Transactions of the American Fisheries Society 147:1030–1041, 2018

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1002/tafs.10104

FEATURED PAPER

Habitat-Specific Reproductive Potential of Red Snapper: A Comparison of Artificial and Natural Reefs in the Western Gulf of Mexico

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Abstract
Energy exploration in the Gulf of Mexico (hereafter, Gulf) has resulted in the addition of numerous oil and gas production platforms that create structurally complex habitat in an area otherwise dominated by barren mud/sand bottom. How these artificial structures affect fish populations is largely unknown, and there is ongoing debate regarding their value as surrogate habitats for ecologically and economically important reef fish species. Thus, the purpose of this study was to characterize trends in Red Snapper *Lutjanus campechanus* reproductive potential in the western Gulf at oil and gas platform reefs relative to reproductive potential at natural banks. Red Snapper (n = 1,585) were collected during 2013–2015 from standing platforms, decommissioned platform artificial reefs, and natural banks by using standardized vertical line gear. Comparisons of gonadosomatic index, male : female ratios, batch fecundity, annual fecundity, spawning frequency, and number of spawning-capable individuals indicated that Red Snapper reproductive biology was similar among natural bank, standing platform, and artificial reef habitats. These results suggest that in terms of reproductive output, fish inhabiting artificial reefs are functionally similar to similar-aged fish on natural banks. This work can be used to make informed management decisions and suggests that there are benefits to converting decommissioned platforms into designated artificial reefs. Future studies should consider site-specific characteristics, such as depth, vertical relief, and proximity to other structures, to elucidate how habitat characteristics may influence reproduction, ultimately improving future artificial reef deployments for fisheries enhancement in the western Gulf.

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Received March 30, 2018; accepted July 12, 2018

The Red Snapper *Lutjanus campechanus* is an economically and ecologically important reef fish that has been pursued commercially and recreationally in the Gulf of Mexico (hereafter, Gulf) since the 1840s (Hood et al. 2007). These fish associate with hard substrate, often occupying natural banks, ridges, and reefs (Patterson et al. 2001; Walter and Ingram 2009; Ajemian et al. 2015; Streich et al. 2017a). However, large portions of the Gulf are dominated by mud bottom, with relatively few areas of natural hard-bottom bank, 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 (hereafter, platforms) that also serve as artificial reef habitat, where the Red Snapper is often the dominant species observed (Stanley and Wilson 2003; Ajemian et al. 2015; Streich et al. 2017a). There is evidence that in some locales, Red Snapper associate with artificial structures over long periods of time (Szedlmayer and Schroepfer 2005), whereas in other areas, Red Snapper exhibit low site fidelity to artificial structure (Peabody and Wilson 2006). One study also showed that larger, older fish inhabit natural banks in comparison to artificial reefs, including standing platforms, while fish on artificial reefs reach a larger size at age, which suggests a faster growth rate (Streich et al. 2017b). Thus, platforms may influence Red Snapper biology, life history characteristics, and population dynamics.

The relative value of artificial reefs compared to natural banks is still widely debated. Several authors have argued that artificial reefs do not provide suitable habitat and may also increase fishing pressure—factors that together create a sink in the population (Jackson et al. 2007; Walters et al. 2008; Cowan et al. 2011). However, other authors have suggested that artificial reefs do provide suitable habitat and may contribute to the recovery and maintenance of Red Snapper in the Gulf (Szedlmayer 2007; Gallaway et al. 2009; Shipp and Bortone 2009; Streich et al. 2017b). Many platforms in the Gulf are mandated for removal due to federal regulations such as "Idle Iron," a recent regulation requiring inactive platforms to be decommissioned (U.S. Department of the Interior 2010). However, some of these structures will be converted to designated artificial reefs through state-run Rigs-to-Reefs programs, like those in Texas and other Gulf states, and will continue to serve as fish habitat. As such, it is important to understand how these artificial structures function in comparison with natural banks so as to determine how these differences in habitat may impact the Gulf Red Snapper population. Therefore, examining the reproductive characteristics of Red Snapper on natural versus artificial reefs is a key parameter that would yield insights as to their value.

Reproductive characteristics of Red Snapper in the Gulf have been previously described. Red Snapper become sexually mature by age 2 and are asynchronous batch spawners that develop oocytes continuously during the spawning season 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 no evident trend of temporal–spatial segregation (Collins et al. 2001; Jackson et al. 2006; Fitzhugh et al. 2012). Red Snapper are long-lived and fecund, capable of reaching over 50 years of age, with the potential to produce 55.5 million eggs over their life span (Szedlmayer and Shipp 1994; Wilson and Nieland 2001; SEDAR 2005). Generally, spawning in the Gulf is thought to occur during April–September (Bradley and Bryan 1975; Gallaway et al. 2009), with peak spawning along the Texas coast from June to August (Collins et al. 2001; Fitzhugh et al. 2012). Fishery managers have cited the need for more detailed information on the reproductive biology of Red Snapper from western Gulf areas, which have been relatively understudied (SEDAR 2013).

