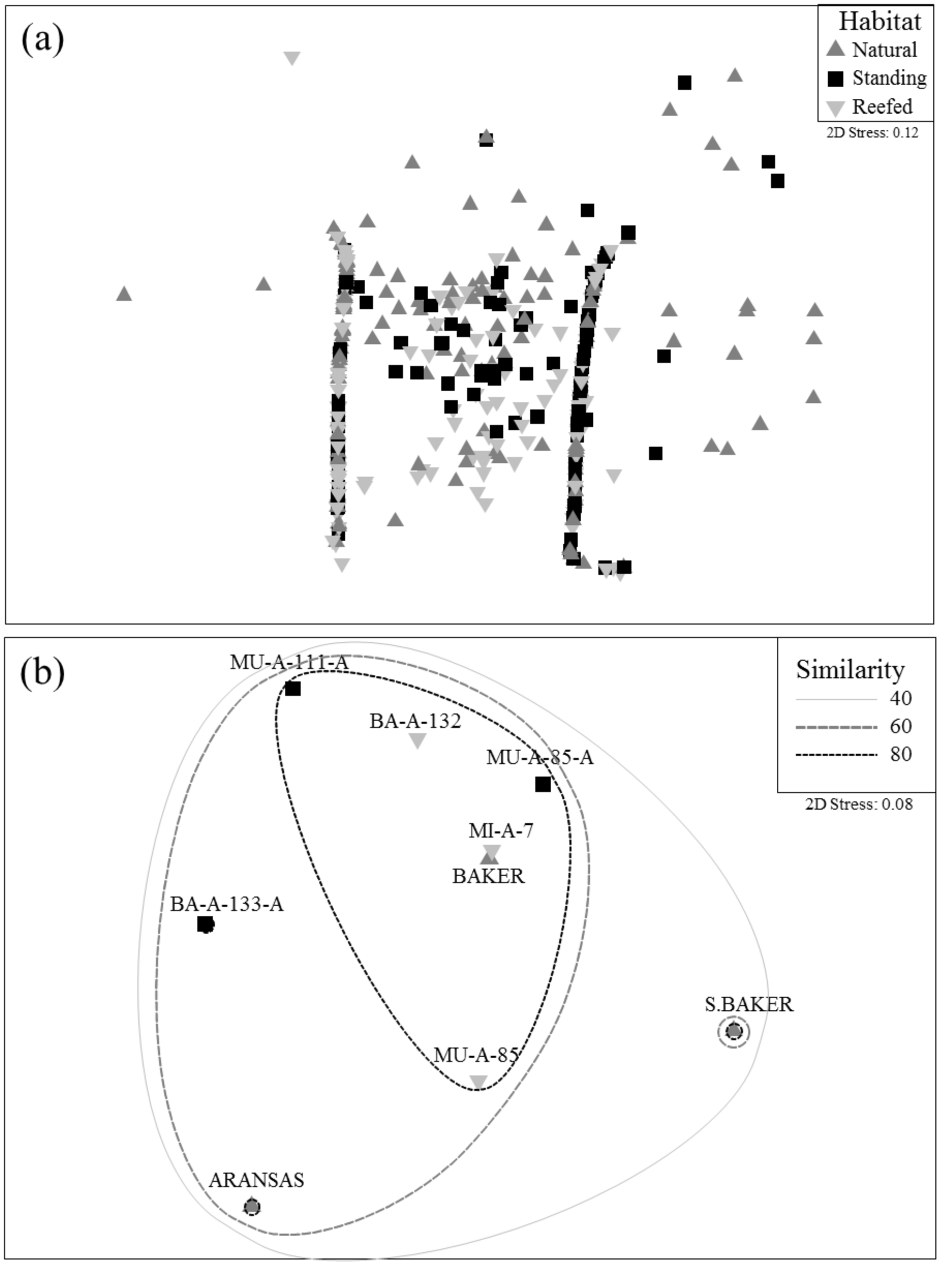

Figure 2.4: Multidimensional scaling (MDS) ordinations of prey taxon composition in Red Snapper *Lutjanus campechanus* diet by habitat type in the northwestern Gulf of Mexico. Standardized weight of prey items were grouped by Class, square-root transformed, and a Bray-Curtis similarity index was calculated, the two tightly grouped sets of points forming lines represent the two most abundant prey taxa: Malacostraca and Osteichthyes (a). Standardized weight of prey items were averaged by site, square-root transformed and a Bray-Curtis similarity index was calculated. A cluster analysis was performed and site was plotted along with the associated habitat type. Six out of nine sites, representing all habitats, were 80% similar, eight sites were 60% similar, and all nine sites were 40% similar (b).

Table 2.2: Results from a two-way crossed PERMANOVA on diet composition among habitat, with site nested, and month (May – October) of Red Snapper *Lutjanus campechanus* collected from natural, standing, and reefed habitats in the northwestern Gulf of Mexico; df = degrees of freedom, SS = sum of squares, MS = mean sum of squares, ** = missing values.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Habitat	2	9396.5	4698.3	1.5162	0.184	998
Month	5	71128	14226	2.4353	0.039	999
Site(Habitat)	6	18860	3143.4	1.3084	0.129	997
HabitatxMonth	10	36871	3687.1	0.6162	0.889	998
Site(Habitat)xMonth**	15	87237	5815.8	2.4208	0.001	997
Res	386	9.27E+05	2402.5			
Total	424	1.29E+06				

Red Snapper diet was affected by month. A trend of decreasing consumption of Malacostraca, 49.84% to 10.40%, and increasing consumption of Osteichthyes, 50.13% to 59.92%, from May to October was evident when analyzing prey Class by month. In addition, pelagic tunicates (Thaliacea, 3.62%), siphonophores (Hydrozoa, 23.23%), and sea butterflies (Gastropoda, 2.84%) became more common in later months (Figure 2.5).

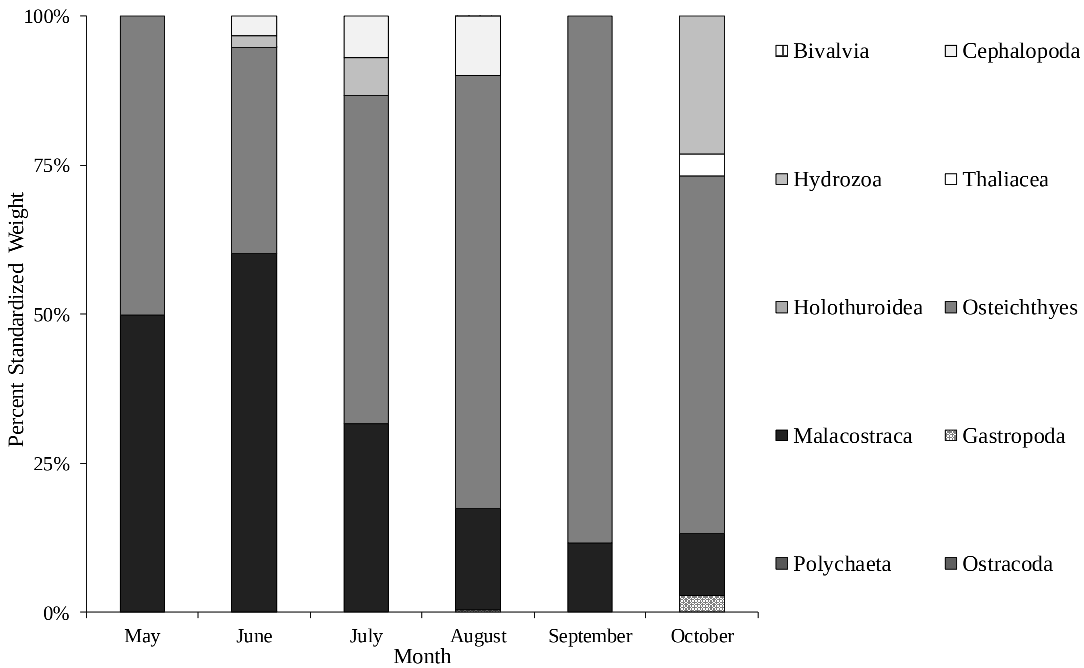

Figure 2.5: Percent standardized weight of Red Snapper *Lutjanus campechanus* diet collected in the northwestern Gulf of Mexico by month from May to October, excluding Unidentified Content. Prey taxa are displayed as Class.

