7-14-2021

Reproductive characteristics of Red Snapper Lutjanus campechanus on artificial reefs in different jurisdictions

Catheline Y. M. Froehlich

Adam M. Lee
The University of Texas Rio Grande Valley

Ramiro Oquita
The University of Texas Rio Grande Valley

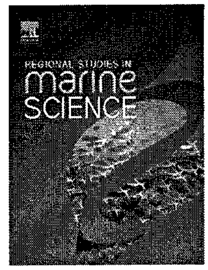
Carlos E. Cintra-Buenrostro
The University of Texas Rio Grande Valley, carlos.cintra@utrgv.edu

J. Dale Shively

Recommended Citation

Froehlich, Catheline Y. M., Adam M. Lee, Ramiro Oquita, Carlos E. Cintra-Buenrostro, and J. Dale Shively. 2021. “Reproductive Characteristics of Red Snapper Lutjanus Campechanus on Artificial Reefs in Different Jurisdictions.” Regional Studies in Marine Science 47 (September): 101936. https://doi.org/10.1016/j.rsma.2021.101936.

Journal Pre-proof



Reproductive characteristics of Red Snapper *Lutjanus campechanus* on artificial reefs in different jurisdictions

Catheline Y.M. Froehlich, Adam M. Lee, Ramiro Oquita, Carlos E. Cintra-Buenrostro, J. Dale Shively

PII: S2352-4855(21)00328-5
DOI: https://doi.org/10.1016/j.rsma.2021.101936
Reference: RSMA 101936

To appear in: *Regional Studies in Marine Science*

Received date : 22 January 2021
Revised date : 25 May 2021
Accepted date : 14 July 2021

Please cite this article as: C.Y.M. Froehlich, A.M. Lee, R. Oquita et al., Reproductive characteristics of Red Snapper *Lutjanus campechanus* on artificial reefs in different jurisdictions. *Regional Studies in Marine Science* (2021), doi: https://doi.org/10.1016/j.rsma.2021.101936.

Reproductive characteristics of Red Snapper *Lutjanus campechanus* on artificial reefs in different jurisdictions

Catheline Y.M. Froehlich[a,b], Adam M. Lee[c], Ramiro Oquita[c], Carlos E. Cintra-Buenrostro[c]*, and J. Dale Shively[d]

[a]School of Earth, Environmental, and Marine Sciences (SEEMS); University of Texas Rio Grande Valley (UTRGV); One West University Blvd.; Brownsville; Texas 78520. [b]School of Earth, Atmospheric, and Life Sciences; University of Wollongong; Northfields Ave.; Wollongong, NSW; Australia: catheline.froehlich@gmail.com. [c]Ocean, Coastal Environmental and Ecological Assessment Lab.; SEEMS; UTRGV; One West University Blvd.; Brownsville; Texas 78520: adam.m.lee1211@gmail.com, ramiro.oquita01@utrgv.edu, carlos.cintra@utrgv.edu. [d]Texas Parks and Wildlife Department; Artificial Reef Program; 4200 Smith School Rd.; Austin; Texas 78744: dale.shively@tpwd.texas.gov.

*Corresponding author: carlos.cintra@utrgv.edu

Highlights

- Red Snapper had similar reproductive capacity among state and federal jurisdiction
- Spawning season spanned April to September with peak spawning starting in June
- Of all females 79% were mature but only 12% of them were from inshore sites
- Further region-based restrictions should be considered to allow successful spawning
- Artificial reefs are essential for reproduction in regions with little natural cover

Abstract

Reproductive activity of Red Snapper *Lutjanus campechanus* (Poey, 1860) at artificial reefs (ARs) are only recently being investigated. Yet, the management of the fishery differs on a regional basis with state and federal jurisdictions, and reproductive differences among regions have not been investigated. To compare the reproductive activity of *L. campechanus* among state (inshore) and federal (offshore) jurisdictions, individuals were collected in the northwestern Gulf of Mexico from four ARs on a quarterly basis for 2 yrs. Inshore sites exhibited fishing pressure year round whereas offshore sites only had fishing season open during a few months of summer. Collected individuals were measured for weight and length, then aged, sexed, and reproductive phase identified using the following metrics: resting, spawning capable, actively spawning, and regressing. Individuals in all reproductive phases were collected at three of the four sites. Spawning season was observed from April to September, with June identified as the induction of the peak spawning period. Hydrated oocytes were observed, which indicated imminent spawning within 12 h. Although 79% of female *L. campechanus* at all sites combined were mature based on reproductive phase, most fish were small, young, and inshore sites only made up 12% of the mature females. Several individuals were mature at offshore sites compared to only a few at inshore sites, yet fishing pressure was higher at inshore sites. We suggest that *L. campechanus* were spawning capable and actively spawning when those individuals were several years of age, but younger, barely mature individuals comprised the majority. Thus, *L. campechanus* include ARs in their life cycle and directly spawn on state and federal ARs when given enough time to achieve reproductive maturity. However, fisheries

management should consider enforcing higher restrictions depending on the jurisdiction to allow individuals to mature and spawn before capture in both state and federal jurisdictions.

