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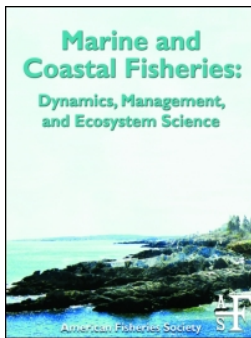
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ARTICLE

A Comparison of Red Snapper Reproductive Potential in the Northwestern Gulf of Mexico: Natural versus Artificial Habitats

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Abstract

The majority of the research on adult Red Snapper *Lutjanus campechanus* in the Gulf of Mexico has been conducted at artificial habitats (in particular, low-relief artificial reefs off the coast of Alabama) and more recently on oil and gas platforms off the coast of Louisiana. However, previous studies indicate that there are differences in Red Snapper demographics and reproductive biology between habitats and regions within the Gulf. Despite the lack of study of natural reefs and banks in the Gulf, these areas are believed to be the historical centers of Red Snapper abundance. This study sampled Red Snapper from habitats that include reefs located more than 125 km offshore, making them difficult to reach for routine sampling. The results indicate significant differences in Red Snapper reproductive biology between females collected on adjacent artificial and natural habitats. Annual fecundity estimates were almost 20-fold higher in fish collected from natural habitats. Due to the high number of artificial habitats in the Gulf, these results suggest that accounting for metapopulation differences in reproductive potential is important in evaluating the status of this resource.

Red Snapper *Lutjanus campechanus* are long-lived (55+ years), periodic life history strategists (Winemiller and Rose 1992) that can reach lengths of 1,000 mm in the Gulf of Mexico (Patterson et al. 2001; Wilson and Nieland 2001). They are gonochoristic broadcast spawners with the ability to spawn multiple times during a season (Grimes 1987; Woods et al. 2003). Further, they are a reef-associated species that will occupy both natural and artificial habitats during all stages of life (Patterson et al. 2001; Workman et al. 2002; Cowan et al. 2011). The fishery for Red Snapper in the northwestern Gulf of Mexico began in 1892 on the shelf edge reefs of Louisiana and Texas. Beginning in the mid-1940s, the placement of thousands of offshore oil and gas platforms resulted in the creation of de facto artificial reefs in the Gulf, which led to a redistribution of adult Red Snapper on the Louisiana shelf. This occurred because many platforms were constructed closer to shore than natural reefs and their high vertical relief provided usable habitat even when Mississippi River discharge was high. Some have even claimed that there were no Red Snapper in the northwestern Gulf until platforms began appearing in waters off the coast of Louisiana (Shipp and Bortone 2009).

The goal of this study was to determine whether there are differences in the reproductive potential of female Red Snapper on the Louisiana continental shelf between natural reefs that increase in habitat complexity from east to west and artificial habitats consisting of standing and toppled oil and gas platforms.

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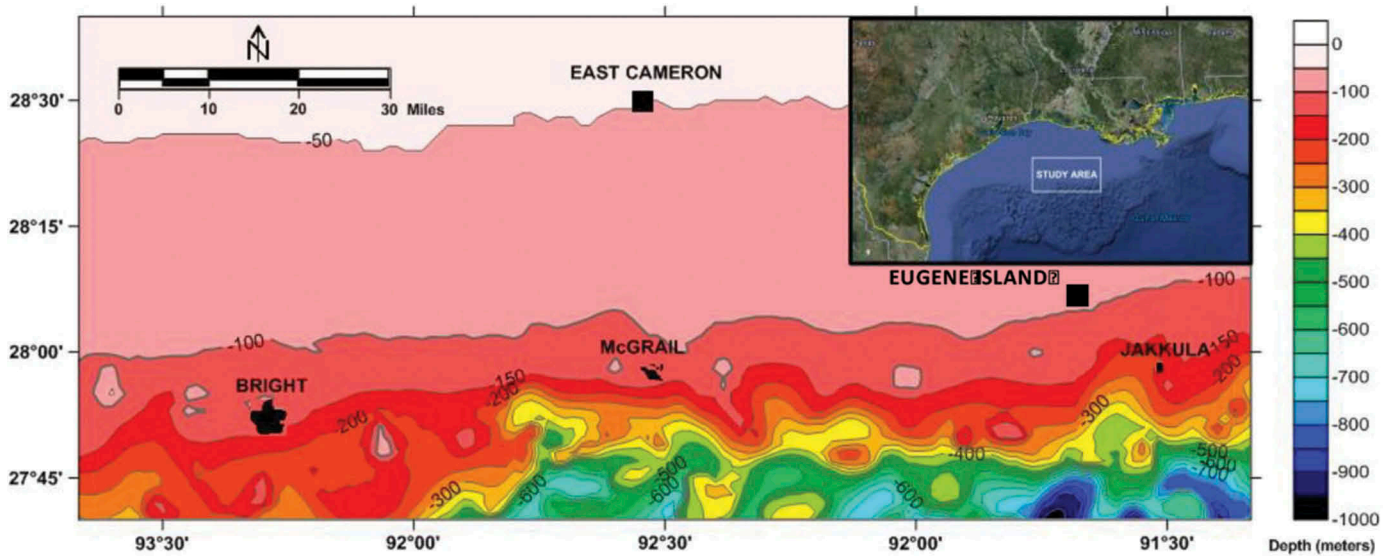
FIGURE 1. Map showing the locations of the three natural reefs (Jakkula, McGrail, and Bright) and two artificial reef sites (East Cameron and Eugene Island, each with multiple structures) that were selected for sampling Red Snapper females. Depth contours are in meters. East Cameron is situated on a large patch of lithified delta mud (Cowan et al. 2007).