Feeding Strategy per Habitat

The feeding strategy diagrams created for natural (2.7b), standing (2.7c), and reefed (2.7d) habitats showed that prey items were mostly rare in the diet of Red Snapper and indicate generalization. Most prey items plotted toward the bottom left and close to the origin indicating that these prey items were preyed upon rarely and contributed little to the diet. Few prey items break this pattern. On natural banks (2.7b) Cavoliniidae was high on the y-axis which indicates a high between phenotype component (2.7a), meaning individual fish may specialize on this particular prey but at a low frequency. At all three habitat types Osteichthyes was close to the within phenotype component (2.7a), which indicates that the Red Snapper diet overall was dominated by fish. On standing (2.7c) and reefed (2.7d) habitats Stomatopoda was more frequent and at a higher abundance than at natural sites. However, on both sites Stomatopoda was still closer to generalization and rare categories than the other categories.

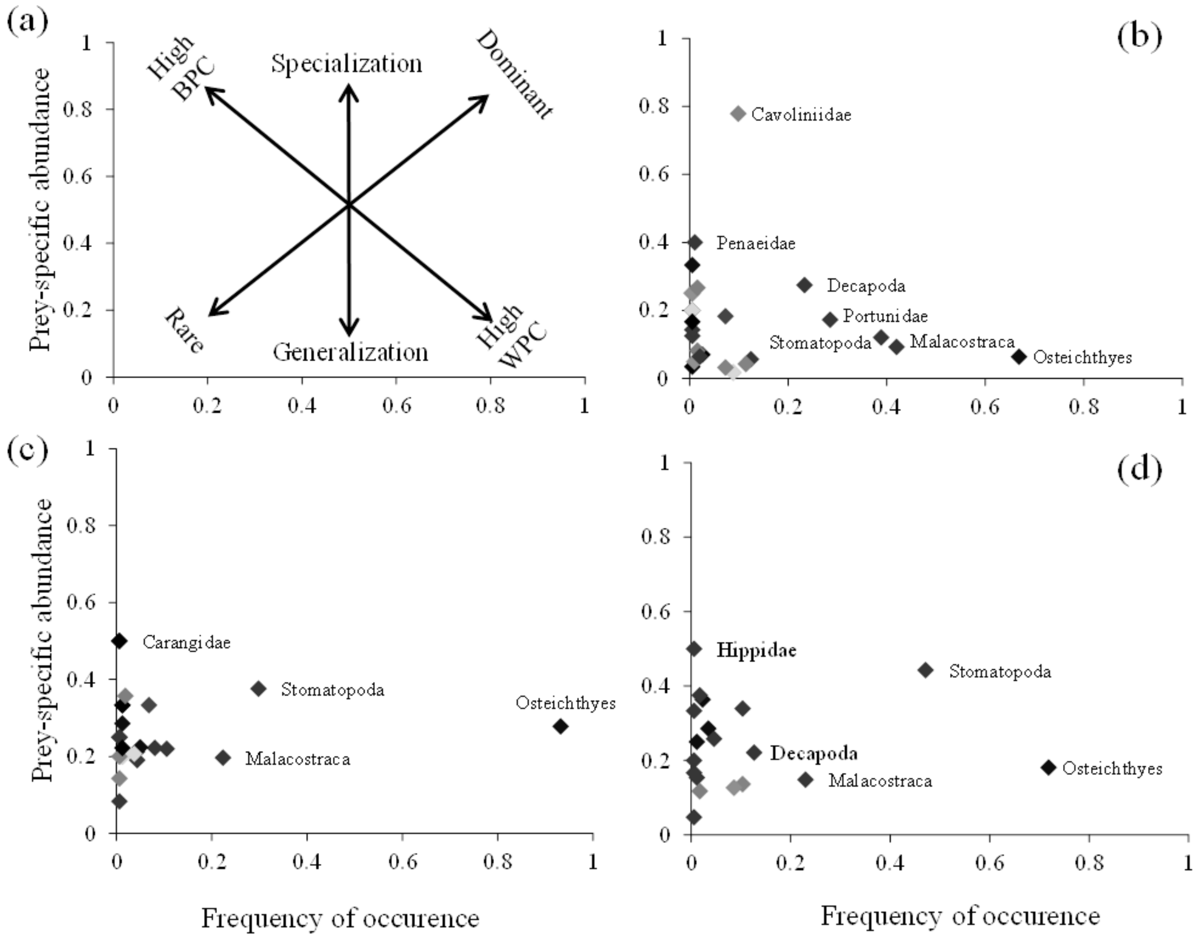

Figure 2.6: Feeding strategy diagrams of Red Snapper *Lutjanus campechanus* collected from natural (b), standing (c), and reefed (d) habitats in the northwestern Gulf of Mexico. The interpretation guide (a) was adapted from Amundsen et al. 1996. BPC stands for between phenotype component and WPC stands for within phenotype component. Prey items are plotted by Family or the next highest taxon identifiable.

Discussion

This purpose of this study was to evaluate the effect of three habitat types, natural banks, standing oil and gas platforms, and reefed platforms, on the diet of Red Snapper in the northwestern Gulf of Mexico. A large sample size was collected from each habitat type that allowed for an accurate representation and comparison of the immediate diet composition of Red Snapper on each of the habitat types. Overall, these findings showed that age, growth, and condition of Red Snapper were not different among the three habitat types. Habitat type was not shown to be a significant influence on diet composition while a temporal effect was identified by month. In general, Red Snapper exhibited a general and opportunistic feeding strategy regardless of the habitat on which they were collected. Thus, prey composition appears to be driven by seasonal influences rather than differences between natural and artificial habitats. This study provides a contrast to those that demonstrate a difference in prey composition between habitat types and conclude artificial reefs do not provide similar foraging opportunities as natural reefs.

Both age and length are capable of influencing the diet of Red Snapper. Mean age and length were not found to be significantly different among habitats; therefore, differences in diet composition among habitats were likely not significantly influenced by age or length differences. Additionally, the quality and quantity of prey in the diet has been shown to affect the condition of fish (Anderson and Neumann 1996; Schwartzkopf 2014). The condition index evaluated, *Wr*, and the ratio of empty, distended, and stomachs containing prey were not different among habitats. Thus, the habitats provided prey of similar quality and similar nutritional value, and whatever patterns found in diet composition can be attributed to the influence of habitat rather than age or length.