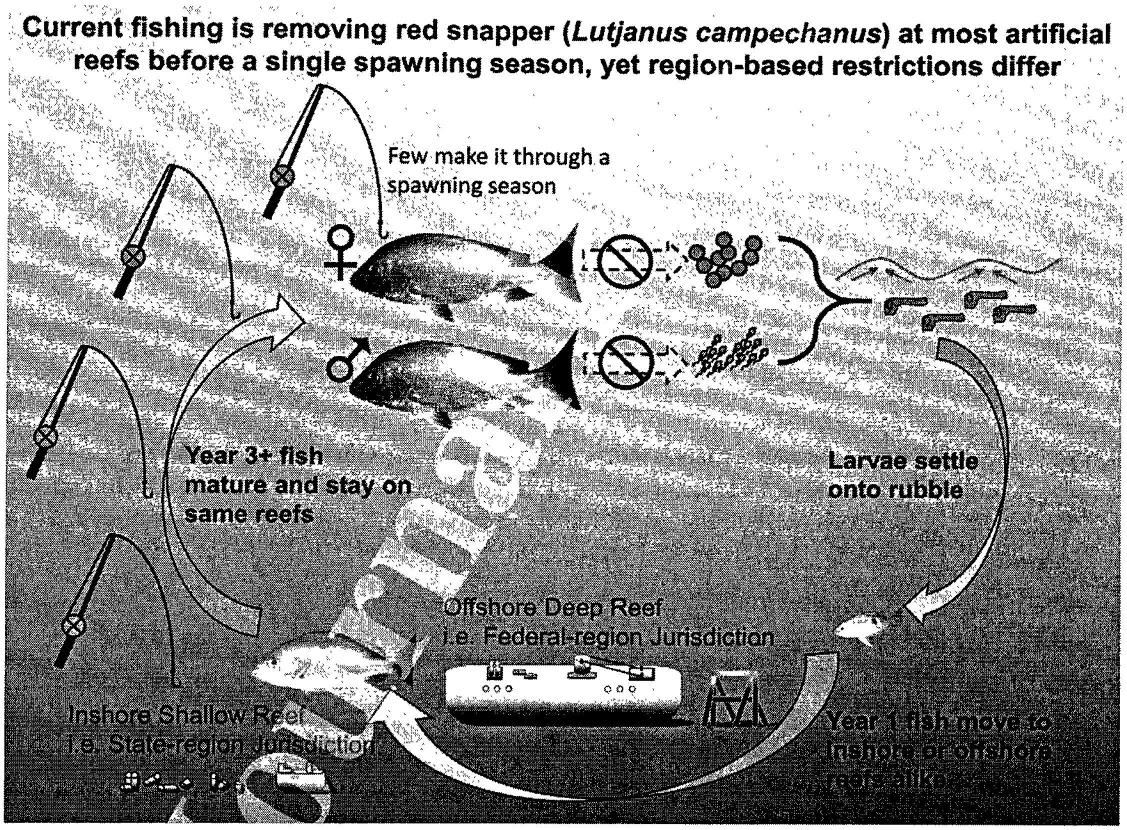
Keywords

Lutjanidae, Reefs, Vertical Longline, Fisheries, Structural Dependence, Gulf of Mexico.

Abbreviations

Artificial Reefs (ARs), Gulf of Mexico (GOM), Gulf of Mexico Fishery Management Council (GMFMC), Southeast Data Assessment Review (SEDAR), National Oceanic and Atmospheric Administration (NOAA), Southeast Monitoring and Assessment Program (SEAMAP), Gulf States Marine Fisheries Commission (GSMFC), Accumulated Variance (ACV), Gonadosomatic Index (GSI), Nested Analysis of Variance (NANOVA).

Graphical Abstract



1. Introduction

Red Snapper (*Lutjanus campechanus*, Poey, 1860) are an ecologically and economically valuable reef fish with a natural range from the Atlantic coast of the United States to the Brazilian state of Ceara (Camber, 1955). *Lutjanus campechanus* are a long-lived (> 50 yrs), voracious and opportunistic predator associated with complex vertical structures, both natural and artificial

(Brewton et al., 2020; Downey et al., 2018; Render, 1995; Wilson and Nieland, 2001). Juvenile *L. campechanus* recruit to low profile structure, and later are thought to move to increasingly complex structure following ontogenetic shifts (Gallaway et al., 1999; Gallaway et al., 2009; Szedlmayer and Conti, 1999; Szedlmayer and Howe, 1997; Workman et al., 2002). Once a predator-adverse size is obtained (8+ yrs), individuals often dissociate from structure and move to open water (Gallaway et al., 2009; Gazey et al., 2008), but can still be recorded on hard structure (Streich et al., 2017). However, the strong structural dependence during their early life make *L. campechanus* especially vulnerable to fishing pressure as fishermen target the species primarily on easily-accessible structures instead of the open ocean.

For several decades, the Gulf of Mexico (GOM) has experienced serious *L. campechanus* stock declines due to habitat destruction, lack of suitable juvenile habitat, overfishing, and high market value (Wells et al., 2008). As the 4th most valuable fishery in the GOM, strict federal fishing regulations and short open seasons attempted to curtail losses and re-establish sustainable stock levels (Cowan et al., 2011; Gallaway et al., 2009; Gillig et al., 2001; Hood et al., 2007). Recent stock assessments determined that *L. campechanus* continue to experience strong fishing pressure, as reported by the Gulf of Mexico Fishery Management Council (GMFMC) and Southeast Data Assessment and Review (SEDAR) (GMFMC, 2014; SEDAR, 2018). An important factor is that available fishing habitat is governed differently based on spatial distributions, which affect temporal and catch limits of *L. campechanus*. In the United States, the federal government oversees fishing habitat passed ~5.6 km (up to 3 nmi), and up to 16.7 km (9 nmi) in some states (Florida's Gulf Coast, Puerto Rico and Texas). The federal government restricts *L. campechanus* fishing to annually specified dates from May to September. The state governments have jurisdiction over the inshore reefs, and some (e.g., Texas) allow open year-round fishing for *L. campechanus*. Fishing pressure may thus be unbalanced depending on the areas targeted and likely affect the reproductive capacity of fish in different jurisdictions.

Many structures visited by fishermen for *L. campechanus* are artificial reefs (ARs), which provide essential habitat for *L. campechanus* spawning in areas with limited natural refuge (Alexander, 2015; Cowan et al., 2011; Downey et al., 2018; Karnauskas et al., 2017; Mueller, 2012; Syc and Szedlmayer, 2012; Wells et al., 2008). Efforts to understand the reproductive characteristics of *L. campechanus* on ARs are essential, because ARs throughout the GOM are used as management tools for the species, which has a history of mismanagement (Cowan et al., op. cit.). *Lutjanus campechanus* associate with ARs throughout the first 8-10 yrs of their life (Gallaway et al., 2009), yet reproductive capacity on ARs are only recently being investigated (Cowan et al., 2012, Downey et al., op. cit.). Because *L. campechanus* grow quickly (legal catch size attained at 2-3 yrs), mature at 3-4 yrs, are asynchronous batch spawners, and increase their reproductive output substantially with size (and by proxy age) (Lowerre-Barbieri et al., 2015; Porch et al., 2015), older individuals are crucial to sustain populations. However, regional variations in the onset of reproduction have been observed across the GOM (Glenn et al., 2017; Kulaw, 2012; Saari et al., 2014). Some reproductive differences may instead be attributed to the type of habitat provided, with ARs near the water surface exhibiting different reproductive outputs than submerged natural and artificial structures (Downey et al., op. cit.). Disparities in fishing pressure from differing jurisdictional restrictions may provide an additional layer of variations observed in spawning capacities since fishing limits vary by jurisdiction.

Accordingly, this study compared the reproductive capacity of *L. campechanus* at inshore (state jurisdiction) and offshore (federal jurisdiction) AR sites in south Texas, northwestern GOM. Fishing pressure varied drastically from a nearly year-round season in inshore sites compared to only a few weeks open season in offshore sites. Sampling sites were all located within 62 km of each other to remove extensive environmental factors, and were within 32 km of the coast to reduce fishing pressure biases against fishermen accessibility. Only submerged ARs were sampled to remove variations attributable to near surface structural or natural reef differences. By investigating reproductive status of *L. campechanus* populations in different jurisdictions, this study provided an opportunity to compare maturity levels of targeted populations, and inform future management practices.