Previous studies of Red Snapper reproduction in the Gulf have been focused offshore of Alabama and Louisiana (Collins et al. 2001; Woods et al. 2003; Jackson et al. 2006, 2007; Kulaw 2012; Glenn et al. 2017), Florida (Brown-Peterson et al. 2008), and the Yucatán Peninsula (Brulé et al. 2010). Off Louisiana, differences in gonadosomatic index (GSI), maturity, and spawning frequency (SFE) were found among natural shelf-edge banks, standing platform sites, and toppled platform sites; however, due to geographical constraints, these habitats were located across a wide depth range (i.e., 55–160 m; Kulaw 2012; Glenn et al. 2017; Kulaw et al. 2017). Additionally, some differences in reproduction, including GSI, SFE, and batch fecundity (BFE), were found among six geographical regions spanning the northern Gulf from central Florida to south Texas (Kulaw 2012). Variation in size at maturity has been found between fish collected off Louisiana and those collected off Alabama, with Alabama Red Snapper reaching maturity benchmarks at smaller sizes and younger ages (Woods et al. 2003). Red Snapper sampled from the east and west (Gulf) coasts of Florida appear to exhibit reproductive differences in spawning seasonality, BFE, and SFE (Brown-Peterson et al. 2008). In addition, Red Snapper from Florida (Brown-Peterson et al. 2008) and the northern Gulf (Woods et al. 2003) show differences in spawning seasonality relative to Red Snapper along the Yucatán Peninsula, with Yucatán fish exhibiting protracted spawning seasons, possibly due to the warmer waters (Brulé et al. 2010). These studies suggest the presence of regional differences in reproduction throughout the Gulf—and, specifically, that there could be differences in the western Gulf compared to previously studied regions as well as localized differences among habitat types. Furthermore, there is growing evidence that subpopulations of Red Snapper exist throughout the Gulf, which could drive important differences in life history parameters, such as reproduction (Gold and Saillant 2007; Puritz et al. 2016). Thus, there may be regional differences in reproductive potential that warrant further investigation.

To address the debate regarding artificial habitat's value for Red Snapper, it is essential to understand whether fish using various habitat types have similar reproductive biology. However, there is a deficit of information on this topic, particularly in the western Gulf. Only one previous study (Glenn et al. 2017) has described localized habitat differences. Glenn et al. (2017) found that Red Snapper on natural banks off Louisiana had higher reproductive potential than those from standing platforms or artificial reefs; however, that study had a relatively small sample size, and the habitats sampled spanned a wide depth range. Given the lack of reproductive life history comparisons between natural banks and artificial habitat in the western Gulf and given the potential for regional differences, the purpose of this study was to further build upon prior studies and further examine regional trends in Red Snapper reproduction in the western Gulf. Of particular interest was the influence of platforms on reproductive parameters relative to natural banks. This study is particularly relevant in that Red Snapper reproductive data from this region of the western Gulf (SEDAR 2013) are needed to inform management.

METHODS

Study site.— The study area was located in the western Gulf, approximately 83–111 km east of Port Aransas, Texas (Figure 1). Three habitat types, each with three replicate sites, were sampled (n = 9 total sites), including natural hard-bottom banks (Aransas, Baker, and South Baker banks), standing platforms (MU-A-111-A, MU-A-85-A, and BA-133-A), and decommissioned platform artificial reefs (MU-A-85, MI-A-7, and BA-A-132). Natural banks consist of naturally hard structure, such as shell ridges, reefs, or banks. In contrast, standing platforms are often located in areas with bare mud bottom, where the only hard structure is the platform itself. Decommissioned platforms are either cut off 25.91 m (85 ft) below the surface of the water or are cut below the sea floor and toppled, removing a large portion of vertical relief. To control for environmental variability as much as reasonably possible, the sites were all located within a 56-km area and were restricted to 60–90-m bottom depth.

Collection and sample processing.— Red Snapper were collected from 2013 to 2015 by using Gulf-wide standardized vertical line sampling following the protocol described by the Southeast Area Monitoring and Assessment Program (SEAMAP 2013; for details, see Streich et al. 2017b). Sampling was conducted throughout the year, and habitats were sampled equally by month across sample years, with a majority of the sampling effort focused on April–October to capture the published extent and peak of the spawning season (Woods et al. 2003; Fitzhugh et al. 2004, 2012; Jackson et al. 2007). All captured individuals were tagged with an identifying label in the field, kept whole on ice, and brought to the laboratory for processing. Total weight (TW; kg) and TL (mm) were recorded. Fish were dissected to collect biological samples, including gonads and otoliths. Sex was determined by macroscopic examination of the gonads, which were also weighed to the nearest gram. A length–weight regression was created for female Red Snapper collected in this study and was used to calculate the predicted weight for each individual (predicted TW = $[2 \times 10^{-8}]\text{TL}^{2.9102}$). A condition index was then calculated for female fish (relative weight [W_r] = [measured TW, kg]/[predicted TW, kg] × 100; Anderson and Neumann 1996). A W_r value of 100 (or 100% of predicted weight based on a fish's length) was interpreted as a healthy individual and was used as a benchmark for comparison among samples and populations (Murphy et al. 1990). Individuals with W_r values below 100 were considered to be in relatively poor condition compared to the population mean, while those with values above 100 were considered to be in better condition relative to the population mean (Murphy et al. 1990).

Red Snapper otoliths were weighed and processed in accordance with the procedures of 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. If a consensus was not reached, the otolith section was excluded from further analyses. Age was determined based on the annulus count and edge code assigned (Allman et al. 2005).