This study determined that the prey composition of Red Snapper was not significantly different among natural, standing and reefed habitats. The diet of Red Snapper was primarily composed of fish and crabs, although stomatopods, squid, octopus, and other invertebrates were also present. Although the percent weight of the two major taxa, Osteichthyes and Malacostraca, varied among habitat types, individual and site variation in the diet of Red Snapper most likely accounted for the inability to detect statistical differences. Unique taxa were also found on each habitat; however, the contributions of these relatively rare taxa were not enough to influence differences among the habitats. Additionally, the prey base on natural habitats appears to be wider than that of standing and reefed habitats, or the forage area available near natural habitats is greater than those of artificial reefs due to the size of natural reefs. While no significant difference in prey composition was found among habitat types, the contribution of each prey item varied among habitats and month, and a greater dispersion at natural reefs was detected. These findings are supported by previous studies which found habitat was not a significant factor with respect to diet or trophic position, and that Red Snapper diet is somewhat variable throughout the year (Wells et al. 2008; Tarnecki and Patterson 2015).

Overall, Red Snapper appear to exhibit a mixed or opportunistic feeding strategy with varying degrees of generalization and slight individual specialization at all habitat types. An examination of feeding strategy diagrams per habitat did not reveal a unique pattern for any of the habitats. Most prey items were located in the rare occurrence area of the feeding strategy diagram for every habitat type, which shows that regardless of habitat Red Snapper are not specializing on any one particular prey item, instead preying on a variety of items as they are available. The prey items spreading up the y-axis, toward the between phenotype component, indicate that individuals within the population may simultaneously specialize on separate prey items (Amundsen et al. 1996; Ajemian and Powers 2012). These results show that Red Snapper exhibit similar feeding patterns on natural, standing, and reefed habitats.

This study suggests that Red Snapper are not dependent on habitat specific prey regardless of the habitat on which they are found. Although there were unique prey items at each of the habitats, the small contribution of those prey and the lack of statistically significant results among habitats suggest that Red Snapper do not depend on habitat specific prey in their diet which is supported by other studies in the Gulf. Comparable diet compositions from other studies identified few reef-dependent taxa regardless of habitat type and prey from all habitat types were equally important at low-relief sites near Alabama (Outz and Szedlmayer 2003; Tarnecki and Patterson 2015). Red Snapper on natural habitats near Alabama were found to feed primarily on non-reef benthic prey such as Synodontidae and Southern Hake while fish on artificial habitat fed on non-reef species as well as more pelagic prey such as harvestfish and Clupeidae (Tarnecki and Patterson 2015). However, studies of other reef-associated fish have found that they do not necessarily feed on reef organisms but instead prey on benthic organisms not associated with natural or artificial reefs (Croker 1962; Eggleston et al. 1998; Duarte and Garcia 1999; Howe 2001). The conclusions of other studies suggest that Red Snapper on artificial reefs are not dependent on reef associated prey; therefore, are merely attracted to the artificial reef and are negatively affected by their association due to lower habitat quality and high fishing pressure (Cowan et al. 1999; McCawley and Cowan et al. 2007; Schwartzkopf 2014). Schwartzkopf (2014) identified reef-specific prey items in the diet of snapper on natural sites but not in the diet of fish from artificial sites. In addition, caloric densities differed between sites and the conclusion was made that Red Snapper at natural reefs are in better condition than fish at artificial reefs. Though some differences may be due to classification of prey habitat preference

(Cowan 2011), there seems to be large variation in the effect of habitat type on diet depending on region and study area.

The results of this study support the idea that artificial reefs may allow Red Snapper to use foraging areas that are otherwise unavailable in areas of little natural structure such as the western Gulf. Unique prey items did not contribute substantially to the diet of fish from natural or artificial reefs indicating that the value of reefs may not be directly related to prey composition present on the reef but to feeding opportunities provided by their placement. For example, habitat interfaces, such as reefs, have been shown to act as crossroads between forage and refuge areas (Davis and Birdsong 1973). Topping and Szedlmayer (2011) determined that artificial reefs and nearby areas (<100m) offer suitable habitat and resources that Red Snapper need on a daily basis. Therefore, lack of significant reef specific prey from both natural and artificial reefs may not be evidence for the species independence from artificial reefs, rather that Red Snapper use artificial and natural structure as a means of accessing foraging areas.

Several factors, other than habitat type, remain to be investigated to better understand the feeding habits of Red Snapper in the northwestern Gulf of Mexico. The diet of Red Snapper has been shown in some studies to change with age, length and distance from shore (Ouzts and Szedlmayer 2003; McCawley and Cowan 2007). Comparatively, this study sampled fish of similar ages and lengths, as well as sites located at approximately similar distances from shore and depths to control for those factors. However, these effects as well as their interaction with habitat types remain unresolved. Additional studies targeting the effects of age and length on the diet of Red Snapper are particularly needed, and especially their interaction with habitat. In addition, the proximity of other reefs in a selected reefing site may negatively affect the forage potential around the reef; on sites containing multiple structures reef fish created overlapping “foraging halos”, areas of depleted resources, in the areas between structures (McCawley and Cowan 2007). Reef sites have also been shown to exhibit changes in prey availability with reef age and location (Palmer-Zwahlen and Aseltine 1994; Relini et al. 1994). Further clarification of the similarity among habitats could be obtained by determining the habitat specificity and caloric content of prey items for Red Snapper in the northwestern Gulf. Finally, some taxa are more easily identifiable due to persistent hard structures, such as Portunidae, Carangidae, Stomatopoda, and Cavoliniidae, which may have lead these taxa to be interpreted disproportionately as a prominent component in the diet of Red Snapper. Incorporation of DNA barcoding into diet content studies would reveal finer differences in diet and remove some of the bias due to the easily identifiable features of some taxa (Szedlmayer 2007; Valdez-Moreno et al. 2012; Cote et al. 2013). The addition of these factors in future diet studies would increase clarity to the question of habitat influence on the diet composition of Red Snapper in the Gulf of Mexico.

The results of this study have several implications for management. There are currently hundreds of oil and gas platforms off the Texas coast coming up for decommissioning and removal. The Texas Parks and Wildlife Department Rigs-to-Reefs program offers an alternate to complete removal where decommissioned platforms can be donated and used as artificial reefs. The results from this study suggest that Red Snapper using artificial reefs are not restricted as far as the prey selection or quality in the northwestern Gulf of Mexico. In addition, there is evidence that suggests removing the platforms may have detrimental effects on the population of Red Snapper through the removal of scarce habitat and the potential for diverting fishing pressure from natural reefs (Peabody and Wilson 2006; Gallaway et al. 2009; Streich et al. in review). If the influence of artificial reefs on other important life history characteristics is determined to be similar to natural reefs, then reefing platforms may be a valid method for creating habitat for Red Snapper in the northwestern Gulf. Furthermore, when the findings of Red Snapper diet studies are examined together, along with studies covering reproduction, the variation among study sites suggests that Red Snapper exhibit different life history characteristics depending on the region and may also interact with artificial reefs in different ways. This suggests that managers should consider regional differences when making decisions regarding the conservation of Red Snapper populations in the Gulf of Mexico.