METHODS

Red Snapper were sampled from five sites, each of which was defined by a specific habitat type (natural or artificial). The natural habitat sites included Jakkula, McGrail, and Bright reefs, which are located on the edge of the Louisiana continental shelf (Figure 1). The artificial habitat sites, East Cameron and Eugene Island, also are located on the continental shelf and are in artificial reef planning areas designated by the state of Louisiana. Both of these planning areas contain toppled and standing platforms (Figure 1). Two toppled and three standing oil and gas platforms were sampled in all years.

Sampling occurred roughly twice per quarter from 2011 to 2013. Because of the distance between sampling sites, it was not always possible to collect Red Snapper on the same day at all sites. We did obtain samples from all sites, however, at a time interval of less than 3 d. Ten-hook vertical longlines with alternating 6/0 and 9/0 circle hooks were used to sample the fish. Each fish was measured for total length (TL; mm), fork length (FL; mm), standard length (SL; mm), total weight (TW; kg), and eviscerated body weight (EW; kg). Muscle tissue, fin clips, livers, stomachs, otoliths, and ovaries were removed at sea, frozen, and transported to the laboratory at Louisiana State University. Ovaries were thawed, weighed (nearest 0.01 g), and preserved in 10% formalin for no less than 2 weeks.

Because the ovarian lobes of Red Snapper are developmentally symmetrical, one sample from each ovary was sufficient for histological slide preparation (Collins et al. 1996). Histological slides were prepared from an ovarian cross section approximately 2 mm thick. The ovary was visually divided into six sections; one section was chosen at random for sample extraction with a six-sided die. Each cross section was embedded in paraffin wax, cut to 4 pm, and mounted on a microscope slide. The slides were then stained and counterstained with hematoxylin and eosin, respectively, and a cover was applied with Permount.

Slides from the peak Red Snapper spawning season (June–August) were examined for maturity at 40× or l00× magnification. Oocytes were classified according to the four stages of oocyte development given by Wallace and Selman (1981) and Brown-Peterson et al. (2011): primary growth, cortical alveoli, vitellogenesis, and hydrated.

The presence of vitellogenic oocytes during the spawning season is the benchmark for maturity in female Red Snapper (Nieland and Wilson 1993; Woods 2003; Jackson et al. 2005; Brown- Peterson et al. 2011). The Red Snapper were first otolith aged (Saari et al. 2014; Kormanec 2015). Mature female Red Snapper then were grouped into both 50-mm TL length classes and age-groups, allowing estimates of both length and age at 50% and 100% maturity.

The gonadosomatic index (GSI) was calculated for all female Red Snapper sampled. The GSI is a ratio of ovary weight to eviscerated body weight:

$$GSI = \frac{\text{ovary weight (g)}}{\text{eviscerated body weight (g)}} \times 100.$$

Seasonal increases in GSI indicate spawning readiness and the potential investment of energy in reproduction; GSI should be at its maximum during peak spawning season (June–August; Davies 1956; Collins et al. 1996). A GSI > 1 indicates spawning readiness in Red Snapper (Phelps et al. 2009; Collins et al. 1996).

Red Snapper ovaries with hydrated oocytes were further examined to estimate batch fecundity (BF):

$$BF = \left(\frac{\text{number of hydrated oocytes}}{\text{sample wt (g)}}\right) \times \text{whole ovary wt (g)}.$$

Batch fecundity is estimated gravimetrically from counts of the number of hydrated oocytes in a subsample of ovarian tissue of known weight (Hunter et al. 1985). That number is then extrapolated to the weight of the entire ovary to obtain the approximate number of eggs that a female would have spawned during the next spawning event. Spawning frequency (SF) was also calculated for all females, providing estimates of the average number of days between consecutive spawning events or the number of days for all females in the population to spawn one time (Hunter and Macewicz 1985; Nieland et al. 2002). There are three different methods for determining SF: the postovulatory follicle (POF) method, the hydrated oocyte method (Hunter and Macewicz 1985; Fitzhugh et al. 1993), and the time-calibrated method (TC) (Fitzhugh et al. 1993; Wilson and Nieland 1994; Nieland et al. 2002; Woods et al. 2003).