Reproductive status was determined via the methods of Fitzhugh et al. (2004), and Kulaw (2012). Ovaries were initially fixed in 10% formalin for a minimum of 2 weeks. After fixation, ovary subsamples (2 mm) were taken from randomly selected sections of the ovary and were 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 progress through stages starting with primary growth followed by the cortical alveolar, vitellogenic (V), and hydrated (H) stages (Wallace and Selman 1981; Brown-Peterson et al. 2011; Glenn et al. 2017). Thus, a reproductive stage was assigned and maturity was

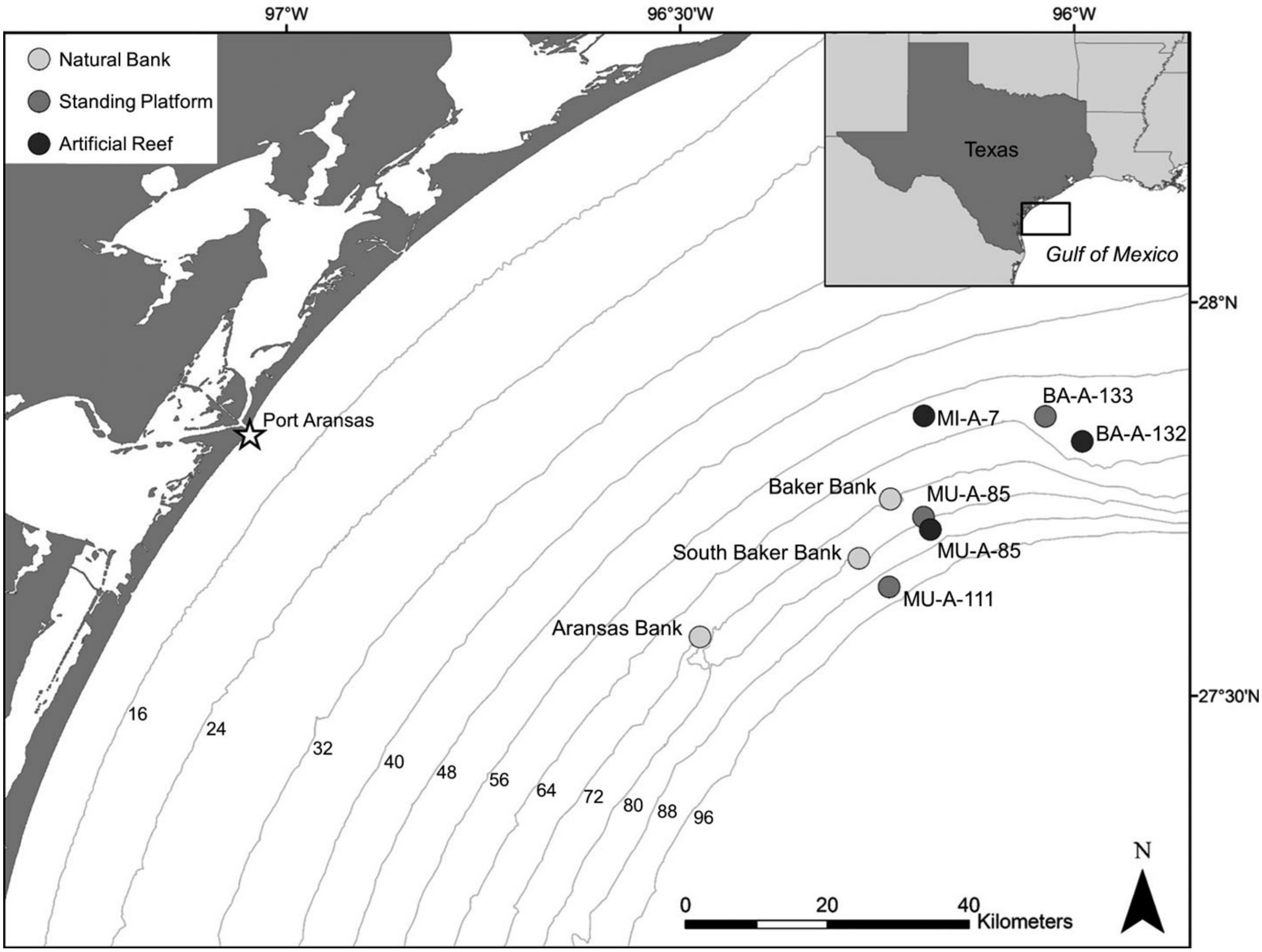

FIGURE 1. Map of the study area in the western Gulf of Mexico offshore of Port Aransas, Texas. The nine study sites represented three habitat types, including natural hard-bottom banks (Baker, South Baker, and Aransas banks), standing oil and gas production platforms (BA-A-133, MU-A-85A, and MU-A-111), and decommissioned platform artificial reefs (MI-A-7, BA-A-132, and MU-A-85).

determined through microscopic examination (Olympus BX51; 40–100×) based on the most advanced oocyte stage present. An individual was considered spawning capable if the ovary exhibited V-stage oocytes (Hunter and Goldberg 1980; Jackson et al. 2007; Brown-Peterson et al. 2011). Two other oocyte spawning markers were also considered: atresia, the breakdown and resorption of oocytes into the body; and postovulatory follicles (POFs), the remains of H cells after spawning, which indicate recent spawning activity.

Reproductive biology metrics.— Since habitat was sampled equally each year, fish data were aggregated across years to obtain a large sample size. Male : female ratios were calculated by habitat for all fish collected. To reduce the influence of season on reproductive characteristics, the remaining analyses were restricted to individuals collected from May to August, which captures the peak spawning period for Red Snapper. The GSI was calculated for each fish by using TW and gonad weight,

$$\mathrm{GSI} = \frac{\text{Gonad weight (g)}}{\text{TW (g)}} \times 100.$$

Estimates of percent maturity, BFE, SFE, and annual fecundity (AFE) were calculated for female Red Snapper collected from each habitat. Based on microscopic evaluation, ovaries containing H oocytes were used to calculate BFE. Three subsamples weighing between 0.03 and 0.05 g were taken from randomly selected sections of ovaries containing H oocytes. The subsamples were spread on a gridded petri dish with a few drops of 10% glycerin, and the H cells were counted under a dissecting microscope