BROADER IMPACTS & CONCLUSION

This study used a design intended to separate the effects of habitat on Red Snapper life history characteristics from extraneous factors, such as depth and distance from shore, as well as provide a large sample size to accurately investigate life history characteristics by region and habitat. The purpose of this work was to determine the relative value of oil and gas platforms to Red Snapper, or artificial reefs, in comparison to natural reefs as well as clarify regional trends in reproduction and diet in the northwestern Gulf of Mexico. Red Snapper life history characteristics have been shown to change with age, so age must be similar among habitats for comparisons to be valid. Ages of the fish collected for this study were not found to be significantly different among habitat types. Length has also been shown to be a factor in the diet and reproduction of Red Snapper, probably due to its relationship with age. However, since length is not completely dependent on age, it must also be similar among habitats. In this study, Red Snapper collected from all habitats were statistically similar in length. Finally, even with the appearance of similar diet compositions among habitats, prey quality could contribute to differing fish condition which affects life history characteristics such as reproductive potential. For habitats to be truly similar, fish condition must be equal among habitats, which was found to be the case in this study. A large sample size was collected from each habitat type which allowed for a more accurate representation of the diet composition and reproductive characteristics of Red Snapper on each of the habitat types. As a result, the influence of habitat on reproduction and diet was comprehensively investigated.

Influence of Habitat on Reproduction

Red Snapper on artificial habitats exhibited similar reproductive capabilities and characteristics to those from natural reefs in terms of gonadosomatic index (GSI), batch fecundity (BFE), spawning frequency (SFE), annual fecundity (SFE), and the number of spawning capable individuals. This shows that artificial reefs provide similar value in terms of reproduction for Red Snapper as natural reefs in the northwestern Gulf. This study is in contrast to those showing that artificial reefs are of poor quality for Red Snapper reproduction when compared to natural banks. Combining the conclusions of this study with previous studies shows that spawning behavior of Red Snapper, and the influence of habitat on reproduction appears to be highly variable among geographic areas in the Gulf, which could be leading to differing values of habitat across the Gulf and determinations about the status of the population. This reinforces the idea that Red Snapper in the northwestern Gulf may have varied reproductive capacities than fish from the other regions in the Gulf.

Influence of Habitat on Diet

The influence of habitat was not found to be significant on the prey composition in the diet of Red Snapper or the feeding strategies exhibited by fish collected from natural, standing, and reefed habitats. The results of this study show that Red Snapper diet on artificial reefs is similar to natural reefs and likely provide similar means for prey selection and feeding strategies. Therefore, artificial reefs are functioning in a similar way to natural banks in terms of Red Snapper feeding habits. This study provides a contrast to those studies which demonstrate a difference in prey composition between habitat types and claim artificial reefs do not provide similar foraging opportunities as natural reefs (McCawley and Cowan. 2007; Schwarztkopf 2014). Nevertheless, together this study highlights the value of artificial reefs to Red Snapper in the northwestern Gulf of Mexico.

Summary

Red Snapper reproduction and diet in the northwestern Gulf of Mexico do not appear to be negatively affected by artificial reefs in comparison to natural reefs. Reproductive potential including GSI, BFE, AFE, SFE, and the number of spawning individuals of Red Snapper were similar among natural banks, standing platforms, and reefed platforms. Furthermore, the diet of Red Snapper is similar among habitat types in that prey composition and feeding strategies among habitats were comparable.

Management

The results of this study have strong implications for management. There are currently hundreds of oil and gas platforms off the Texas coast scheduled for decommissioning and removal due to Idle Iron policies. The Texas Parks and Wildlife Department Rigs-to-Reefs program offers an alternative to complete removal where decommissioned platforms can be donated and used as artificial reefs. The results from this study show that artificial reefs appear to offer similar value to Red Snapper reproduction and diet as natural habitat in the northwestern Gulf of Mexico. If other life history characteristics such as age and growth of Red Snapper are shown to be similar between artificial and natural reefs then the use of decommissioned platforms may be a valid method for creating additional habitat in the northwestern Gulf. Thus, these structures likely perform a valuable role through enhancement of the Red Snapper population. Furthermore, differences between this study and previous studies from other areas of the Gulf indicate the possibility of important regional differences in reproductive and diet characteristics of Red Snapper as well as the influence of habitat type on these characteristics. Managers should consider regional management as it would provide flexibility in the management of the recreational sector's harvest of red snapper by allowing for regional biological differences among regions in the Gulf.

Future Studies

Several factors other than habitat type remain to be investigated to better understand the feeding habits and reproductive potential of Red Snapper in the northwestern Gulf of Mexico. A greater range of sizes and ages are needed to investigate the effect of these on diet and reproduction in the northwestern Gulf, as they are known to influence dietary habits and reproductive output. The interactions of size and age with habitat on diet and reproduction also deserve consideration. In addition, site specific differences due to characteristics like depth, vertical relief, distance to shore, habitat complexity, proximity to other structures, age of the structure, and recent disturbance remain to be investigated to determine the best practice for reefing strategies. In Red Snapper stomach content, some species are easily identifiable due to persistent hard structures which may contribute to an apparent dominance of these prey items in the diet. To improve accuracy of the dietary data, DNA barcoding of prey items has begun to be incorporated to further clarify specific contents and obtain a finer resolution of Red Snapper diet. Obtaining a genetic description of the diet would account for bias associated with easily identifiable taxa. The quality of the prey is also an important component of diet and should be investigated by determining the caloric density of prey items to compare among habitats and regions. Finally, stomach content is a snapshot of the short-term diet composition for fish. The use of stable isotope analysis in conjunction with stomach contents would provide a longer time-frame picture of Red Snapper diets for comparing among regions and habitats. The inclusion of these factors in future studies would increase clarity to the question of habitat influence on the reproduction and diet of Red Snapper.

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APPENDIX

Table 1: Spawning frequency calculations of female Red Snapper collected from natural, standing, and reefed habitats in the northwestern Gulf of Mexico. Day-0 refers to individuals with hydrated oocytes; day-1 refers to individuals with post ovulatory follicles (POF). SFE = spawning frequency estimate, H = hydrated, TC = time calibrated.

Habitat	day-0	day-1	mature	SFE_H	SFE_POF	SFE_TC	Spawns/Season_H	Spawns/Season_POF	Spawns/Season_TC
Natural	21	10	153	7	15	9	21	10	15
Standing	27	6	130	5	22	7	31	7	19
Reefed	23	4	138	6	35	10	25	4	14
All	71	20	421	6	21	9	25	7	16

Table 2: A description of stomach condition of Red Snapper collected from natural, standing, and reefed habitats in the northwestern Gulf of Mexico classified as distended, empty or with prey per habitat. Classifications were determined upon capture, during processing, and during content identification.

Habitat	Distended	Empty	With Prey	Total
Natural	204	79	222	505
Standing	154	102	238	494
Reefed	200	152	234	586
Total	558	333	694	1585

Table 3: The number (N), occurrence (O), and frequency of occurrence (FO) of gastric parasites found in the stomachs of Red Snapper collected from natural, standing, and reefed habitats in the northwestern Gulf of Mexico.

	Female			Male			Total		
Habitat	O	N	FO	O	N	FO	O	N	FO
Natural	30	72	0.28	26	55	0.24	85	127	0.40
Standing	10	14	0.10	12	15	0.11	25	29	0.12
Reefed	17	37	0.17	31	61	0.23	78	98	0.33
Total	57	123	0.19	69	131	0.19	188	254	0.28

Table 2: Overall stomach content results of Red Snapper collected from natural, standing, and reefed habitats in the northwestern Gulf of Mexico. Results are sorted by Class, Order, Family, and Lowes Possible Taxon (LPT). %Wu = Percent weight with Unidentified content included, %W = percent weight without unidentified content, O = occurrence, FO = frequency of occurrence, %FO = percent frequency of occurrence, N = number, %N = percent number, IRI = index of relative importance, %IRI = percent index of relative importance.