We chose the TC method because it takes into account the numbers of females with both hydrated oocytes (day 0) and POFs (day 1). The spawning fraction, or proportion of females currently spawning, is calculated by dividing the average of the numbers of day-0 and day-1 females by the total number of mature females.

$$\text{Spawning frequency}_{\text{TC Method}} = \frac{\text{total number of mature females}}{\left(\left(\begin{array}{c}\text{total number of}\\\text{mature females}\\\text{with hydrated}\\\text{oocytes + number}\\\text{with POFs}\end{array}\right) \times 0.5\right)}$$

The inverse of the spawning fraction represents the number of days between spawning events for the population during the spawning season. To estimate the spawning events per season, we used a 150-d spawning season following Woods (2003):

$$\text{Spawning events per season} = \frac{150\text{ d}}{\text{SF}}.$$

Annual fecundity (AF) was calculated from the spawning fraction (SF), a 150-d spawning season, and batch fecundity (BF) (Nieland and Wilson 1993; Woods et al. 2003):

$$AF = \frac{150\text{ d}}{\text{SF}} \times BF.$$

A number of statistical analyses were used to compare reproductive parameters between habitats. The sex ratios of Red Snapper were compared between habitats using analysis of variance (ANOVA). Multivariate analysis of variance (MANOVA) was used to compare Red Snapper habitat-specific demographics, including mean age, percent maturity, GSI, mean TL, mean TW, and seasonal bottom water temperature. Simple linear regression was used to calculate Red Snapper weight–length relationships and analysis of covariance (ANCOVA) to compare those relationships between habitats. All statistical tests were done with the Statistical Analysis System (SAS version 9.3); statistical significance was determined at $\alpha = 0.05$ for all tests.

Analysis of variance was also used to test mean GSI values by month, habitat, and the interaction between month and habitat. Year, water temperature, and a nested site effect within habitat were included in the model as random effects. A post hoc Tukey's test was also run to provide information concerning individual comparisons. Further, ANOVA was used to determine whether there were significant differences between sites over the entire (May–September) spawning season; ANOVA was also used to analyze just the peak spawning months (June, July, and August). Mean GSI values were tested by habitat, size-class, and the interaction between month and habitat. Year, water temperature, and a nested site effect within habitat were included in the ANOVA as random effects.

RESULTS

A total of 718 Red Snapper were collected, of which 346 (48%) were collected during the peak spawning months. Of the specimens collected during the peak spawning season, 161 (46%) were females. The ratio of females to males during the peak spawning season was 50% at artificial habitats and 42% at natural reefs, but this difference was not significant (Table 1; ANOVA; $P < 0.1420$).

Among the female Red Snapper sampled during the spawning season, total length ranged from 301 to 793 mm; the largest individual was found on natural habitat, while the smallest was found on artificial habitat. Mean TL was significantly higher at natural habitats (MANOVA; $P = 0.0015$; Table 2). The heaviest Red Snapper was found on natural

TABLE 1. Sex ratios of Red Snapper sampled in the northwestern Gulf of Mexico during peak spawning months (June, July and August) at artificial and natural habitats, by sex.

Habitat	Female	Male	Percent female
Artificial	98	99	50
Natural	63	86	42

TABLE 2. Characteristics of female Red Snapper (least-squares means ± SEs unless indicated otherwise). Asterisks denote significant differences ($P < 0.05$) between artificial and natural habitats as determined by MANOVA.

Characteristic	Artificial habitat	Natural habitat
N^a	98	93
Age range (years)[a]	2–9	4–17
Mean age (years)	5 ± 1	7 ± 1*
Total length (mm)	529 ± 11	580 ± 14*
Total weight (kg)	2.18 ± 0.14	2.71 ± 0.17*
Percent mature	50 (52)	62 (98)*
Gonadosomatic index	0.63 ± 0.09	1.87 ± 0.12*
Bottom water temperature (°C)	24 ± 1	23 ± 1*

[a]Not included in the MANOVA model, used only to show trends.

FIGURE 2. Least-squares (LS) monthly mean gonadosomatic indices for female Red Snapper by **(A)** individual sites and **(B)** habitats. The vertical bars represent standard errors of the monthly means; asterisks denote significant differences between habitat types (ANOVA; $P < 0.05$).

habitat, while the lightest was found on artificial habitat. Mean weight was significantly higher at natural habitats (MANOVA; $P = 0.0172$; Table 2).

Red Snapper GSI ranged from 0.14 to 7.59. Mean GSI during the peak spawning months was significantly higher on natural reefs than at artificial habitats (MANOVA; $P < 0.0001$; Table 2). When GSI was examined by site, natural reef sites were found to be more similar to one another than to artificial habitat sites (Figure 2A; post hoc Tukey's test; $\alpha < 0.05$). For the remainder of the paper, therefore, the sites will be grouped by habitat (Figure 2B). Mean GSI began to decline earlier at the artificial habitats than at the natural reefs and was significantly different during May ($P = 0.0194$), June ($P < 0.0001$), July ($P = 0.0008$), and August ($P = 0.0025$). The temporal pattern observed at natural habitats corresponds to the traditional Red Snapper spawning season, whereas the spawning season was truncated at the artificial habitats. Female Red Snapper not caught during peak spawning months were not assessed for maturity because mature regenerating females can be mistaken for immature females. The smallest specimen to reach maturity, a 301-mm TL female, was from artificial habitat and was 3 years old. The smallest mature female Red Snapper from natural habitat had a TL of 446 mm, and the youngest was 4 years old.