2. Methods

Four AR sites were sampled quarterly from December 2014 until December 2016: December-February, March-May, June-August, and September-November. Two reef sites resided in Texas state waters (< 15 km from shore) and were considered inshore and shallow (< 25-m depth) sites: PS-1169L Port Isabel reef (hereafter inshore south = INSO, 24-m depth, latitude 25.968407° longitude -97.066917°), and PS-1047 South Padre Island Nearshore reef (hereafter inshore north = INNO, 21-m depth, latitude 26.525583° longitude -97.153587°). The remaining sites resided in federal waters (> 15 km from shore) and were considered offshore and deep (> 30-m depth) sites: PS-1122 Texas Clipper reef (hereafter offshore south = OFSO, 35-m depth, latitude 26.189154° longitude -96.85215°), and PS-1070 Port Mansfield Liberty Ships (hereafter offshore north = OFNO, 31-m depth, latitude 26.426607° longitude -97.024338°). The main differences between inshore and offshore sites were depth, structure and vertical relief. Offshore sites were deeper than inshore sites and exhibited high vertical relief (> 15 m) and were dominated by decommissioned oil platforms and large (145 m) vessels. Inshore sites exhibited low vertical relief (< 15 m) and were dominated by concrete culverts, smaller vessels, small oil jackets, and reef balls. Detailed descriptions and images of sampled sites were published in Bollinger and Kline (2017).

Lutjanus campechanus individuals were collected each quarter per site utilizing a modified National Oceanic and Atmospheric Administration Southeast Monitoring and Assessment Program (NOAA SEAMAP) vertical long line protocol (Gulf States Marine Fisheries Commission (GSMFC), 2016). Commercial bandit rigs with 10 equally-sized hooks were deployed either starboard or portside randomly (modification from NOAA SEAMAP, which outlined bandit rigs to be simultaneously deployed starboard, portside, and at the stern) with one of three hook sizes (8/0, 11/0, and 15/0 also selected at random). Each site was fished with one line at a time, each for a 5-min soaking time until all hook sizes were used. The size of fish varied based on the hook size used, as discussed in Froehlich et al. (2018), which provided a sample of most fish sizes present at each site. Specimens were placed on ice and processed within 48 h of catch.

Morphometric measures of total length (TL, ± 1.0 mm), total weight (W, ± 0.0001 kg), eviscerated weight (EW, ± 0.0001 kg), and gonad weight (GW, ± 0.0001 kg) were collected from wet dissections for all but one fish (weight measurement missing). Age (± 0.1 yrs) of individuals was determined by otolith annulation and margin analysis. Age was calculated to ± 0.1 yrs by counting the number of annuli on otoliths compared to a shared birth date for GOM *L. campechanus* and the month of capture (VanderKooy and Guindon-Tisdel, 2003). Accumulated variance (ACV) between three independent readers was 0.49% for annulations and 0.14% for margin characterizations, thus no otoliths were excluded from the analysis. Fulton's condition factor (K) was used as an indicator of fish health by assuming the weight of a fish was proportional to its cubed length (Bardon-Albaret and Saillant, 2017). The general condition of *L. campechanus* was approximated using K, where:

$$K = \text{Weight (kg)} / \text{Total Length (mm)}^3 \times 100$$

A value of $K > 1$ suggested a fish in good health, and K was used as a general indicator for individual health condition.

Gonads were preserved in Prefer®, which is a glyoxal fixative found to have a safer profile and faster reaction rate than formaldehyde (Dapson, 2007), for at least 48 h but no more than 14 d. A 5-mm section from an individual gonad lobe (right or left), and area (top, middle, lower or bottom) was removed according to a random number table generated in SPSS v.23 (IBM, 2013). Due to symmetrical development of ovarian lobes, a single sample from a female *L. campechanus* was used to estimate reproductive status (Glenn et al., 2017). The tissues were embedded in paraffin using a KD-TS3D tissue cassette processing system, and thin sections (5-10 μm) were cut on a rotary microtome. Tissue sections were affixed to glass slides and stained utilizing Gil hematoxylin and counterstained with EOSIN-Y.

Sex and reproductive phases were assigned after identification of reproductive and accessory tissues with specific features following Brown-Peterson et al. (2011). Reproductive phases were confirmed by three readers with phase confirmation dependent upon at least two identical phase assignments. There was a 100% agreement among at least two readers. Gonadosomatic index (GSI) measures were used to assign reproductive capability (Kjesbu, 2009), where:

$$GSI = \text{Gonad Weight} / (\text{Total Weight} - \text{Eviscerated Weight}) \times 100$$

Individuals with a $GSI > 1$ suggested reproductive activity (Brown-Peterson et al., 2011). Means of GSI for males and females were calculated across month. A fish was identified as mature and reproductively active that season when a reproductive phase of spawning capable, actively spawning, or regressing was assigned. The spawning season was determined as the months in which females and males exhibited a mean $GSI > 1$. Peak spawning period was determined as the month with the highest percent of reproductively active females, highest mean female GSI, and the largest proportion of mature females.

Statistical analyses were performed in SPSS v.23 (IBM, 2013) with $\alpha = 0.05$. All results where means are reported are followed by ± standard errors. A Chi-square test (χ^2) was utilized to identify sex ratios at sampling sites. Size frequency (TL mm) and distribution of individuals in different reproductive phases were compared with a Kolmogorov-Smirnov test. Morphometric and age characteristics were subject to tests of normality with visual Q-Q plots and Kolmogorov-Smirnov, and homoscedasticity was tested with Levene's test (Sokal and Rohlf, 2011). A logistic transformation (Log+1) of W was completed to obtain normality (hereafter LogW). Differences in GSI and K among sites were determined through a nested analysis of variance (NANOVA). Morphometrics and reproductive status were used in binary logistic regressions to calculate maturity proportions (per quarter per site) for total length (TL_{50}), LogW ($LogW_{50}$), and age (Age_{50}) at which 50% of females exhibited maturity (Sokal and Rohlf, op. cit.). Reproductive maturity as a function of morphometric measures was only calculated for females as the species exhibits asynchronous ovarian development, and are characterized as heterochronal (batch) spawning with indeterminate annual fecundity (Brulé et al., 2010). Heterochronal batch spawners are not sperm limited (Grimes, 1987; Woods et al., 2003), thus males play a limited role in the management of *L. campechanus*, and are excluded in proportion mature analyses. Differences in maturity proportions (TL_{50}, $LogW_{50}$, and Age_{50}) among locations, sites and quarters of collection were tested with a NANOVA (Sokal and Rohlf, op. cit.).

All NANOVAs used location (inshore or offshore) as the main factor with collection site (INSO, INNO, OFSO and OFNO), and quarter of collection (December-February, March-May, June-August, September-November) subsequently nested. Post hoc testing of statistical results were performed through Tukey's HSD test to identify homogeneous subsets if significant differences were observed (Sokal and Rohlf, 2011).