								Overall					
Class	**Order**	**Family**	**LPT**	**Weight (g)**	**%Wu**	**%W**	**O**	**FO**	**%FO**	**N**	**%N**	**IRI**	**%IRI**
Bivalvia	Unidentified Bivalve	Unidentified Bivalve	Bivalvia	**0.12**	**0.00**	**0.00**	**3.00**	**0.01**	**0.25**	**3.00**	**0.08**	**0.08**	**0.06**
Cephalopoda				**2008.98**	**51.36**	**69.67**	**582.00**	**1.10**	**49.16**	**732.00**	**20.04**	**44.80**	**34.63**
	Octopoda	Unidentified Octopus	Octopoda	8.22	0.21	0.29	3.00	0.01	0.25	4.00	0.11	0.11	0.09
	Teuthida	Unidentified Squid	Teuthida	53.57	1.37	1.86	9.00	0.02	0.76	13.00	0.36	0.39	0.30
Chondrichthyes	Rajiformes	Rajidae	Rajidae	**3.32**	**0.08**	**0.12**	**1.00**	**0.00**	**0.08**	**1.00**	**0.03**	**0.03**	**0.02**
Gastropoda				**2005.17**	**51.27**	**69.53**	**533.00**	**1.01**	**45.02**	**656.00**	**17.96**	**42.72**	**33.02**
	Litorinimorpha	Atlantidae	*Atlanta spp.*	0.49	0.01	0.02	48.00	0.09	4.05	75.00	2.05	2.05	1.59
	Thecosomata	Cavoliniidae	*Cavolinia tridentata*	11.96	0.31	0.41	19.00	0.04	1.60	1115.00	30.52	30.54	23.60
		Janthinidae	*Janthina janthina*	0.00	0.00	0.00	1.00	0.00	0.08	1.00	0.03	0.03	0.02
Holothuroidea	Unidentified Sea Cucumber	Unidentified Sea Cucumber	Holothuroidea	**0.00**	**0.00**	**0.00**	**1.00**	**0.00**	**0.08**	**1.00**	**0.03**	**0.03**	**0.02**
Hydrozoa	Siphonophora	Unidentified Siphonophore	Siphonophora	**153.49**	**3.92**	**5.32**	**23.00**	**0.04**	**1.94**	**23.00**	**0.63**	**0.86**	**0.67**
Malacostraca				**1831.37**	**46.82**	**63.51**	**454.00**	**0.86**	**38.34**	**514.00**	**14.07**	**38.52**	**29.78**
	Amphipoda	Unidentified Amphipod	Amphipoda	20.31	0.52	0.70	55.00	0.10	4.65	118.00	3.23	3.30	2.55
	Decapoda	Hippidae	Hippidae	1.91	0.05	0.07	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Decapoda	Ogyridae	*Ogyrides spp.*	0.00	0.00	0.00	2.00	0.00	0.17	3.00	0.08	0.08	0.06
	Decapoda	Peneaidae	*Farfantepenaeus spp.*	78.71	2.01	2.73	5.00	0.01	0.42	5.00	0.14	0.16	0.13
	Decapoda	Portunidae	*Portunus Gibbesii*	24.24	0.62	0.84	4.00	0.01	0.34	8.00	0.22	0.23	0.17
	Decapoda	Portunidae	*Portunus spinicarpus*	224.18	5.73	7.77	46.00	0.09	3.89	102.00	2.79	3.47	2.68
	Decapoda	Portunidae	*Portunus spinimanus*	3.62	0.09	0.13	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Decapoda	Portunidae	*Portunus spp.*	72.13	1.84	2.50	21.00	0.04	1.77	34.00	0.93	1.03	0.80
	Decapoda	Unidentified Lobster	Achelata	0.07	0.00	0.00	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Decapoda	Xanthidae	*Speocarcinus lobatus*	2.41	0.06	0.08	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Decapoda	Unidentified Crab	Decapoda	92.22	2.36	3.20	87.00	0.16	7.35	624.00	17.08	17.61	13.61
	Isopoda	Unidentified Isopod	Isopoda	0.44	0.01	0.02	5.00	0.01	0.42	5.00	0.14	0.14	0.11
	Stomatopoda	Unidentified Stomatopod	Stomatopoda	61.20	1.56	2.12	211.00	0.40	17.82	794.00	21.74	22.58	17.46
	Tanaidacea	Tanaidacea	Tanaidacea	0.00	0.00	0.00	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Unidentified Crustacean	Unidentified Crustacean	Malacostraca	216.51	5.54	7.51	166.00	0.31	14.02	175.00	4.79	7.15	5.53
Osteichthyes				**7845.93**	**126.87**	**100.81**	**2388.00**	**2.28**	**101.60**	**3687.00**	**100.93**	**130.33**	**100.74**
	Anguilliformes	Anguilliformes	Anguilliformes	90.04	2.30	3.12	18.00	0.03	1.52	23.00	0.63	0.74	0.57
	Anguilliformes	Nettastomatidae	*Hoplunnis spp.*	87.41	2.23	3.03	4.00	0.01	0.34	4.00	0.11	0.13	0.10
	Anguilliformes	Ophichthidae	Ophichthidae	298.12	7.62	10.34	10.00	0.02	0.84	10.00	0.27	0.47	0.36
	Ophidiiformes	Ophidiidae	Ophidiidae	0.47	0.01	0.02	2.00	0.00	0.17	2.00	0.05	0.05	0.04
	Perciformes	Carangidae	Carangidae	55.28	1.41	1.92	2.00	0.00	0.17	3.00	0.08	0.09	0.07
	Perciformes	Clupeidae	Clupeidae	2.52	0.06	0.09	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Perciformes	Congidae	Congridae	283.24	7.24	9.82	3.00	0.01	0.25	3.00	0.08	0.14	0.11
	Perciformes	Haemulidae	Haemulidae	0.23	0.01	0.01	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Perciformes	Haemulidae	*Orthopristis chrysoptera*	66.58	1.70	2.31	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Perciformes	Lutjanidae	*Pristipomoides aquilonaris*	11.71	0.30	0.41	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Perciformes	Sparidae	*Calamus leucosteus*	33.56	0.86	1.16	1.00	0.00	0.08	1.00	0.03	0.03	0.02
	Unidentified Fish	Unidentified Fish	Osteichthyes	902.21	23.07	31.29	406.00	0.77	34.29	460.00	12.59	36.65	28.33
Ostracoda	Unidentified Ostracod	Ostracoda	Ostracoda	**0.00**	**0.00**	**0.00**	**2.00**	**0.00**	**0.17**	**2.00**	**0.05**	**0.05**	**0.04**
Polychaeta	Unidentified Polychaete	Polychaeta	Polychaeta	**0.00**	**0.00**	**0.00**	**2.00**	**0.00**	**0.17**	**2.00**	**0.05**	**0.05**	**0.04**
Thaliacea	Unidentified Tunicate	Thaliacea	Thaliacea	**23.26**	**0.59**	**0.81**	**15.00**	**0.03**	**1.27**	**30.00**	**0.82**	**0.84**	**0.65**
Unidentified Content	Unidentified Content	Unidentified Content	Unidentified Content	**1027.58**	**26.27**	-	-	-	-	-	-	-	-

Table 3: Stomach content results of Red Snapper collected from natural habitats in the northwestern Gulf of Mexico. Results are sorted by Class, Order, Family, and Lowes Possible Taxon (LPT). %Wu = Percent weight with Unidentified content included, %W = percent weight without unidentified content, O = occurrence, FO = frequency of occurrence, %FO = percent frequency of occurrence, N = number, %N = percent number, IRI = index of relative importance, %IRI = percent index of relative importance.