Every female Red Snapper caught at natural habitats was mature, with the exception of one small (352-mm) 6-year-old female (Figure 3). Red Snapper from natural reefs reached 100% maturity at 401–449 mm and at 4 years of age. Red Snapper on artificial habitats reached 50% maturity at 350–399 mm and 7 years of age. No size-class reach 100% maturity at artificial habitats. The percentage of females that were mature was significantly higher at natural reefs (MANOVA; $P < 0.0001$; Table 2).

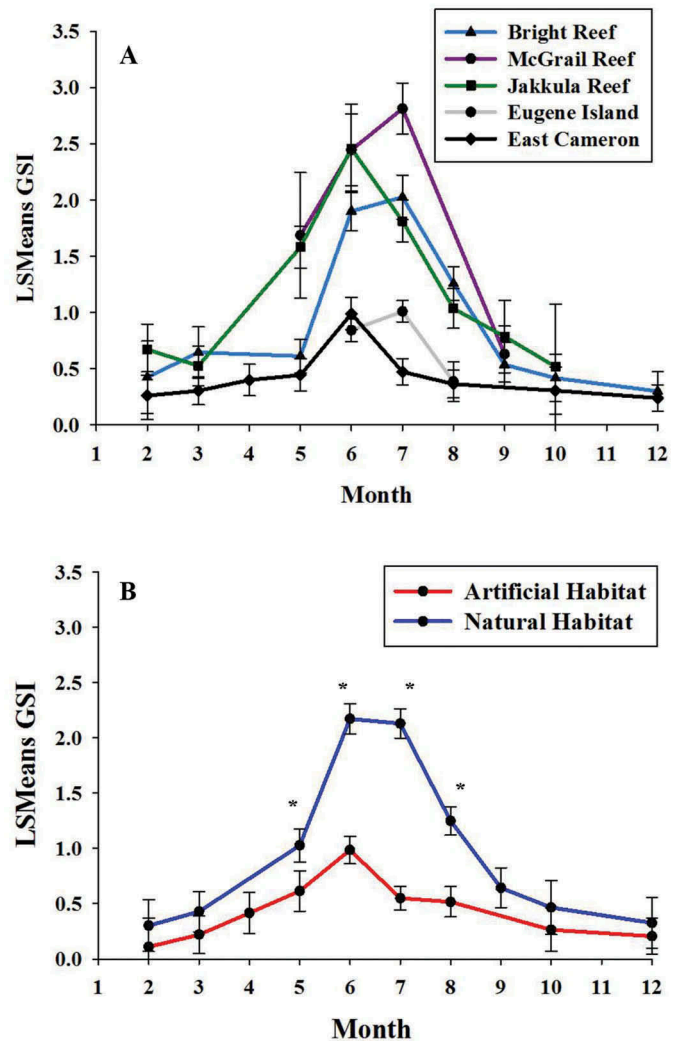Only nine Red Snapper had ovaries with hydrated oocytes, seven from artificial habitat and two from natural reefs. The smallest individual with hydrated oocytes was 4 years old, had a TL of 351 mm, and was from an artificial habitat. The largest individual with hydrated oocytes came from natural habitat, was 10 years old, and had a TL of 789 mm. Red Snapper from natural reefs had a higher percentage of ovaries with POFs, despite there being fewer samples of individual females (Table 3).

The batch fecundity (BF) estimated for female Red Snapper with hydrated oocytes ranged from 6,991 to 1,194,993 eggs per batch. The mean BF was higher at natural reefs than at artificial habitats (Table 3). Batch fecundity estimates for the Red Snapper from artificial habitats were generally low, regardless of the size or age of the female (Figure 4).
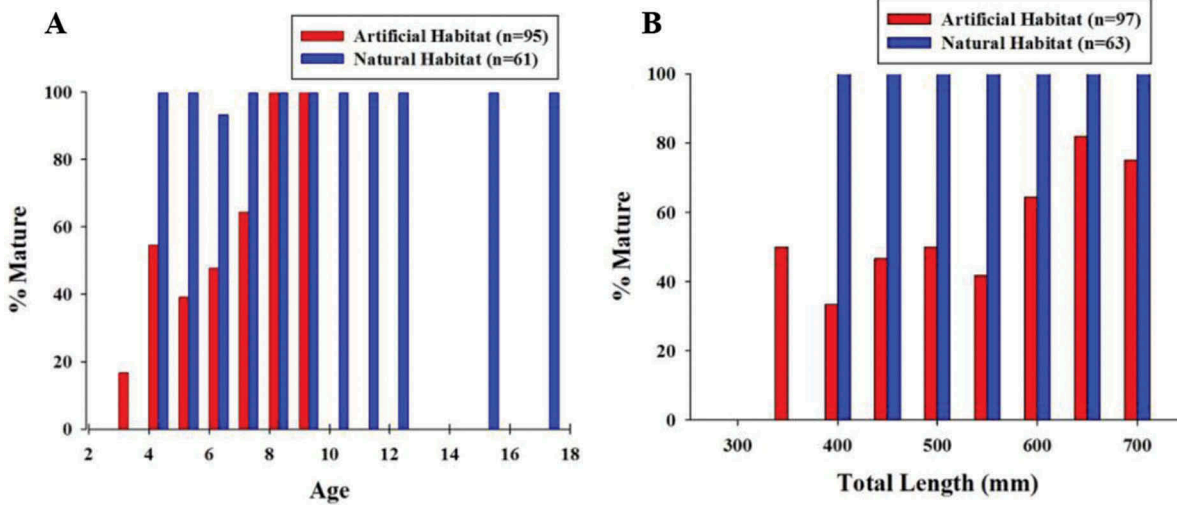
FIGURE 3. Percentages of mature female Red Snapper caught during peak spawning months by **(A)** age and **(B)** 50 mm size-class. Maturity was determined by oocyte stage analysis of histological slides. Four individuals could not be aged due to missing or damaged otoliths.