3. Results

A total of 398 individuals were collected from December 2014 to December 2016. From individuals collected, mean TL was 467 ± 90 mm (max 721 mm), mean W was 1.65 ± 0.97 kg (max 5.53 kg), and mean age was 3.8 ± 1.5 yrs (max 10.8 yrs). Only 18 out of 184 females and 13 out of 214 males were of large sizes (> 600 mm, see Froehlich et al., 2018 for additional morphometric information on *L. campechanus* at these sites). A 1:1 sex ratio ($p > 0.05$, see Table 1 for all statistical outputs) was observed in *L. campechanus* overall, with INSO, INNO and OFSO also retaining a 1:1 ratio. Offshore north however, was significantly dominated by males with a 1:1.39 sex ratio ($p \leq 0.04$). All individuals, except for one, were in good condition (K) from all sites. Less fish were caught on inshore reefs (121 inshore vs. 277 offshore), but no significant differences in condition were observed among locations ($p > 0.05$), neither sites ($p > 0.05$) nor sex ($p \geq 0.05$).

Histological characterization identified *L. campechanus* in all stages: resting, developing, spawn capable, and regression in both females and males. No significant difference in the frequency of histological characterization was observed by locations ($p > 0.05$) or sites ($p > 0.05$), but differences were observed by sex ($p < 0.01$) and quarter ($p < 0.01$). There were significant interactions between locations and quarters ($p < 0.01$), sites and quarters ($p < 0.01$), and sex and quarters ($p < 0.05$). Hydrated oocytes, which indicated imminent spawning within 12 h, were observed at OFSO.

Mean GSI for females was 0.53 ± 0.06 (0.08 to 7.55 range), and for males was 0.61 ± 0.04 (0.04 to 3.24 range). Mean female GSI was slightly higher offshore (0.56 ± 0.06) than inshore (0.45 ± 0.13), although there were no significant differences among locations ($p > 0.05$) nor sites ($p > 0.05$), but differences were observed among quarters ($p < 0.01$). There was a significant interaction between locations and quarters ($p < 0.05$), however no significant interaction was found between sites and quarters ($p > 0.05$). Spawning capable individuals were observed at all locations (inshore and offshore) and sites (INNO, OFSO and OFNO) with the exception of INSO, at which zero spawning capable females were observed. Male and female fish exhibited a mean GSI/month > 1 only in June, but females got close in May (Fig. 1). From all individuals collected, 82% of fish (male and female) were identified as reproductively active (in which gonadosomatic characterization is either developing or spawn capable) across April, May, June and September. At all sites combined, 79% of females were mature, but, inshore sites accounted for only 12% (INSO = 9%, INNO = 3%) of mature females observed. Gonadosomatic indices for females and males were observed at their highest levels in June (Fig. 1). Over 90% of all fish, regardless of sex or location, were reproductively active in June at inshore and offshore sites. Since samples were not collected in July or August (due to weather constraints), June could not be confirmed as the peak spawning month. However, June could be delineated as the induction of peak spawning period.

Based on calculations of maturity proportions, half of females would reach maturity at 458 mm in total length (TL_{50}), 1.14 kg in weight ($LogW_{50}$), and 3 yrs of age (Age_{50}) (Fig. 2). No females collected were at or above the estimated length for 99% maturation (968 mm). The legal catch size for *L. campechanus* in Texas state waters was 381 mm at the time the study was performed, and 84% of the females collected were of legal retention size. Of the females collected (n = 184), 79% displayed maturity (n = 146) but 57% did not achieve TL_{50} before capture (n = 104). Furthermore, only 18% of females collected (n = 34) were at least 5 yrs old. Out of all females sampled only 41% met the maturity benchmarks for TL, 41% for LogW, and 71% for age. No significant differences were found in the proportional maturity of females as determined by length, LogW, and age between locations or quarters of capture ($p > 0.05$). Less than half of females met the TL_{50}, $LogW_{50}$, and Age_{50} benchmarks at INSO, which set INSO significantly apart from all other sites ($p < 0.05$, Fig. 3). There were some differences in maturity proportions for all other sites, but no site had more than 65% of females meeting any maturity benchmarks (Fig. 3). However, the proportion of females that met maturation benchmarks were different among other reefs in the GOM (Table 2). Total length benchmarks (458 mm) were higher in our study than in other studies, but age benchmarks (3 yrs) were generally similar to others (Table 2).

4. Discussion

Lutjanus campechanus collected in the current study were assessed for reproductive capacity on inshore artificial sites within state jurisdiction compared to offshore artificial sites within federal management. Twice as many fish were caught offshore even though the same fishing effort was completed in both jurisdictions, and offshore sites had fish with marginally higher GSI. Reproductively active females and males were observed on all four ARs, and a sex ratio of 1:1 was observed on most sites. A recurring spawning season was identified from April to September with the peak spawning period likely beginning in June. Although 82% of fish were reproductively active during the spawning season, < 65% of females met maturity benchmarks based on TL, W and age values (TL_{50} = 458 mm, $LogW_{50}$ = 1.14 kg, Age_{50} = 3 yrs). Out of 79% mature females, only 12% were observed at inshore sites. All fish but one were in good condition and several were reproductively active and spawning. Thus ARs sampled in this study provided essential habitat suitable for reproduction in the otherwise relatively barren seafloor in the region.

Histological characterizations support a spawning capable population at inshore and offshore sites, with spawning capable individuals identified at all offshore sites, but few at inshore sites. It is unknown at this time if spawning aggregations occur at all sites, however a hydrated oocyte was identified at an inshore site in Alexander (2015) and an offshore site in our study, indicating imminent spawning within 12 h. Histological assessments, GSI levels, and previously observed imminent spacing characterizations (Alexander, op. cit.) suggest that artificial habitat inshore and offshore are used reproductively by *L. campechanus*. There are some limitations with using gonadosomatic characterization alone to characterize reproductive capacity, since the tissues represent only a snapshot of reproductive parameters, but our findings support previous studies that identify ARs as essential habitat for *L. campechanus* in the GOM (Brock, 1994; Cowan et al., 2011; Downey et al., 2018; Gallaway et al., 2009; Render, 1995; Syc and Szedlmayer, 2012). Utilization of both inshore and offshore sites throughout ontogeny suggests that movement offshore upon maturity (Gallaway et al., op. cit.) may not be a characteristic of *L. campechanus* everywhere. *Lutjanus campechanus* are capable swimmers, and the greatest distance between offshore and inshore sites in the current study is 30 km. Such a distance among sites is within the species' reported mean distances travelled (Patterson et al., 2001). However, *L. campechanus* tagged at the two sites farthest from each other in the current study (INNO and OFSO) are found to exhibit relatively high fidelity and no movement between both sites (Garcia, 2013). Finding mature individuals at inshore and offshore sites counters a previously held belief that *L.*

campechanus move to deeper offshore sites as they mature (Gallaway et al., op. cit.). Thus, the lack of mobility (Garcia, op. cit.) coupled with finding mature females and males at inshore and offshore sites suggests that ARs in both regions of the northwestern GOM provide adequate habitat for sexual maturation and spawning activity.