				Natural									
Class	**Order**	**Family**	**LPT**	**Weight (g)**	**%Wu**	**%W**	**O**	**FO**	**%FO**	**N**	**%N**	**IRI**	**%IRI**
Bivalvia	Unidentified Bivalve	Unidentified Bivalve	Bivalvia	**0.02**	**0.00**	**0.00**	**1.00**	**0.01**	**0.20**	**1.00**	**0.04**	**0.04**	**0.03**
Cephalopoda				**740.81**	**43.82**	**58.01**	**209.00**	**1.08**	**40.98**	**260.00**	**10.31**	**26.25**	**22.39**
	Octopoda	Unidentified Octopus	Octopoda	8.22	0.49	0.64	3.00	0.02	0.59	4.00	0.16	0.17	0.14
	Teuthida	Unidentified Squid	Teuthida	3.24	0.19	0.25	3.00	0.02	0.59	4.00	0.16	0.16	0.14
Chondrichthyes	Rajiformes	Rajidae	Rajidae	-	-	-	-	-	-	-	-	-	-
Gastropoda				**740.65**	**43.81**	**58.00**	**187.00**	**0.97**	**36.67**	**224.00**	**8.88**	**24.82**	**21.17**
	Litorinimorpha	Atlantidae	*Atlanta spp.*	0.16	0.01	0.01	22.00	0.11	4.31	36.00	1.43	1.43	1.22
	Thecosomata	Cavoliniidae	*Cavolinia tridentata*	11.96	0.71	0.94	19.00	0.10	3.73	1115.00	44.19	44.29	37.77
		Janthinidae	*Janthina janthina*	-	-	-	-	-	-	-	-	-	-
Holothuroidea	Unidentified Sea Cucumber	Unidentified Sea Cucumber	Holothuroidea	**0.00**	**0.00**	**0.00**	**1.00**	**0.01**	**0.20**	**1.00**	**0.04**	**0.04**	**0.03**
Hydrozoa	Siphonophora	Unidentified Siphonophore	Siphonophora	**129.22**	**7.64**	**10.12**	**17.00**	**0.09**	**3.33**	**17.00**	**0.67**	**1.57**	**1.33**
Malacostraca				**591.30**	**34.98**	**46.30**	**145.00**	**0.75**	**28.43**	**162.00**	**6.42**	**21.28**	**18.15**
	Amphipoda	Unidentified Amphipod	Amphipoda	20.13	1.19	1.58	24.00	0.12	4.71	44.00	1.74	1.94	1.65
	Decapoda	Hippidae	Hippidae	-	-	-	-	-	-	-	-	-	-
	Decapoda	Ogyridae	*Ogyrides spp.*	-	-	-	-	-	-	-	-	-	-
	Decapoda	Peneaidae	*Farfantepenaeus spp.*	16.89	1.00	1.32	2.00	0.01	0.39	2.00	0.08	0.09	0.08
	Decapoda	Portunidae	*Portunus Gibbesii*	11.23	0.66	0.88	2.00	0.01	0.39	5.00	0.20	0.21	0.18
	Decapoda	Portunidae	*Portunus spinicarpus*	193.17	11.43	15.13	38.00	0.20	7.45	92.00	3.65	6.62	5.65
	Decapoda	Portunidae	*Portunus spinimanus*	-	-	-	-	-	-	-	-	-	-
	Decapoda	Portunidae	*Portunus spp.*	59.42	3.51	4.65	15.00	0.08	2.94	28.00	1.11	1.47	1.26
	Decapoda	Unidentified Lobster	Achelata	0.07	0.00	0.01	1.00	0.01	0.20	1.00	0.04	0.04	0.03
	Decapoda	Xanthidae	*Speocarcinus lobatus*	-	-	-	-	-	-	-	-	-	-
	Decapoda	Unidentified Crab	Decapoda	56.12	3.32	4.39	44.00	0.23	8.63	463.00	18.35	19.35	16.51
	Isopoda	Unidentified Isopod	Isopoda	0.44	0.03	0.03	2.00	0.01	0.39	2.00	0.08	0.08	0.07
	Stomatopoda	Unidentified Stomatopod	Stomatopoda	28.16	1.67	2.21	75.00	0.39	14.71	222.00	8.80	9.66	8.24
	Tanaidacea	Tanaidacea	Tanaidacea	0.00	0.00	0.00	1.00	0.01	0.20	1.00	0.04	0.04	0.03
	Unidentified Crustacean	Unidentified Crustacean	Malacostraca	124.09	7.34	9.72	81.00	0.42	15.88	86.00	3.41	7.49	6.39
Osteichthyes				**1208.76**	**90.29**	**88.34**	**216.00**	**1.33**	**67.24**	**279.00**	**39.86**	**77.77**	**72.32**
	Anguilliformes	Anguilliformes	Anguilliformes	24.78	1.47	1.94	5.00	0.03	0.98	7.00	0.28	0.33	0.28
	Anguilliformes	Nettastomatidae	*Hoplunnis spp.*	-	-	-	-	-	-	-	-	-	-
	Anguilliformes	Ophichthidae	Ophichthidae	101.45	6.00	7.94	4.00	0.02	0.78	4.00	0.16	0.32	0.28
	Ophidiiformes	Ophidiidae	Ophidiidae	-	-	-	-	-	-	-	-	-	-
	Perciformes	Carangidae	Carangidae	30.20	1.79	2.36	1.00	0.01	0.20	1.00	0.04	0.05	0.04
	Perciformes	Clupeidae	Clupeidae	2.52	0.15	0.20	1.00	0.01	0.20	1.00	0.04	0.04	0.03
	Perciformes	Congidae	Congridae	120.21	7.11	9.41	1.00	0.01	0.20	1.00	0.04	0.09	0.08
	Perciformes	Haemulidae	Haemulidae	0.23	0.01	0.02	1.00	0.01	0.20	1.00	0.04	0.04	0.03
	Perciformes	Haemulidae	*Orthopristis chrysoptera*	-	-	-	-	-	-	-	-	-	-
	Perciformes	Lutjanidae	*Pristipomoides aquilonaris*	-	-	-	-	-	-	-	-	-	-
	Perciformes	Sparidae	*Calamus leucosteus*	33.56	1.99	2.63	1.00	0.01	0.20	1.00	0.04	0.05	0.05
	Unidentified Fish	Unidentified Fish	Osteichthyes	278.35	16.47	21.80	129.00	0.67	25.29	144.00	5.71	20.28	17.29
Ostracoda	Unidentified Ostracod	Ostracoda	Ostracoda	**0.00**	**0.00**	**0.00**	**1.00**	**0.01**	**0.20**	**1.00**	**0.04**	**0.04**	**0.03**
Polychaeta	Unidentified Polychaete	Polychaeta	Polychaeta	**0.00**	**0.00**	**0.00**	**1.00**	**0.01**	**0.20**	**1.00**	**0.04**	**0.04**	**0.03**
Thaliacea	Unidentified Tunicate	Thaliacea	Thaliacea	**23.24**	**1.37**	**1.82**	**14.00**	**0.07**	**2.75**	**29.00**	**1.15**	**1.28**	**1.09**
Unidentified Content	Unidentified Content	Unidentified Content	Unidentified Content	**413.41**	**24.46**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**

Table 4: Stomach content results of Red Snapper collected from standing habitats in the northwestern Gulf of Mexico. Results are sorted by Class, Order, Family, and Lowes Possible Taxon (LPT). %Wu = Percent weight with Unidentified content included, %W = percent weight without unidentified content, O = occurrence, FO = frequency of occurrence, %FO = percent frequency of occurrence, N = number, %N = percent number, IRI = index of relative importance, %IRI = percent index of relative importance.