TABLE 3. Descriptive fecundity variables for female Red Snapper sampled during the peak spawning season. The values for the first two characteristics are the numbers observed (percentages of the total samples in parentheses); the values for the second two characteristics are means ± SDs.

Characteristic	Artificial habitat	Natural habitat
Ovaries with hydrated oocytes	7 (5)	2 (3)
Postovulatory follicles in ovaries	5 (4)	14 (22)
Batch fecundity estimate (eggs/batch)	$41{,}878 \pm 48{,}027$	$704{,}563 \pm 693{,}573$
Annual fecundity estimate (eggs/season)	$1{,}369{,}334 \pm 1{,}600{,}920$	$26{,}323{,}179 \pm 26{,}147{,}495$

Given a 150-d spawning season, according to the time-calibrated method 39 spawning events would be expected on natural reefs, whereas only 33 spawning events would be expected at artificial habitats (Table 4). Mature female Red Snapper on natural reefs were estimated to be 4% more likely to be spawning during any given day in peak spawning season. Red Snapper at artificial habitats had lower mean annual fecundities than those at natural reefs (Table 3). The large standard deviation of AF is most likely due to a small sample size.
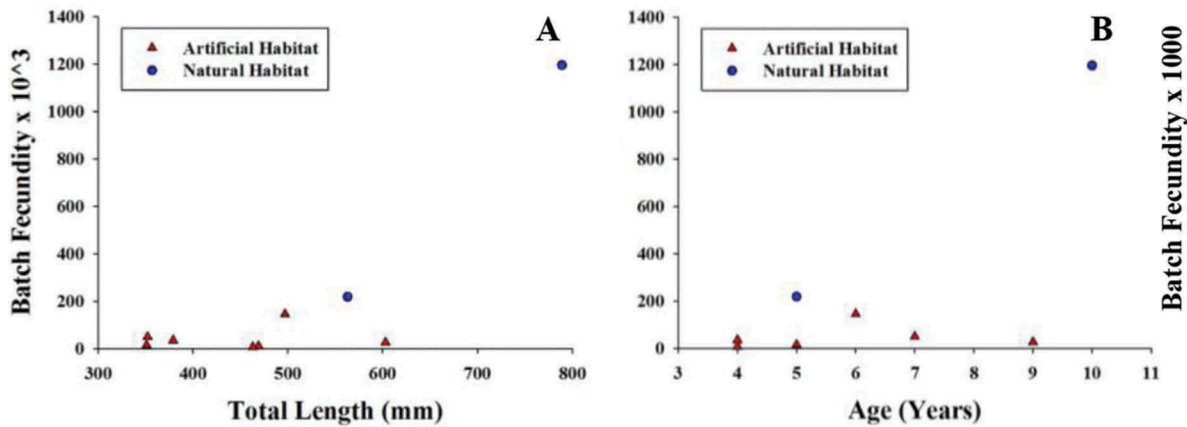

FIGURE 4. Batch fecundity of female Red Snapper by **(A)** total length and **(B)** age.

TABLE 4. Estimated spawning frequency of female Red Snapper sampled during the peak spawning season. Spawning events were calculated in terms of a 150-d spawning season.

Variable	Artificial habitat	Natural habitat
Mature females	50	62
Postovulatory follicles (day 1)	5	14
Ovaries with hydrated oocytes (day 0)	7	2
Late vitollegenic oocytes (day 0)	10	16
Spawning fraction[a]	22	26
Spawning frequency estimate[b]	4.5	3.9

[a]Percentage of mature females spawning during any day in the spawning season.
[b]Days between spawning.