(Olympus SZ61; 6.7–10×). The BFE was calculated for each subsample according to Hunter et al. (1983), and the subsamples were averaged to obtain the mean BFE for the fish as

$$\mathrm{BFE} = \frac{\text{Number of H oocytes}}{\text{Subsample weight (g)}} \times \text{Gonad weight (g)}.$$

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

$$\mathrm{SFE\ (d)} = \frac{\text{Number of mature females}}{(\text{Number with POFs only} + \text{Number with H oocytes})/2}.$$

Woods et al. (2003) and Fitzhugh et al. (2004) estimated a spawning season duration of 150 d for Red Snapper. Since evidence of temporal–spatial segregation of spawning in the Gulf has not been identified, the value of 150 d was used for AFE calculations in this study. Individual AFE was calculated using the formula based on Nieland and Wilson (1993) and was averaged to obtain the mean AFE per habitat,

$$\mathrm{AFE} = \frac{\text{Spawning season (d)}}{\text{SFE (d)}} \times \mathrm{BFE}.$$

Statistical analyses.— Differences in Red Snapper TL, age, W_r, and GSI among habitat types were assessed using nested ANOVA (site nested within habitat; Pinheiro et al. 2017). The GSI values were arcsine–square root transformed to correct for ratio data (Gotelli and Ellison 2004) and were then transformed ($1/Y$) to satisfy assumptions (Venables and Ripley 2002). Tukey contrasts were used for pairwise comparisons when ANOVA detected significance among months (Hothorn et al. 2008). Differences in fecundity at TL among habitat types were tested by log transforming BFE, AFE, and TL and then performing an ANCOVA. Chi-square tests were used to examine differences in the male : female ratio, SFE, and number of spawning-capable individuals among habitat types. Univariate statistics were performed using R version 3.3.1 (R Core Team 2013). Results were considered significant at P-values ≤ 0.05.

RESULTS

Overall, 1,585 Red Snapper were collected; of these, 863 were male, 717 were female, and 5 were of indeterminate sex. There were significantly more males collected across all habitats combined in this study ($\chi^2 = 13.49$, df = 1, $P < 0.01$). Fewer females than males were collected on artificial reefs ($\chi^2 = 16.45$, df = 1, $P < 0.01$); however, the male : female ratios were not significantly different on natural banks or standing platforms (natural: $\chi^2 = 0.33$, df = 1, $P = 0.56$; standing: $\chi^2 = 2.49$, df = 1, $P = 0.11$).

Out of the 717 female Red Snapper, 544 were collected in May–August from natural ($n = 175$), standing ($n = 177$), and artificial ($n = 192$) habitats and were included in spawning season analyses. The age and length of females collected during the spawning season were generally similar among habitats, ranging from 2 to 14 years and from 276 to 767 mm TL (Figure 2). Red Snapper from natural banks were 2–10 years old, with TLs from 294 to 739 mm; individuals from standing platforms were 2–14 years old, with TLs from 300 to 694 mm; and individuals collected from artificial reefs were 2–14 years old, with TLs from 276 to 767 mm. The mean ages and TLs (natural: 6.2 years, 549 mm; standing: 5.0 years, 503 mm; artificial: 5.8 years, 545 mm) of female Red Snapper collected during the spawning season were similar among habitats (ANOVA, age: $F = 0.39$, df = 2, $P = 0.19$; TL: $F = 0.23$, df = 2, $P = 0.28$). The W_r of Red Snapper on natural (mean $W_r \pm$ SD = 105 ± 8), standing (107 ± 11), and artificial (106 ± 7) habitats was not significantly different (ANOVA: $F = 2.70$, df = 2, $P = 0.07$; Figure 3).

No difference was found among habitats for the GSI of female Red Snapper. Mean female GSI values at all habitats were low in May and increased to a peak in June before decreasing in July and August. In July, mean female GSI values on standing platforms were lower than those on both natural banks and artificial reefs, whereas in August, GSI values on both standing and artificial habitats appeared lower than those on natural banks. 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: $F = 1.92$, df = 6, $P = 0.08$; Figure 4), although month was significant overall (ANOVA: $F = 33.97$, df = 3, $P < 0.01$; Figure 4). Pairwise testing revealed that Red Snapper GSI was significantly higher in June than in May or August, while GSI was similar in other months (Table 1).

In total, 526 females were assigned a reproductive stage, and the percentages of spawning-capable fish at each habitat type were 87% at natural banks, 79% at standing platforms, and 73% at artificial reefs. Percentages of spawning-capable individuals were not significantly different among habitats ($\chi^2 = 1.24$, $P = 0.53$). The BFE and AFE values were calculated for all females with H oocytes (total $n = 71$; natural: $n = 21$, standing: $n = 27$, artificial: $n = 23$; Table 2), and time-calibrated SFE was calculated for fish exhibiting spawning markers (V oocytes, H oocytes, and POFs; $n = 421$). The largest mean BFE was calculated for Red Snapper from natural