				Standing									
Class	**Order**	**Family**	**LPT**	**Weight (g)**	**%Wu**	**%W**	**O**	**FO**	**%FO**	**N**	**%N**	**IRI**	**%IRI**
Bivalvia	Unidentified Bivalve	Unidentified Bivalve	Bivalvia	**0.10**	**0.01**	**0.01**	**2.00**	**0.01**	**0.64**	**2.00**	**0.31**	**0.31**	**0.29**
Cephalopoda				**736.58**	**61.49**	**82.54**	**195.00**	**1.21**	**62.50**	**241.00**	**37.54**	**75.25**	**70.08**
	Octopoda	Unidentified Octopus	Octopoda	-	-	-	-	-	-	-	-	-	-
	Teuthida	Unidentified Squid	Teuthida	35.43	2.96	3.97	3.00	0.02	0.96	5.00	0.78	0.85	0.79
Chondrichthyes	Rajiformes	Rajidae	Rajidae	-	-	-	-	-	-	-	-	-	-
Gastropoda				**736.56**	**61.49**	**82.54**	**187.00**	**1.16**	**59.94**	**226.00**	**35.20**	**72.91**	**67.90**
	Litorinimorpha	Atlantidae	*Atlanta spp.*	0.02	0.00	0.00	8.00	0.05	2.56	15.00	2.34	2.34	2.18
	Thecosomata	Cavoliniidae	*Cavolinia tridentata*	-	-	-	-	-	-	-	-	-	-
		Janthinidae	*Janthina janthina*	0.00	0.00	0.00	1.00	0.01	0.32	1.00	0.16	0.16	0.15
Holothuroidea	Unidentified Sea Cucumber	Unidentified Sea Cucumber	Holothuroidea	-	-	-	-	-	-	-	-	-	-
Hydrozoa	Siphonophora	Unidentified Siphonophore	Siphonophora	**24.27**	**2.03**	**2.72**	**6.00**	**0.04**	**1.92**	**6.00**	**0.93**	**1.04**	**0.96**
Malacostraca				**712.19**	**59.45**	**79.80**	**168.00**	**1.04**	**53.85**	**202.00**	**31.46**	**69.07**	**64.33**
	Amphipoda	Unidentified Amphipod	Amphipoda	0.10	0.01	0.01	13.00	0.08	4.17	18.00	2.80	2.80	2.61
	Decapoda	Hippidae	Hippidae	-	-	-	-	-	-	-	-	-	-
	Decapoda	Ogyridae	*Ogyrides spp.*	0.00	0.00	0.00	1.00	0.01	0.32	1.00	0.16	0.16	0.15
	Decapoda	Peneaidae	*Farfantepenaeus spp.*	-	-	-	-	-	-	-	-	-	-
	Decapoda	Portunidae	*Portunus Gibbesii*	6.88	0.57	0.77	1.00	0.01	0.32	2.00	0.31	0.32	0.29
	Decapoda	Portunidae	*Portunus spinicarpus*	10.48	0.87	1.17	4.00	0.02	1.28	4.00	0.62	0.65	0.61
	Decapoda	Portunidae	*Portunus spinimanus*	-	-	-	-	-	-	-	-	-	-
	Decapoda	Portunidae	*Portunus spp.*	7.38	0.62	0.83	2.00	0.01	0.64	2.00	0.31	0.32	0.30
	Decapoda	Unidentified Lobster	Achelata	-	-	-	-	-	-	-	-	-	-
	Decapoda	Xanthidae	*Speocarcinus lobatus*	-	-	-	-	-	-	-	-	-	-
	Decapoda	Unidentified Crab	Decapoda	29.85	2.49	3.34	17.00	0.11	5.45	20.00	3.12	3.47	3.23
	Isopoda	Unidentified Isopod	Isopoda	0.00	0.00	0.00	1.00	0.01	0.32	1.00	0.16	0.16	0.15
	Stomatopoda	Unidentified Stomatopod	Stomatopoda	12.57	1.05	1.41	48.00	0.30	15.38	117.00	18.22	18.64	17.36
	Tanaidacea	Tanaidacea	Tanaidacea	-	-	-	-	-	-	-	-	-	-
	Unidentified Crustacean	Unidentified Crustacean	Malacostraca	53.13	4.44	5.95	36.00	0.22	11.54	36.00	5.61	6.94	6.46
Osteichthyes				**855.31**	**79.25**	**76.98**	**183.00**	**1.05**	**50.60**	**237.00**	**20.62**	**48.89**	**44.40**
	Anguilliformes	Anguilliformes	Anguilliformes	27.80	2.32	3.12	7.00	0.04	2.24	10.00	1.56	1.69	1.58
	Anguilliformes	Nettastomatidae	*Hoplunnis spp.*	10.80	0.90	1.21	2.00	0.01	0.64	2.00	0.31	0.33	0.30
	Anguilliformes	Ophichthidae	Ophichthidae	51.48	4.30	5.77	2.00	0.01	0.64	2.00	0.31	0.38	0.36
	Ophidiiformes	Ophidiidae	Ophidiidae	0.47	0.04	0.05	2.00	0.01	0.64	2.00	0.31	0.31	0.29
	Perciformes	Carangidae	Carangidae	25.08	2.09	2.81	1.00	0.01	0.32	2.00	0.31	0.33	0.31
	Perciformes	Clupeidae	Clupeidae	-	-	-	-	-	-	-	-	-	-
	Perciformes	Congidae	Congridae	163.03	13.61	18.27	2.00	0.01	0.64	2.00	0.31	0.54	0.50
	Perciformes	Haemulidae	Haemulidae	-	-	-	-	-	-	-	-	-	-
	Perciformes	Haemulidae	*Orthopristis chrysoptera*	66.58	5.56	7.46	1.00	0.01	0.32	1.00	0.16	0.20	0.19
	Perciformes	Lutjanidae	*Pristipomoides aquilonaris*	11.71	0.98	1.31	1.00	0.01	0.32	1.00	0.16	0.16	0.15
	Perciformes	Sparidae	*Calamus leucosteus*	-	-	-	-	-	-	-	-	-	-
	Unidentified Fish	Unidentified Fish	Osteichthyes	355.24	29.66	39.81	150.00	0.93	48.08	180.00	28.04	65.12	60.65
Ostracoda	Unidentified Ostracod	Ostracoda	Ostracoda	-	-	-	-	-	-	-	-	-	-
Polychaeta	Unidentified Polychaete	Polychaeta	Polychaeta	-	-	-	-	-	-	-	-	-	-
Thaliacea	Unidentified Tunicate	Thaliacea	Thaliacea	**0.02**	**0.00**	**0.00**	**1.00**	**0.01**	**0.32**	**1.00**	**0.16**	**0.16**	**0.15**
Unidentified Content	Unidentified Content	Unidentified Content	Unidentified Content	**305.48**	**25.50**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**

Table 5: Stomach content results of Red Snapper collected from reefed habitats in the northwestern Gulf of Mexico. Results are sorted by Class, Order, Family, and Lowes Possible Taxon (LPT). %Wu = Percent weight with Unidentified content included, %W = percent weight without unidentified content, O = occurrence, FO = frequency of occurrence, %FO = percent frequency of occurrence, N = number, %N = percent number, IRI = index of relative importance, %IRI = percent index of relative importance.