A genetic relationship among populations of *L. campechanus* throughout the GOM (Gold and Saillant, 2007) suggests that reproductive cues and periodicity should be similar across populations even at great distances. Previous studies of reproduction for *L. campechanus* indicate similar spawning seasons to the current study ± 1 mo in the GOM (Alexander, 2015; Brulé et al., 2010; Collins et al., 1996; Downey et al., 2018; Kulaw et al., 2017), and the Atlantic Ocean (White and Palmer, 2004). A latitudinal shift in population distribution and associated differences in environmental conditions may be responsible for slightly offset spawning seasons (Brulé et al., op. cit.). In the northwestern GOM, peak spawning in June was corroborated by Downey et al., (op. cit.), even though one study observed a peak in April —attributing it to differences in fish condition (Alexander, op. cit.). Without additional sampling, the current study cannot confidently identify the breadth of the peak spawning period in the northwestern GOM region (Brulé et al., op. cit.) since July and August were not sampled. However, the current study can confidently attest to the induction of peak spawning period in June and the spawning season from April to September.

The current study's combined estimates of maturity benchmarks for TL and age are not similar to previous measures of maturity for *L. campechanus* in the GOM. The TL at which 50% of females exhibit reproductive maturity (TL_{50} = 458 mm) in the current study is larger than other studies (Brulé et al., 2010; Camber, 1955; Cowan et al., 2012; Jackson et al., 2007; Kulaw, 2012; Wilson et al., 1994; Woods et al., 2003; Table 2), which may be due to habitat type because some sampling occurred from large ARs and natural banks (Cowan et al., op. cit.). The age at which 50% of females exhibit reproductive maturity (Age_{50} = 3 yrs) is similar to ARs sampled in Cowan et al. (op. cit.), older than samples in Woods et al. (op. cit.), and younger than natural structures studied in Cowan et al. (op. cit.). On the contrary, Downey et al. (2018) did not find reproductive differences between natural and ARs in the northwestern GOM. Because manmade structures deployed in the region generally vastly outnumber natural habitats of *L. campechanus* (Froehlich and Kline, 2015; Gallaway et al., 2009), differences observed in our current study compared to other areas may be a response to the size of the habitat instead of artificial vs. natural habitat (Downey et al., op. cit.). Although the current study cannot speculate on *L. campechanus* maturation at local natural sites, reproductive biology may be similar across different habitats in the region (Downey et al., op. cit.).

If instead a delayed maturity in *L. campechanus* is a consequence of life on ARs, then management concerns exist. The current study only encountered 9.7% females and 6.1% males that were of large sizes (TL ≥ 600 mm). Large females are of particular interest, because larger females (by proxy older females) contribute a larger proportion of reproductive output (Barneche et al., 2018; Hixon et al., 2014). Older females can partake in longer spawning periods than newly mature females, and their batch fecundity increases as well (Lowerre-Barbieri et al., 2015). Finding fewer large females is not only an outcome of the current study, but one of several other studies in other regions (Kulaw et al., 2017; Lowerre-Barbieri et al., op. cit.; Saari et al., 2014). A lack of larger and older females at habitats suitable for reproductive activity suggests that females are likely being removed before optimal reproductive output.

Maturation characteristics of *L. campechanus* observed in the current study suggests that individuals may grow to legal catch size in both Texas state (381 mm TL) and federal waters (406 mm TL) before reaching maturity (458 mm TL and age 3 yrs). *Lutjanus campechanus* at these sites can reach Texas state and federal legal catch size by age 2 yrs (Alexander, 2015; Froehlich et al., 2018). Up to 84% of females collected are of legal retention size, but many are not reaching maturity levels before capture. Inshore sites (Texas jurisdiction) have similarly-sized and aged *L campechanus* compared to offshore (federal) sites (Froehlich et al., op. cit.), but there are far less mature individuals at inshore sites (only 12% mature females). Either a depth bias exists with inshore sites being at 5 to 10-m shallower than offshore sites, or, more likely, fishing pressure is explaining observed differences given recreational fishing is a year-round activity allowed at inshore sites compared to only a few months in federal waters. Fishermen are always observed targeting *L. campechanus* during sampling events at inshore sites (pers. obs.), especially at INSO. Accordingly, such high presence of fishermen at INSO, and the fact that INSO is closest to the busiest coastal port in the area, may explain why mature females were never observed at INSO compared to the other inshore site, INNO. Individuals may be harvested before reaching maturity, resulting in less proportionally mature populations inshore. There may be structural factors that influence reproductive biology, such as habitat complexity, vertical relief, and underlying substrate (Alexander, op. cit.; Arney et al., 2017; Downey et al., 2018; Froehlich and Kline, 2015), and improving ARs accordingly may help offset some consequences of fishing pressure. However, management of inshore reefs (state jurisdiction) should strongly consider truncating the region's fishing effort because most fish are immature at capture. There may also be a benefit towards both state and federal management working in tandem to provide a combined effort and relieve excessive fishing pressure on immature fish.

Lutjanus campechanus are experiencing age truncation in several studies, including the current study, Alexander (2015) and Saari et al. (2014). Compared to 10 yrs ago, significantly lower reproductive capacity of *L. campechanus* has been observed among common age classes (Kulaw et al., 2017). Brown-Peterson et al. (2018) found an overall decrease in *L. campechanus* egg output from 1997-2017, particularly in the northwestern GOM. Identifying essential spawning habitat and environmental factors that support reproductively active populations are crucial for the future management of *L. campechanus*. The current study, and Alexander (op. cit.) suggests that inshore and offshore sites provide essential habitat for reproduction, and fish are actively spawning at ARs. Although spawning is observed at these sites, *L. campechanus* are small, young, and barely mature before harvest within legal catch limits, especially at inshore sites. Additional management restrictions, like commercial and recreational fishing closures during spawning periods, should be implemented to allow populations to become sustainable and allow fish to mature and spawn often prior to removal. Similar restrictions among regions may need to be implemented and with higher frequencies to reduce excessing fishing on young, and barely mature individuals, because our study finds that inshore and offshore sites serve similar purposes for *L. campechanus* reproduction even though management practices differ. Failing to implement additional restrictions reduces benefits of ARs and further hampers the attempts of reaching a sustainable *L. campechanus* fishery and removing a long-standing overfished status (Brown et al., 1989; Gallaway et al., 2017).

5. Conflict of Interest

We declare none of us have a conflict of interest.

Acknowledgements

We thank the University of Texas Rio Grande Valley boat crew and dive team for assistance collecting samples, particularly R. Alexander in the earlier sampling periods. We thank Seth

Patterson, Gwyn Carmean, Al Alder, and Andres Garcia for photography. The project could not have been completed without the funding [contract numbers 439189, 475342 to CCB and his collaborators], guidance, or support of the Texas Parks and Wildlife Department (TPWD) Artificial Reef Program (ARP). The TPWD ARP granted Scientific Permit SPR-0314–050 to collect specimens in Texas waters. In addition, the National Oceanic and Atmospheric Administration National Marine Fisheries Service provided an essential letter of acknowledgment, which allowed for collection outside the boundaries of fishing regulations.