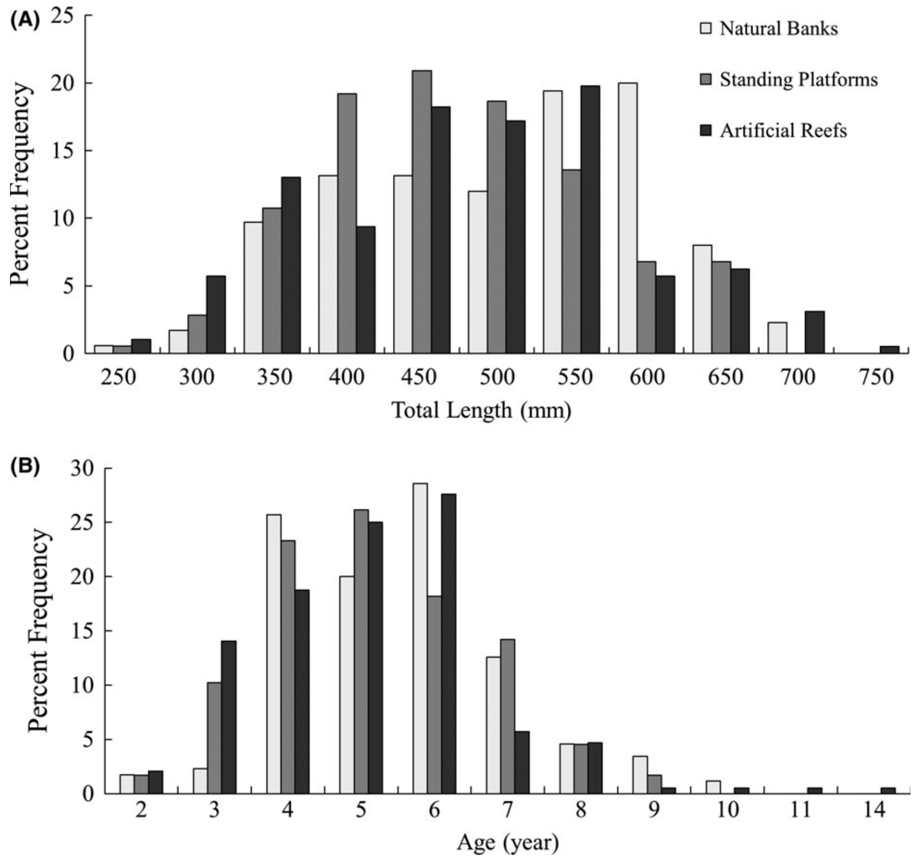

FIGURE 2. Percent frequency of occurrence for **(A)** TL in 50-mm bins and **(B)** age (years) of female Red Snapper collected on natural banks, standing platforms, and artificial reefs in the northwestern Gulf of Mexico.

banks, which also exhibited the largest mean AFE. Fish from standing platforms had the next-largest mean BFE and mean AFE values, while those from artificial reefs exhibited the lowest of both mean BFE and mean AFE. However, Red Snapper collected from standing platforms had the highest SFE, which resulted in the most spawning events per season, followed by fish from natural banks and then artificial reefs. Although apparent differences existed in SFE, it was not significantly different among habitat types ($\chi^2 = 0.54$, $P = 0.76$; Table 2). Both BFE and AFE showed an increasing trend with TL for Red Snapper (Figure 5). However, neither TL (ANCOVA: $F = 3.45$, df = 1, $P = 0.07$) nor habitat ($F = 1.55$, df = 2, $P = 0.22$; Figure 5A) was significant in predicting BFE. A similar trend was apparent for AFE, wherein TL was not a significant predictor (ANCOVA: $F = 2.83$, df = 1, $P = 0.10$; Figure 5B) and habitat was not significant ($F = 1.85$, df = 2, $P = 0.17$).

DISCUSSION

This study investigated the reproductive characteristics of Red Snapper collected from natural and artificial habitats in the western Gulf. Red Snapper on artificial habitats—both standing platforms and artificial reefs—generally exhibited reproductive capabilities and characteristics that were congruent with those from natural banks in the region. The spawning season was similar among habitats, as evidenced by similar GSI values during each month of the season. Furthermore, females that were collected during the spawning season exhibited analogous spawning traits in terms of fecundity and SFE among all habitats, and the percentage of mature females and the distribution of oocyte stages did not differ among habitats. Together, these results suggest that Red Snapper living on artificial reefs and natural banks in the western Gulf have comparable reproductive potential and thus have the potential to contribute similarly to the population.

Although our study showed that reproductive characteristics were similar among habitats, differences in Red Snapper reproductive characteristics between natural and artificial habitats have been reported in other studies. Kulaw (2012) found that natural banks yielded the highest GSI among the habitats sampled; however, no differences in SFE were observed, and the study was characterized by a relatively low sample size of females with H oocytes