DISCUSSION

In this study female Red Snapper on natural reef habitat had greater reproductive potential than those on artificial habitats. Prior to this, little work had been done on the reproductive potential of Red Snapper at natural bank and reef habitats in the Gulf. It is possible that the size of the reef or its structure (i.e., available habitat) and the density of Red Snapper at those habitats (artificial reefs consistently have higher density/area, so that there is more competition for resources) have a major effect on reproductive output. If this is true and the density of spawning females is too high at artificial reefs, one could argue that artificial habitats are reducing stock productivity. Moreover, the fish collected at artificial reefs were smaller at age and in poorer nutritional condition than those found on the shelf edge reefs (Saari et al. 2014; Kormanec 2015; Schwartzkopf and Cowan 2017), suggesting that high density is making Red Snapper more vulnerable to exploitation while decreasing their potential to influence the recovery of spawning stock biomass (Cowan et al. 2011).

In previous studies, growth rates, feeding habits, liver somatic index, and some reproductive parameters differed substantially for Red Snapper inhabiting natural and artificial habitats in the Gulf (Kulaw 2012; Saari et al. 2014; Simonsen et al. 2015; Schwartzkopf and Cowan 2017). A decade ago, female Red Snapper at artificial reefs off Louisiana reached 50% maturity at 400–450 mm TL and 100% maturity above 700 mm (Woods et al. 2003; Fitzhugh et al. 2004; Kulaw et al., in press). More recently, Kulaw et al. (in press) found that female Red Snapper from Jakkula (a natural shelf edge reef; see Figure 1) had significantly higher gonadosomatic indices during the spawning season than females collected from adjacent artificial habitats, indicating that habitat-based differences in Red Snapper reproduction may have been overlooked.

In teleost species, both reproductive effort and somatic growth require a significant storage of energy (Rijnsdorp 1990; Schreck et al. 2001). The exact process by which a fish "chooses" how to allocate energy, however, are poorly known (Karlsen et al. 1995; Nash et al. 2000). Better nutritional condition is linked to increased reproductive output, whereas diminished nutritional condition and stress are known to reduce reproductive output in most teleosts (Trippel 1995; Schreck et al. 2001; Marteinsdottir and Begg 2002; Morgan 2004). In a study done concurrently, Red Snapper at natural reefs were found to be in better nutritional condition and to have higher liver somatic indices than Red Snapper on artificial habitats (Schwartzkopf and Cowan 2017).

A fish in poor nutritional condition is more likely to use its energy stores for somatic growth instead of reproduction, because basic survival is more important than reproduction in the short term (Trippel 1995; Rideout et al. 2006). At natural habitats, female Red Snapper may be maturing earlier because they can afford to trade somatic growth for reproductive potential. Conversely, Red Snapper at artificial habitats may be bioenergetically forced to favor somatic growth over reproduction just to survive.

The liver somatic index (LSI), a measure of liver size in relation to body size, is linked to reproductive maturity (Morgan 2004). The livers of female fish produce the hormone vitellogenin (Morgan 2004; McMillan 2007), which triggers the maturation of cortical alveoli oocytes into vitellogenic oocytes, signaling maturity during the spawning season (McMillan 2007). LSI is normally correlated with GSI because vitellogenic oocytes are larger than immature oocytes, thus increasing the size and weight of the ovaries (Morgan 2004). Studies have shown that female fish with high LSIs are more likely to be mature than fish with lower LSIs, regardless of size or age (Silverstein et al. 1997; Marteinsdottir and Begg 2002; Morgan 2004). We believe that female Red Snapper at natural reefs are capable of accelerated maturation because they are in better nutritional condition and have more energy stored in their livers (Table 5; Schwartzkopf 2014; Schwartzkopf and Cowan 2017).

Evidence suggests that 100% maturity for Red Snapper in the northwestern Gulf is reached between 6 and 8 years of age, which is consistent with the maturity schedule seen

TABLE 5. Mean, standard error, minimum, and maximum values of the liver-somatic index of Red Snapper collected on Jakkula and Bright reefs and in the East Cameron artificial reef planning area (from Schwartzkopf 2014).

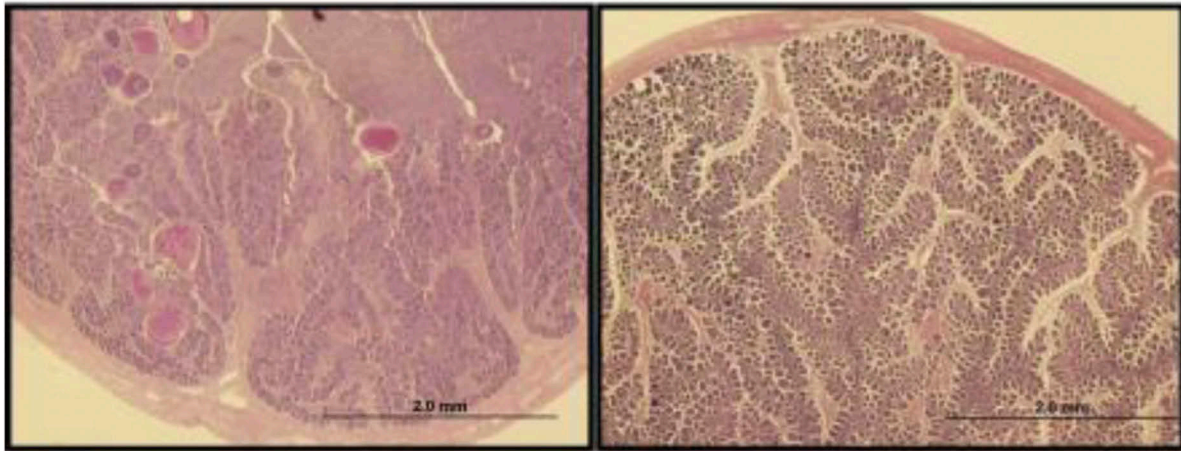| Site	Mean	SE	Minimum	Maximum
Jakkula	0.66	0.03	0.35	1.78
Bright	0.50	0.01	0.23	1.13
East Cameron	0.47	0.009	0.26	0.92