References

Alexander, R.J., 2015. Comparing reproductive capacity of nearshore and offshore Red Snapper, *Lutjanus campechanus*, on artificial reefs in the western Gulf of Mexico. MS thesis, University of Texas Rio Grande Valley, Brownsville. 84 p.

Allman, R.J., Lombardi-Carlson, L.A., Fitzhugh, G.R., Fable, W.A., 2002. Age structure of Red Snapper (*Lutjanus campechanus*) in the Gulf of Mexico by fishing mode and region. Presented at the Proceedings of the Gulf and Caribbean Fisheries Institute, pp. 482–495.

Arney, R.N., Froehlich, C.Y.M., Kline, R.J., 2017. Recruitment patterns of juvenile fish at an artificial reef area in the Gulf of Mexico. Marine and Coastal Fisheries 9, 79–92. https://doi.org/10.1080/19425120.2016.1265031

Bardon-Albaret, A., Saillant, E., 2017. Egg quality traits and predictors of embryo and fry viability in Red Snapper *Lutjanus campechanus*. Aquaculture Reports 7, 48–56. https://doi.org/10.1016/j.aqrep.2017.05.004

Barneche, D.R., Robertson, D.R., White, C.R., Marshall, D.J., 2018. Fish reproductive-energy output increases disproportionately with body size. Science 360, 642–645. https://doi.org/10.1126/science.aao6868

Bollinger, M.A., Kline, R.J., 2017. Validating sidescan sonar as a fish survey tool over artificial reefs. Journal of Coastal Research 33, 1397–1407. https://doi.org/10.2112/JCOASTRES-D-16-00174.1

Brewton, R.A., Downey, C.H., Streich, M.K., Wetz, J.J., Ajemian, M.J., Stunz, G.W., 2020. Trophic ecology of Red Snapper *Lutjanus campechanus* on natural and artificial reefs: interactions between annual variability, habitat, and ontogeny. Marine Ecology Progress Series 635, 105–122. https://doi.org/10.3354/meps13210

Brock, R.E., 1994. Beyond fisheries enhancement: artificial reefs and ecotourism. Bulletin of Marine Science 55, 1181–1188.

Brown, A.Jr., Bohnsack, J.A., Harper, D., 1989. Automated Landings Assessment for Responsive Management (ALARM): Gulf of Mexico commercial reef fish landings (No. CRD-89/90-02). NOAA, NMFS, Southeast Fisheries Center, Miami Laboratory, Miami, FL.

Brown-Peterson, N.J., Peterson, C.R., Fitzhugh, G.R., 2018. Multidecadal meta-analysis of reproductive parameters of female Red Snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico. FB 117, 37–49. https://doi.org/10.7755/FB.117.1.5

Brown-Peterson, N.J., Wyanski, D.M., Saborido-Rey, F., Macewicz, B.J., Lowerre-Barbieri, S.K., 2011. A standardized terminology for describing reproductive development in fishes. Marine and Coastal Fisheries 3, 52–70. https://doi.org/10.1080/19425120.2011.555724

Brulé, T., Colás-Marrufo, T., Pérez-Díaz, E., Sámano-Zapata, J.C., 2010. Red Snapper reproductive biology in the southern Gulf of Mexico. Transactions of the American Fisheries Society 139, 957–968. https://doi.org/10.1577/T09-125.1

Camber, C.I., 1955. A survey of the Red Snapper fishery of the Gulf of Mexico, with special reference to the Campeche Banks. Florida State Board of Conservation Marine Laboratory Technical Series 12, 1–64.

Collins, L.A., Johnson, A.G., Keim, C.P., 1996. Spawning and annual fecundity of the Red Snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico, in: Arreguin-Sanchez, F., Munro, J.L., Balgos, M.C., Pauly, D. (Eds.), Biology, Fisheries and Culture of Tropical Groupers and Snappers. International Center for Living Aquatic Resources Management, Manila, Philippines, pp. 174–188.

Cowan, J.H.Jr., Boswell, K.M., Simonsen, K.A., Saari, C.R., Kulaw, D.H., 2012. Working paper for Red Snapper data workshop (SEDAR 31) (No. SEDAR31-DW03). SEDAR, North Charleston, South Carolina.

Cowan, J.H.Jr., Grimes, C.B., Patterson, W.F.I., Walters, C.J., Jones, A.C., Lindberg, W.J., Sheehy, D.J., Pine, W.E.I., Powers, J.E., Campbell, M.D., Lindeman, K.C., Diamond, S.L., Hilborn, R., Gibson, H.T., Rose, K.A., 2011. Red Snapper management in the Gulf of Mexico: science- or faith-based? Reviews in Fish Biology and Fisheries 21, 187–204. https://doi.org/10.1007/s11160-010-9165-7

Dapson, R.W., 2007. Glyoxal fixation: how it works and why it only occasionally needs antigen retrieval. Biotech Histochem 82, 161–166. https://doi.org/10.1080/10520290701488113

Downey, C.H., Streich, M.K., Brewton, R.A., Ajemian, M.J., Wetz, J.J., Stunz, G.W., 2018. Habitat-specific reproductive potential of Red Snapper: a comparison of artificial and natural reefs in the western Gulf of Mexico. Transactions of the American Fisheries Society 147, 1030–1041. https://doi.org/10.1002/tafs.10104

Froehlich, C.Y.M., Kline, R.J., 2015. Using fish population metrics to compare the effects of artificial reef density. PLoS ONE 10, e0139444. https://doi.org/10.1371/journal.pone.0139444

Froehlich, C.Y.M., Lee, A.M., Oquita, R., Cintra-Buenrostro, C.E., Shively, J.D., Shipley, J.B., 2018. A comparison of population dynamics from Red Snapper associated with inshore and offshore artificial reefs in the northwestern Gulf of Mexico, in: Bortone, S.A. (Ed.), Marine Artificial Reef Research and Development: Integrating Fisheries Management Objectives. American Fisheries Society Symposium 86, Florida, USA, pp. 81–95.

Gallaway, B.J., Cole, J.G., Meyer, R., Roscigno, P., 1999. Delineation of essential habitat for juvenile Red Snapper in the northwestern Gulf of Mexico. Transactions of the American Fisheries Society 128, 713–726. https://doi.org/10.1577/1548-8659(1999)128<0713:DOEHFJ>2.0.CO;2

Gallaway, B.J., Gazey, W.J., Cole, J.G., 2017. An updated description of the benefits and consequences of Red Snapper shrimp trawl bycatch management actions in the Gulf of Mexico. North American Journal of Fisheries Management 37, 414–419. https://doi.org/10.1080/02755947.2016.1271842

Gallaway, B.J., Szedlmayer, S.T., Gazey, W.J., 2009. A life history review for Red Snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Reviews in Fisheries Science 17, 48–67. https://doi.org/10.1080/10641260802160717

Garcia, A., 2013. A comparison of site fidelity and habitat use of Red Snapper (*Lutjanus campechanus*) to evaluate the performance of two artificial reefs in South Texas utilizing acoustic telemetry. MS thesis, University of Texas at Brownsville, Brownsville. 55 p.