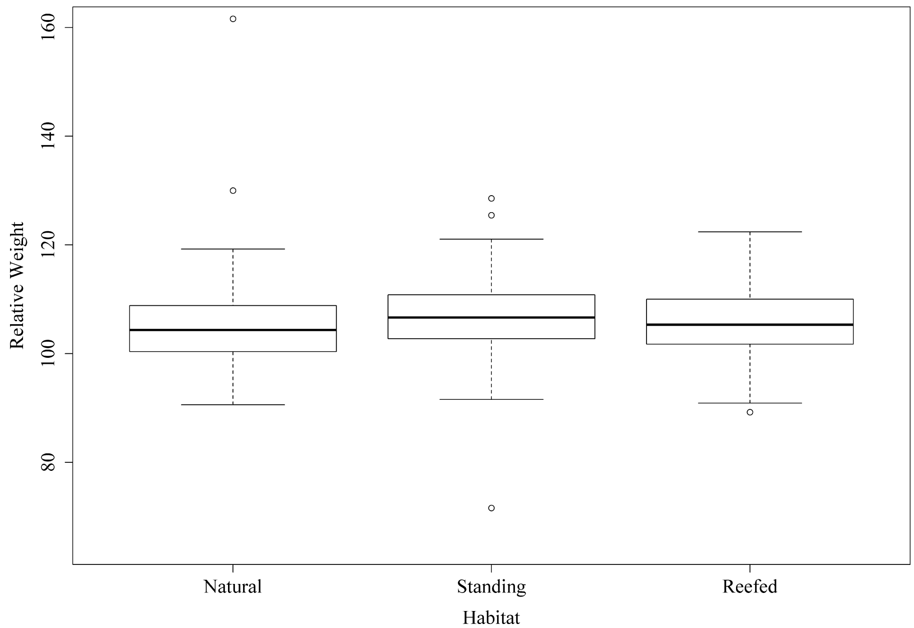

FIGURE 3. Box plot of relative weight (W_r) for Red Snapper collected on natural bank, standing platform, and artificial reef (Reefed) habitats in the northwestern Gulf of Mexico. The line within each box indicates the median; ends of the box represent the 25–75% interquartile range; ends of whiskers delineate the 95% confidence interval; and open circles denote outliers. The W_r among habitats was tested by using nested ANOVA (site nested within habitat); no statistical differences were found (F = 2.70, df = 2, P = 0.07).

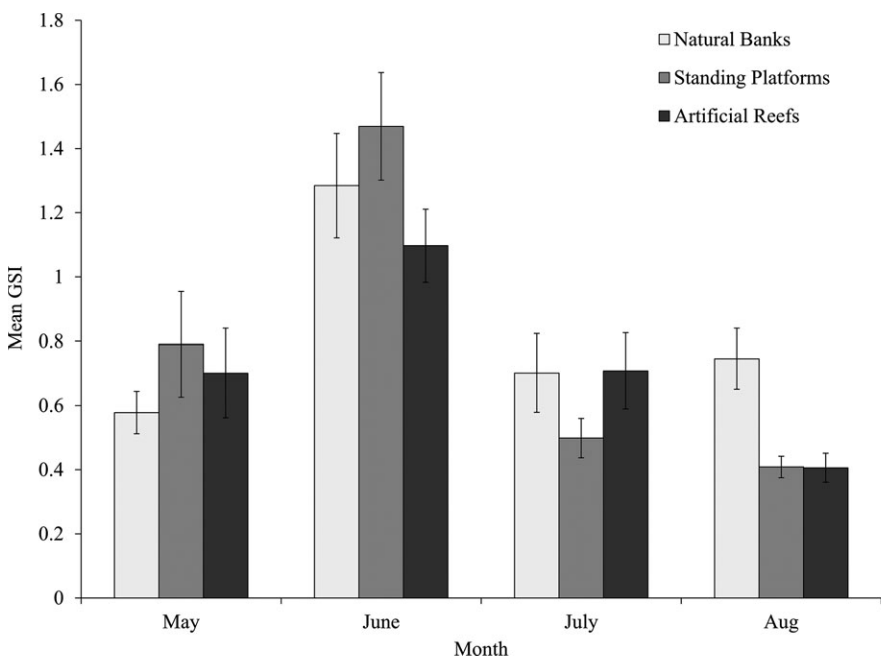

FIGURE 4. Mean (±SE) gonadosomatic index (GSI) per month and habitat for female Red Snapper collected during the spawning season in the western Gulf of Mexico. The effects of habitat within each month on mean GSI was tested using nested ANOVA (site nested within habitat), and there were no significant differences among habitats within each month (F = 1.92, df = 6, P = 0.08). The effect of month on mean GSI was also tested and was found to be significant (F = 33.97, df = 3, P < 0.01).

TABLE 1. Results from nested ANOVAs (site nested within habitat) examining female Red Snapper gonadosomatic index (GSI) by habitat. Female GSI was also tested by month and by habitat per month. Pairwise testing with Tukey's test and corrected using the Shaffer method was also performed on month (df_{num} = numerator degrees of freedom; df_{den} = denominator degrees of freedom; asterisks indicate significant results at $\alpha = 0.05$).

Effect or comparison	df_{num}	df_{den}	F	P	Estimate	SE	Z	Pr(>|Z|)
(Intercept)	1	335	563.5869	<0.0001*				
Habitat(Site)	2	6	1.075	0.399				
Month	3	335	33.9733	<0.0001*				
Habitat × Month	6	335	1.9162	0.0776				
Jun versus May					−3.9037	1.44714	−2.698	0.0419*
Jul versus May					−0.6767	2.25801	−0.300	1.0000
Aug versus May					−0.7043	1.48334	−0.475	1.0000
Jul versus Jun					3.22698	1.95019	1.655	0.1960
Aug versus Jun					3.1994	1.23749	2.585	0.0419*
Aug versus Jul					−0.0276	2.13551	−0.013	1.0000

TABLE 2. Overview of reproductive characteristics for female Red Snapper collected in the western Gulf of Mexico on natural bank, standing platform, and artificial reef habitats from May to August 2013–2015. Spawning frequency (SFE) is reported in days. Batch fecundity (BFE; eggs/spawn) and annual fecundity (AFE; eggs/spawning season) are reported as mean ± SE.