FIGURE 5. Two histological preparations showing evidence of skip spawning in Red Snapper. The image on the left is from a 707-mm, 9-year-old female collected from a standing platform in the Eugene Island artificial reef planning area. The image on the right is from a 587-mm, 6-year-old female collected in the East Cameron planning area. Both fish were collected during the peak of the Red Snapper spawning season. Note the lack of vitolleginc oocytes as well as postovulatory follicles.

at artificial habitats in this study (Woods et al. 2003; Kulaw et al., in press). However, we found that female Red Snapper at natural reefs reached 100% maturity at age 4. Moreover, although the results of previous length-at-maturity studies are consistent with our results for Red Snapper at artificial habitats, at natural reefs our Red Snapper were 100% mature at smaller sizes than previously reported by studies elsewhere in the northern Gulf (Collins et al. 1996; Fitzhugh et al. 2004; Jackson et al. 2007). Brule et al. (2010) found Red Snapper on the Campeche Banks (off the Yucatan Peninsula of Mexico) to be 50% mature at 314 mm TL and 100% mature at 526 mm. Thus, the maturity patterns for Red Snapper on natural reefs in the northwestern Gulf more closely resemble those collected on the Campeche Banks than those in previous studies in the northern Gulf. We have evidence of more complex and calorically rich diets at natural habitats (Simonsen et al. 2015; Schwartzkopf and Cowan 2017). Moreover, the natural reefs we studied are located on the shelf edge, where prevailing southwesterly bottom currents provide oceanographic conditions (i.e., water temperature, salinity, and water clarity) similar to those found at lower latitudes (Rezak et al. 1985).

However, because there is now evidence that Red Snapper at natural habitats are in better nutritional condition, we conclude that juvenescence is not likely the reason for early maturation on these habitats. In a previous study (Woods et al. 2003), we suggested that the early maturation of Red Snapper in the eastern Gulf off Alabama and the Florida panhandle was attributable to juvenescence and that the slower maturation schedule of Red Snapper collected off Louisiana was caused by density dependence in a larger population. We now believe this to be incorrect, as the female Red Snapper studied by Woods et al. (2003) were

on standing platforms at the time of collection. We caution the reader here because of the small sample of young and small female Red Snapper that we collected at natural habitats. Nevertheless, the sample as a whole is likely representative of the populations on large natural reefs and/or standing or toppled oil and gas platforms because younger Red Snapper do not normally recruit to these habitats until they are older (~2 years). The small sample size does not negate the fact that female Red Snapper at natural habitats were mature when female Red Snapper of the same age and size at artificial habitats were not.

It is also possible that the female Red Snapper at artificial habitats were skip spawning (Figure 5), a phenomenon whereby a female teleost that has reproduced in previous seasons "chooses" not spawn in the current season (Morgan and Lilly 2006; Rideout et al. 2006; Rideout and Tomkiewicz 2011). Skip spawning is not based on size or age but is associated with poor condition, poor diet, and intraspecies competition and is perhaps more common than first thought (Thresher 1983; Trippel 1995; Morgan and Lilly 2006; Rideout et al. 2006; Brown-Peterson et al. 2011; Rideout and Tomkiewicz 2011). The presence of larger (over 600 mm) and older females (6 years of age) from artificial habitats that were not exhibiting signs of maturity lends evidence to the possibility of skip spawning and may be attributable to crowding on artificial habitats. Based on previous studies, we would expect females of that size or age to be spawning during the aforementioned spawning season, but we saw almost no signs of maturation of fish of this size at artificial habitats (Woods et al. 2003; Fitzhugh et al. 2004; Jackson et al. 2007).