Gazey, W.J., Gallaway, B.J., Cole, J.G., Fournier, D.A., 2008. Age composition, growth, and density-dependent mortality in juvenile Red Snapper estimated from observer data from the Gulf of Mexico Penaeid shrimp fishery. North American Journal of Fisheries Management 28, 1828–1842. https://doi.org/10.1577/M07-216.1

Gillig, D., Griffin, W.L., Ozuna, T.Jr., 2001. A bioeconomic assessment of Gulf of Mexico Red Snapper management policies. Transactions of the American Fisheries Society 130, 117–129. https://doi.org/10.1577/1548-8659(2001)130%3C0117:ABAOGO%3E2.0.CO;2

Glenn, H.D., Cowan, J.H.Jr., Powers, J.E., 2017. A comparison of Red Snapper reproductive potential in the northwestern Gulf of Mexico: natural versus artificial habitats. Marine and Coastal Fisheries 9, 139–148. https://doi.org/10.1080/19425120.2017.1282896

GMFMC, 2014. Final framework action to the fishery management plan for the reef fish resources of the Gulf of Mexico including environmental assessment, regulatory impact review, and regulatory flexibility act analysis: recreational accountability measures for Red Snapper (No. NA10NMF4410011). Gulf of Mexico Fishery Management Council.

Gold, J.R., Saillant, E., 2007. Population structure of Red Snapper in the northern Gulf of Mexico, in: Patterson, W.F. III, Cowan, J.H. Jr., Fitzhugh, G.R., Nieland, D.L. (Eds.), Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico. American Fisheries Society Symposium 60, Bethesda, Maryland, p. 15.

Grimes, C.B., 1987. Reproductive biology of the Lutjanidae: a review, in: Polovina, J.J., Ralston, S. (Eds.) Tropical Snappers and Groupers: Biology and Fisheries Management. Westview Press, Boulder, CO, pp. 239–294.

GSMFC, 2016. SEAMAP vertical line operations manual. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

Hixon, M.A., Johnson, D.W., Sogard, S.M., 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science 71, 2171–2185. https://doi.org/10.1093/icesjms/fst200

Hood, P.B., Strelcheck, A.J., Steele, P., 2007. A history of Red Snapper management in the Gulf of Mexico, in: Patterson, W.F. III, Cowan, J.H. Jr., Fitzhugh, G.R., Nieland, D.A., (Eds.) Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico. American Fisheries Society Symposium 60, Bethesda, Maryland, pp. 267–284.

IBM, 2013. IBM SPSS Statistics for Macintosh. IBM, Corp., Armonk, New York.

Jackson, M.C., Cowan, J.H.Jr., Nieland, D.L., 2007. Demographic differences in northern Gulf of Mexico Red Snapper reproductive maturation: implications for the unit stock hypothesis. in: Patterson, W.F. III, Cowan, J.H. Jr., Fitzhugh, G.R., Nieland, D.A., (Eds.), Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico. American Fisheries Society Symposium 60. Bethesda, Maryland, pp. 217–228.

Karnauskas, M., Walter, J.F.I., Campbell, M.D., Pollack, A.G., Drymon, J.M., Powers, S., 2017. Red Snapper distribution on natural habitats and artificial structures in the northern Gulf of Mexico. Marine and Coastal Fisheries 9, 50–67. https://doi.org/10.1080/19425120.2016.1255684

Kjesbu, O.S., 2009. Applied fish reproductive biology: contribution of individual reproductive potential to recruitment and fisheries management, in: Jakobsen, T., Fogarty, M.J., Megrey, B.A., Moksness, E. (Eds.), Fish Reproductive Biology: Implications for

Assessment and Management. Blackwell Publishing Ltd., Oxford, England, pp. 293–332. https://doi.org/10.1002/9781444312133.ch8

Kulaw, D.H., 2012. Habitat- and region-specific reproductive biology of female Red Snapper (*Lutjanus campechanus*) in the Gulf of Mexico. MS thesis, Louisiana State University and Agricultural and Mechanical College, Baton Rouge. 165 p.

Kulaw, D.H., Cowan, J.H.Jr., Jackson, M.W., 2017. Temporal and spatial comparisons of the reproductive biology of northern Gulf of Mexico (USA) Red Snapper (*Lutjanus campechanus*) collected a decade apart. PLoS ONE 12, e0172360. https://doi.org/10.1371/journal.pone.0172360

Lowerre-Barbieri, S., Crabtree, L., Switzer, T., Walters Burnsed, S., Guenther, C., 2015. Assessing reproductive resilience: an example with South Atlantic Red Snapper *Lutjanus campechanus*. Marine Ecology Progress Series 526, 125–141. https://doi.org/10.3354/meps11212

Mueller, M., 2012. Artificial structure and hard-bottom spatial coverage in the Gulf of Mexico. SEDAR31-DW-29. SEDAR, North Charleston, South Carolina.

Patterson, W.F.I., Watterson, J.C., Shipp, R.L., Cowan, J.H.Jr., 2001. Movement of tagged Red Snapper in the northern Gulf of Mexico. Transactions of the American Fisheries Society 130, 533–545. https://doi.org/10.1577/1548-8659(2001)130<0533:MOTRSI>2.0.CO;2

Porch, C.E., Fitzhugh, G.R., Lang, E.T., Lyon, H.M., Linton, B.C., 2015. Estimating the dependence of spawning frequency on size and age in Gulf of Mexico Red Snapper. Marine and Coastal Fisheries 7, 233–245. https://doi.org/10.1080/19425120.2015.1040567

Render, J.H., 1995. The life history (age, growth and reproduction) of Red Snapper (*Lutjanus campechanus*) and its affinity for oil and gas platforms. PhD dissertation, Louisiana State University and Agricultural and Mechanical College, Baton Rouge. 76 p.

Saari, C.R., Cowan, J.H.Jr., Boswell, K.M., 2014. Regional differences in the age and growth of Red Snapper (*Lutjanus campechanus*) in the US Gulf of Mexico. Fishery Bulletin 112, 261–273. https://doi.org/10.7755/FB.112.4.3

SEDAR, 2018. SEDAR 52 - South Atlantic Red Snapper Assessment Report - Gulf of Mexico Red Snapper. SEDAR, North Charleston, South Carolina.

Sokal, R.R., Rohlf, F.J., 2011. Biometry, 4th ed. W.H. Freeman, London.