Habitat	n	SFE (d)	Spawns per season	BFE ± SE	AFE ± SE
Natural banks	21	9.9	15.2	133,552 ± 130,409	2,029,474 ± 505,297
Standing platforms	27	7.9	19.0	84,018 ± 78,377	1,599,580 ± 398,906
Artificial reefs	23	10.2	14.7	77,601 ± 69,309	1,138,724 ± 321,443
All	71	9.3	16.2	96,590 ± 89,889	1,577,440 ± 237,338

(n = 8 females), thereby preventing statistical comparisons of BFE and AFE between habitats. Glenn et al. (2017) also reported that the reproductive potential of Red Snapper at artificial reefs differed significantly from that at natural banks located on the Louisiana shelf edge. A GSI value greater than 1 has been associated with spawning (Grimes 1987; Collins et al. 1996); during observations throughout the year on artificial reefs, Glenn et al. (2017) detected these "spawning" values only in June, which was interpreted as a truncated spawning season for fish on artificial habitat. In contrast, we observed similar GSI patterns for all habitats. Additionally, females that were spawning capable and females with H oocytes were identified during all months of the spawning season, at times with mean GSI values less than 1, which correlates with GSI values above 0.5 indicating the onset of vitellogenesis as found by Fitzhugh et al. (2004). Glenn et al. (2017) also reported that mean BFE was lower at the artificial reef site than at the natural sites; however, these results were based on (1) a relatively small sample size (only nine H-stage females were identified: two from natural banks and seven from the artificial site) and (2) an unequal size distribution of fish with H oocytes (one of the two fish from natural sites was the largest fish sampled in the study and correspondingly exhibited the highest fecundity). Results from the current study showed similar spawning characteristics among habitats, with a much larger representation of H-stage fish (71 individuals) having similar lengths and an approximately equal distribution among habitat types (natural: n = 21; standing: n = 27; artificial: n = 23).

A directed effort was made in this research to control for environmental factors, such as depth and distance to shore. For example, site selection in the study by Glenn et al. (2017) was limited due to the distribution of natural habitat along the Louisiana shelf edge, which resulted in differences in site depths ranging from 55 m at artificial reefs to 160 m at natural banks. In contrast, sites selected for this study were all within the 60–90-m depth range. Therefore, reproductive differences identified between habitats in previous studies may also have been related to physical differences of sample location rather than habitat.

No statistical differences in fish condition, TL, or age were found among habitats during the spawning season, suggesting that the similarities in reproductive characteristics among habitats were not influenced by the age or length of fish. In prior studies, the differences between Red Snapper reproduction on artificial habitats and natural banks were attributed to several factors, including fish size and age as well as nutritional condition. For example,