Batch fecundity estimates are normally a powerful gauge of reproductive potential. Unfortunately, very few female Red Snapper with hydrated oocytes were collected during the

course of this study. The BF estimates for Red Snapper at artificial habitats were lower than previously reported estimates at artificial reefs in the western Gulf (Collins et al. 1996; Jackson et al. 2007). However, the BF estimates for Red Snapper at natural habitats were similar to previously reported ranges (Collins et al. 1996; Woods 2003; Kulaw 2012). Reduced fecundity has been linked to poor diet and poor nutritional condition in teleost species, both of which are likely contributing to the low BF estimates for Red Snapper at artificial habitats (Trippel 1995; Marteinsdottir and Begg 2002; Rideout et al. 2006).

Spawning frequency estimates for Red Snapper at artificial habitats have been reported to range from 4.2 to 7.0 d (Woods 2003; Kulaw 2012; Porch et al. 2015), which compares well with the value from this study of 4.5 d. A previous spawning frequency estimate for Red Snapper at natural habitats was 9.5 d between spawning events (Kulaw 2012), whereas the spawning frequency at natural habitats in our study was every 3.9 d. The conflicting results are likely due to the lack of small and young Red Snapper females in our sample and the lack of information from the more complex natural habitats that we sampled in this study.

Annual fecundity estimates for Red Snapper are relatively few in number, and AF estimates from natural habitats in the Gulf are even rarer. Kulaw (2012) estimated the AF of Red Snapper at toppled platforms to be 3.4 ± 2.5 million eggs per season and that at standing platforms to be 3.4 ± 2.2 million eggs per season. The AF estimate at artificial habitats in our study was 1.4 ± 1.6 million eggs per year, which is lower than in previous studies. Obviously, the estimates of the AF of Red Snapper in this study were highly variable, as they have been in other studies. Still, our study shows that the estimates for Red Snapper in natural habitats are higher than those for Red Snapper at artificial habitats.

Overall, this study shows that Red Snapper in natural habitats are reproducing earlier and at a smaller size than those at artificial habitats and that over their lifetimes they will be more fecund. We also show that Red Snapper in natural habitats have higher GSIs, larger batch fecundities, increased spawning frequencies, and greater annual fecundities than Red Snapper at artificial habitats. It is possible that Red Snapper who spend extended periods of time in artificial habitats never realize their full reproductive potential for the first few years in which they are capable of spawning, before they move to less structured natural soft bottoms.

These findings are fundamentally different from what we previously knew about Red Snapper on natural habitats in the Gulf. Although a large number of Red Snapper inhabit artificial habitats in the northwestern Gulf, these individuals appear to be unable to devote as much of their stored energy to reproduction as Red Snapper occupying natural habitats. We believe that Red Snapper at artificial habitats are less important to the productivity of the stock in the Gulf than those found on the natural shelf edge reefs. In a recent review of the literature, Cowan and Rose (2016) reported that the mean number of Red Snapper on standing oil and gas platforms was 1,884 (range, 905–4,632), putting the total number at all platforms combined (2,300 as of late 2015) in the vicinity of 4,333,200. More research is needed on Red Snapper from these natural shelf edge reefs to fully understand the reproductive consequences of this recreationally and commercially important finfish on these habitats and the populations in the Gulf. We are continuing to sample Red Snapper at both habitat types to derive estimates of per capita reproductive output per female at each age in order to create a vector of multipliers at age that can be used in the next Red Snapper benchmark stock assessment.

Current management criteria for determining the status of Red Snapper resources in the Gulf of Mexico include the use of spawning potential ratios (SPRs). These ratios measure the reproductive output of a cohort over its lifespan when it is undergoing fishing relative to when it is not (Goodyear 1996). Clearly, understanding the species' reproductive biology is important for defining that management criterion. The results of our studies indicate that the different reproductive characteristics of Red Snapper at artificial and natural habitats need to be addressed in the process of stock assessment. The impact of these differences on stock productivity is likely limited, however, as Karnauskas et al. (2017) found that while Red Snapper catch rates in the northern Gulf were very high at artificial structures, these represented only a small fraction of the total area and that artificial habitats (especially oil and gas platforms) mostly attract the youngest individuals. They estimated that the Red Snapper found on these structures contributed only about 8% to population biomass, or 6.5% to spawning potential.

Nevertheless, this represents the broader problem of defining management criteria (biological reference points) and taking appropriate measurements when a population is composed of several metapopulations that share vital rates at certain stages of their life but not at others. This problem has arisen in many contexts (Thresher 1983; Jackson et al. 2005, 2007), such as shifts in productivity regimes, the variable movements of fish between areas, and the use of multiple spawning grounds. In particular, the structure of the stock–recruitment model is essential (Powers 2005; Brooks and Powers 2007; Brooks et al. 2010): does the density-dependent recruitment process occur independently for each metapopulation, or is recruitment density dependence occurring at the aggregate of the metapopulations?

Our results for Red Snapper are important because a large proportion of the Gulf of Mexico catch occurs in association with artificial habitats. This suggests that there are metapopulations with different life history and fishing experiences, which will affect the determination of SPR. Models that incorporate these differences into SPR determination and status assessment need to be developed. Additionally, status and SPR criteria that encompass the effect of the differences

between artificial and natural habitats on Red Snapper population dynamics are needed.

ACKNOWLEDGMENTS

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