				Reefed									
Class	**Order**	**Family**	**LPT**	**Weight (g)**	**%Wu**	**%W**	**O**	**FO**	**%FO**	**N**	**%N**	**IRI**	**%IRI**
Bivalvia	Unidentified Bivalve	Unidentified Bivalve	Bivalvia	-	-	-	-	-	-	-	-	-	-
Cephalopoda				**531.59**	**51.97**	**74.43**	**178.00**	**1.02**	**49.17**	**231.00**	**20.03**	**48.26**	**43.83**
	Octopoda	Unidentified Octopus	Octopoda	-	-	-	-	-	-	-	-	-	-
	Teuthida	Unidentified Squid	Teuthida	14.90	1.46	2.09	3.00	0.02	0.83	4.00	0.35	0.38	0.35
Chondrichthyes	Rajiformes	Rajidae	Rajidae	**3.32**	**0.32**	**0.46**	**1.00**	**0.01**	**0.28**	**1.00**	**0.09**	**0.09**	**0.08**
Gastropoda				**527.96**	**51.61**	**73.92**	**159.00**	**0.91**	**43.92**	**206.00**	**17.87**	**46.09**	**41.85**
	Litorinimorpha	Atlantidae	*Atlanta spp.*	0.31	0.03	0.04	18.00	0.10	4.97	24.00	2.08	2.09	1.89
	Thecosomata	Cavoliniidae	*Cavolinia tridentata*	-	-	-	-	-	-	-	-	-	-
		Janthinidae	*Janthina janthina*	-	-	-	-	-	-	-	-	-	-
Holothuroidea	Unidentified Sea Cucumber	Unidentified Sea Cucumber	Holothuroidea	-	-	-	-	-	-	-	-	-	-
Hydrozoa	Siphonophora	Unidentified Siphonophore	Siphonophora	-	-	-	-	-	-	-	-	-	-
Malacostraca				**527.88**	**51.60**	**73.91**	**141.00**	**0.81**	**38.95**	**150.00**	**13.01**	**41.23**	**37.44**
	Amphipoda	Unidentified Amphipod	Amphipoda	0.08	0.01	0.01	18.00	0.10	4.97	56.00	4.86	4.86	4.41
	Decapoda	Hippidae	Hippidae	1.91	0.19	0.27	1.00	0.01	0.28	1.00	0.09	0.09	0.08
	Decapoda	Ogyridae	*Ogyrides spp.*	0.00	0.00	0.00	1.00	0.01	0.28	2.00	0.17	0.17	0.16
	Decapoda	Peneaidae	*Farfantepenaeus spp.*	61.82	6.04	8.66	3.00	0.02	0.83	3.00	0.26	0.41	0.37
	Decapoda	Portunidae	*Portunus Gibbesii*	6.13	0.60	0.86	1.00	0.01	0.28	1.00	0.09	0.09	0.08
	Decapoda	Portunidae	*Portunus spinicarpus*	20.53	2.01	2.87	4.00	0.02	1.10	6.00	0.52	0.59	0.53
	Decapoda	Portunidae	*Portunus spinimanus*	3.62	0.35	0.51	1.00	0.01	0.28	1.00	0.09	0.09	0.08
	Decapoda	Portunidae	*Portunus spp.*	5.33	0.52	0.75	4.00	0.02	1.10	4.00	0.35	0.36	0.33
	Decapoda	Unidentified Lobster	Achelata	-	-	-	-	-	-	-	-	-	-
	Decapoda	Xanthidae	*Speocarcinus lobatus*	2.41	0.24	0.34	1.00	0.01	0.28	1.00	0.09	0.09	0.08
	Decapoda	Unidentified Crab	Decapoda	6.25	0.61	0.88	26.00	0.15	7.18	141.00	12.23	12.36	11.22
	Isopoda	Unidentified Isopod	Isopoda	0.00	0.00	0.00	2.00	0.01	0.55	2.00	0.17	0.17	0.16
	Stomatopoda	Unidentified Stomatopod	Stomatopoda	20.47	2.00	2.87	88.00	0.51	24.31	455.00	39.46	40.91	37.15
	Tanaidacea	Tanaidacea	Tanaidacea	-	-	-	-	-	-	-	-	-	-
	Unidentified Crustacean	Unidentified Crustacean	Malacostraca	39.29	3.84	5.50	49.00	0.28	13.54	53.00	4.60	6.15	5.58
Osteichthyes				**308.69**	**30.18**	**0.00**	**2.00**	**0.01**	**0.55**	**2.00**	**0.17**	**0.17**	**0.16**
	Anguilliformes	Anguilliformes	Anguilliformes	37.46	3.66	5.24	6.00	0.03	1.66	6.00	0.52	0.70	0.64
	Anguilliformes	Nettastomatidae	*Hoplunnis spp.*	76.61	7.49	10.73	2.00	0.01	0.55	2.00	0.17	0.30	0.27
	Anguilliformes	Ophichthidae	Ophichthidae	145.19	14.19	20.33	4.00	0.02	1.10	4.00	0.35	0.81	0.74
	Ophidiiformes	Ophidiidae	Ophidiidae	-	-	-	-	-	-	-	-	-	-
	Perciformes	Carangidae	Carangidae	-	-	-	-	-	-	-	-	-	-
	Perciformes	Clupeidae	Clupeidae	-	-	-	-	-	-	-	-	-	-
	Perciformes	Congidae	Congridae	-	-	-	-	-	-	-	-	-	-
	Perciformes	Haemulidae	Haemulidae	-	-	-	-	-	-	-	-	-	-
	Perciformes	Haemulidae	*Orthopristis chrysoptera*	-	-	-	-	-	-	-	-	-	-
	Perciformes	Lutjanidae	*Pristipomoides aquilonaris*	-	-	-	-	-	-	-	-	-	-
	Perciformes	Sparidae	*Calamus leucosteus*	-	-	-	-	-	-	-	-	-	-
	Unidentified Fish	Unidentified Fish	Osteichthyes	268.62	26.26	37.61	127.00	0.73	35.08	136.00	11.80	39.25	35.64
Ostracoda	Unidentified Ostracod	Ostracoda	Ostracoda	**0.00**	**0.00**	**0.00**	**1.00**	**0.01**	**0.28**	**1.00**	**0.09**	**0.09**	**0.08**
Polychaeta	Unidentified Polychaete	Polychaeta	Polychaeta	**0.00**	**0.00**	**0.00**	**1.00**	**0.01**	**0.28**	**1.00**	**0.09**	**0.09**	**0.08**
Thaliacea	Unidentified Tunicate	Thaliacea	Thaliacea	-	-	-	-	-	-	-	-	-	-
Unidentified Content	Unidentified Content	Unidentified Content	Unidentified Content	**308.69**	**30.18**	-	-	-	-	-	-	-	-