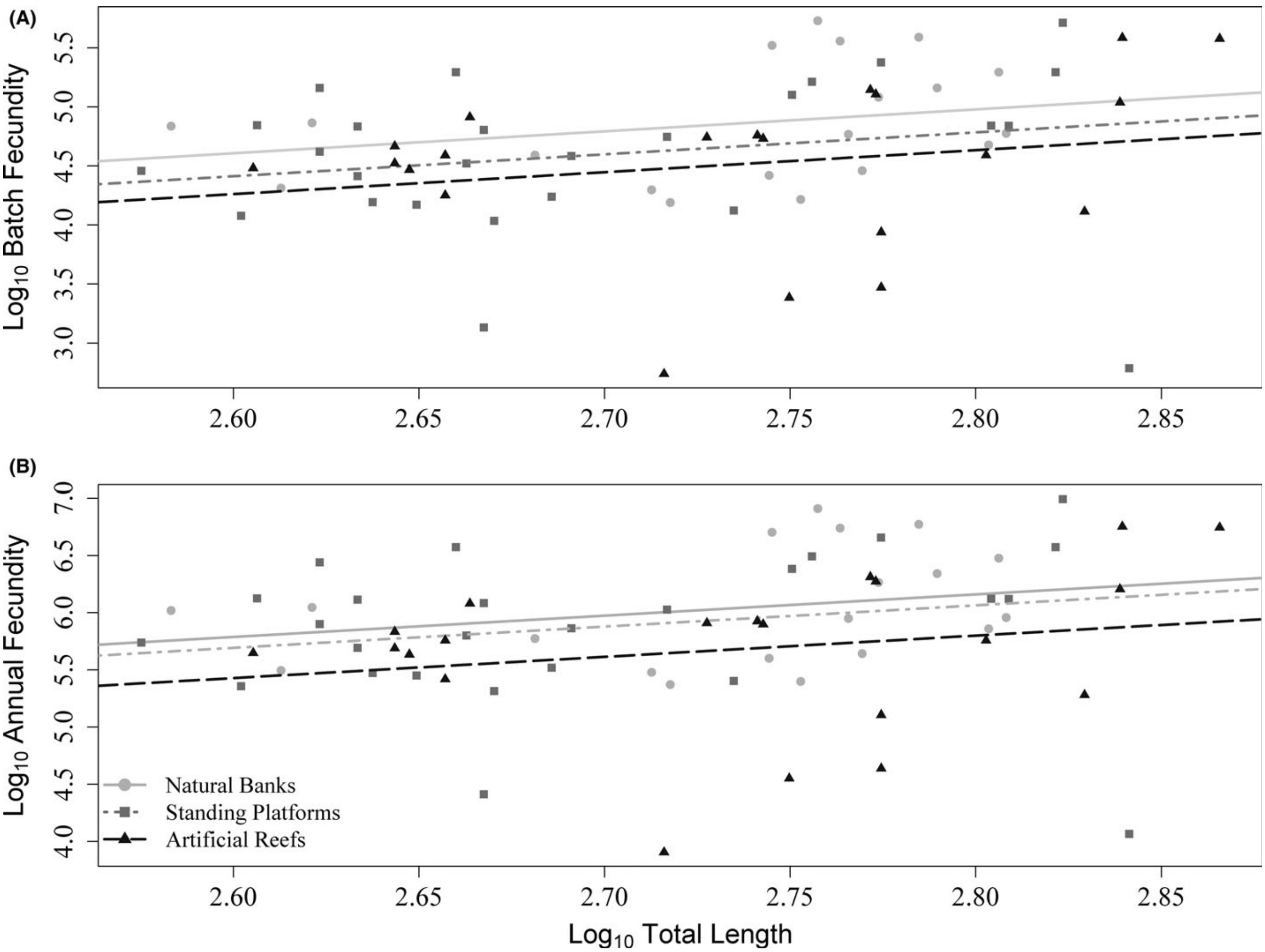

FIGURE 5. **(A)** Log_{10}(batch fecundity [BFE]) versus $\log_{10}$(TL) and **(B)** $\log_{10}$(annual fecundity [AFE]) versus $\log_{10}$(TL) by habitat for female Red Snapper collected in the western Gulf of Mexico. Differences in $\log_{10}$(BFE) and $\log_{10}$(AFE) by $\log_{10}$(TL) were tested among habitats with ANCOVA. There were no statistical differences in BFE (F = 1.54, df = 2, P = 0.22) or AFE (F = 1.85, df = 2, P = 0.17) among habitat types by TL. Log_{10}(TL) was also not significant (BFE: F = 3.45, df = 2, P = 0.07; AFE: F = 2.83, df = 2, P = 0.10).

Kulaw (2012) and Glenn et al. (2017) identified differences in fish size and age among habitats. In addition, natural banks had a larger slope in 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).

We observed similar fish condition among natural and artificial reefs. Reproductive differences by habitat have been attributed to poor nutritional condition of the fish located on artificial reefs based on a concurrent diet study (Glenn et al. 2017; Schwartzkopf and Cowan 2017; Schwartzkopf et al. 2017) and previous literature stating that reduced fecundity can be linked to poor diet and poor condition (Marteinsdottir and Begg 2002; Rideout et al. 2006). However, we did not observe any of these differences in the present study. Additionally, the differences between this study and other Gulf studies are not simply an effect of age or size, as fish ages and sizes were not so different to influence discrepancies in their respective results. For example, the size range of Red Snapper in this study (276–767 mm) was similar to the ranges reported by Kulaw (2012; 235–864 mm) and Glenn et al. (2017; 327–793 mm). Furthermore, the age range of female Red Snapper (2–14 years) was similar to the age ranges reported by Kulaw (2012; 1–12 years) and Glenn et al. (2017; 3–17 years). This reinforces the hypothesis that Red Snapper in the western Gulf may have more varied reproductive potential than fish in the northern Gulf (Lyczkowski-Shultz and Hanisko 2007; Porch et al. 2015).

Comparing the reproduction of Red Snapper across the Gulf can reveal apparent regional or demographic differences among semi-distinct populations. Higher larval concentration and spawning potential have been found in the western Gulf compared to the eastern Gulf (Lyczkowski-Shultz and Hanisko 2007). Interestingly, the BFE, SFE, and AFE calculated in this study were generally lower than previous estimates for the Gulf. Both the minimum and maximum BFE values throughout the Gulf were reported from Florida and ranged from 458 to 1,704,736 eggs per spawn (Collins et al. 1996); in Alabama, BFE values were 304,996 (Woods et al. 2003); and in Louisiana, mean BFE values ranged from 219,258 to 704,563, with a low value of 41,878 for artificial habitats (Kulaw 2012; Glenn et al. 2017). Mean BFE in the present study was 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 per year estimated between 14.7 (this study) and 44 (in Alabama; Woods et al. 2003). These patterns translate to AFE as well because AFE is calculated from BFE and SFE. However, the method used to preserve the sampled ovaries could also be a contributing factor in the observed differences between studies: freezing the gonads, which was done in other studies, tends to slightly overestimate BFE estimates and affects the ability to detect spawning markers (Porch et al. 2015; Glenn et al. 2017; Kulaw et al. 2017). Although BFE and SFE were lower in this study, Porch et al. (2015) found that the western Gulf, including the western Louisiana shelf and central to south Texas shelf, was the area with the highest spawning activity, which corresponds with the greater larval abundance detected by Lyczkowski-Shultz and Hanisko (2007). These results indicate that the spawning behavior of Red Snapper is highly variable among geographic areas in the Gulf, which may influence conclusions about the reproductive potential of the population, depending on the region sampled.

This research has several important management implications. First, reproductive traits of individual Red Snapper appear to be similar on natural and artificial habitats in this region of the western Gulf. With thousands of platforms in the Gulf scheduled for decommissioning and removal, the identification of an artificial reef's potential habitat 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 western Gulf population of Red Snapper in terms of reproduction, and the removal of platforms may in fact be detrimental to their reproduction by removing scarce complex habitat (Peabody and Wilson 2006; Gallaway et al. 2009; Streich et al. 2017b). These implications should be considered in the Gulf to identify best practices for reefing efforts and the sustainable management of the Red Snapper fishery.

ACKNOWLEDGMENTS

We are grateful to the students and staff of the Center for Sportfish Science and Conservation at the Harte Research Institute for Gulf of Mexico Studies, Texas A&M University–Corpus Christi, for help in collecting and processing fish. We also appreciate Jim Cowan and Dannielle Kulaw at Louisiana State University for sharing their histological expertise. Funding for this research was provided by the National Oceanic and Atmospheric Administration's Marine Fisheries Initiative Program (Grant Number NA14NMF4330219), the Texas Parks and Wildlife Department's Artificial Reef Program (Interagency Contract Numbers 415254, 439195, and 474362), and a grant from the Gulf of Mexico Research Initiative/ C-IMAGE II. Data are publicly available through the Gulf of Mexico Research Initiative's Information and Data Cooperative. There is no conflict of interest declared in this article.

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