Streich, M.K., Ajemian, M.J., Wetz, J.J., Williams, J.A., Shipley, J.B., Stunz, G.W., 2017. A comparison of size structure, age, and growth of Red Snapper from artificial and natural habitats in the western Gulf of Mexico. Transactions of the American Fisheries Society 146, 762–777. https://doi.org/10.1080/00028487.2017.1308884

Syc, T.S., Szedlmayer, S.T., 2012. A comparison of size and age of Red Snapper (*Lutjanus campechanus*) with the age of artificial reefs in the northern Gulf of Mexico. Fishery Bulletin 110, 458–469.

Szedlmayer, S.T., Conti, J., 1999. Nursery habitats, growth rates, and seasonality of age-0 Red Snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. Fishery Bulletin 97, 626–635.

Szedlmayer, S.T., Howe, J.C., 1997. Substrate preference in age-0 Red Snapper, *Lutjanus campechanus*. Environmental Biology of Fishes 50, 203–207. https://doi.org/10.1023/A:1007371514250

VanderKooy, S., Guindon-Tisdel, K., 2003. A practical handbook for determining the ages of Gulf of Mexico fishes (Number 111). Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

Wells, R.J.D., Cowan, J.H.Jr., Patterson, W.F.I., Walters, C.J., 2008. Effect of trawling on juvenile Red Snapper (*Lutjanus campechanus*) habitat selection and life history parameters. Canadian Journal of Fisheries and Aquatic Sciences 65, 2399–2411. https://doi.org/10.1139/F08-145

White, D.B., Palmer, S.M., 2004. Age, growth, and reproduction of the Red Snapper, *Lutjanus campechanus*, from the Atlantic waters of the southeastern U.S. Bulletin of Marine Science 75, 335–360.

Wilson, C.A., Nieland, D.L., 2001. Age and growth of Red Snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. Fishery Bulletin 99, 653–664.

Wilson, C.A., Render, J.H., Nieland, D.L., 1994. Life history gaps in Red Snapper (*Lutjanus campechanus*), Swordfish (*Xiphias gladius*), and Red Drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico: age distribution, growth, and some reproductive biology (No. NA17FF0383-02). Final report to U.S. Department of Commerce, Marine Fisheries Initiative (MARFIN) Program, NMFS, St. Petersburg, Florida.

Woods, M.K., Fischer, A.J., Cowan, J.H.Jr., Nieland, D.L., 2003. Size and age at maturity of female Red Snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Presented at the Proceedings of the 54th Gulf and Caribbean Fisheries Institute, Turks and Caicos, pp. 526–537.

Workman, I., Shah, A., Foster, D., Hataway, B., 2002. Habitat preferences and site fidelity of juvenile Red Snapper (*Lutjanus campechanus*). ICES Journal of Marine Science 59, S43–S50. https://doi.org/10.1006/jmsc.2002.1211

Table 1. Statistical output of all analyses for the reproductive capacity of red snapper (*Lutjanus campechanus*) from four artificial reefs in the northwestern Gulf of Mexico. Note: NANOVA = nested analysis of variance; parentheses identify factors that the predictor variables are nested within; morphometric values at which 50% of females were mature (maturity proportion) = X_{50}; GSI = gonadosomatic index; N/A = not available.

Response Variable	Predictor Variable (s)	Test Used	Factor Type	Degrees of Freedom	Test-value	p-value
Sex ratio	N/A	χ^2 statistic	N/A	1.388	2.261	> 0.05
Condition (K)	Location	NANOVA	Fixed	1.390	10.55	> 0.05
	Site(Location)	F-value	Fixed	3.390	1.60	> 0.05
	Sex(Site(Location))	statistic	Fixed	1.390	2.45	> 0.05
Histological Characteristics	Location	NANOVA	Fixed	1,390	4.69	> 0.05
	Site(Location)	F-value	Fixed	3.390	0.32	> 0.05
	Sex(Site(Location))	statistic	Fixed	1.390	6.17	< 0.01
	Quarter		Fixed	3.390	6.213	< 0.01
	Quarters*Location		Fixed	3.390	9.665	< 0.01
	Quarters*Site(Location)		Fixed	6,385	5.85	< 0.01
	Quarters*Sex(Site(Location))		Fixed	3.390	3.10	< 0.05
GSI	Location	NANOVA	Fixed	1.389	0.42	> 0.05
	Site(Location)	F-value	Fixed	3.389	0.356	> 0.05
	Quarter	statistic	Fixed	3.384	17.111	< 0.01
	Quarters*Location		Fixed	3.389	3.525	< 0.05
	Quarters*Site(Location)		Fixed	6.384	1.60	> 0.05
Total Length (X_{50})	Location	NANOVA	Fixed	1.171	5.98	> 0.05
	Site	F-value	Fixed	3.171	5.25	< 0.05
	Quarter	statistic	Fixed	8.171	1.27	> 0.05
Logarithmic Transformation of Total Weight (X_{50})	Location	NANOVA	Fixed	1.171	5.43	> 0.05
	Site	F-value	Fixed	3.171	5.41	< 0.05
	Quarter	statistic	Fixed	8.171	1.57	> 0.05
Age (X_{50})	Location	NANOVA	Fixed	1.171	3.83	> 0.05
	Site	F-value	Fixed	3.171	14.25	< 0.01
	Quarter	statistic	Fixed	8.171	0.81	> 0.05

Table 2. The total length (mm) at 50% (TL_{50}) maturity and biological age (yrs.) at 50% (Age_{50}) maturity of *Lutjanus campechanus* from studies throughout the Gulf of Mexico. Asterisks denote fork length (FL, mm), and data were converted to TL (mm) using a previously developed equation: TL = 2.651 + 1.061 × FL (Allman et al., 2002). Benchmarks obtained from 375-424 mm = [1]; N/A = not available.

Study	TL_{50}	Age_{50}	Region	Reef Type
Current Study	458	3	South Texas	Artificial - platforms, ships, pipes
Cowan et al. (2012)	450	5	Louisiana	Natural banks
	450	4	Louisiana	Artificial - standing platforms
	400	3	Louisiana	Artificial - toppled platforms
Kulaw (2012)[1]	400	3	Central Florida	N/A = fisheries landings
	400	3	Northwest Florida	N/A = fisheries landings
	400	3	Alabama	N/A = fisheries landings
	400	3	Louisiana	N/A = fisheries landings
	400	3	North Texas	N/A = fisheries landings
	400	3	South Texas	N/A = fisheries landings
Brulé et al. (2010)	314		Campeche Banks	N/A = fisheries landings
Jackson et al. (2007)*	371		Louisiana	N/A
Woods et al. (2003)[1]*	294	2	Alabama	N/A = fisheries landings
	321	2	Louisiana	N/A = fisheries landings
Wilson et al. (1994)	313		Louisiana	N/A
Camber (1955)	345		Campeche Banks	N/A = fisheries landings

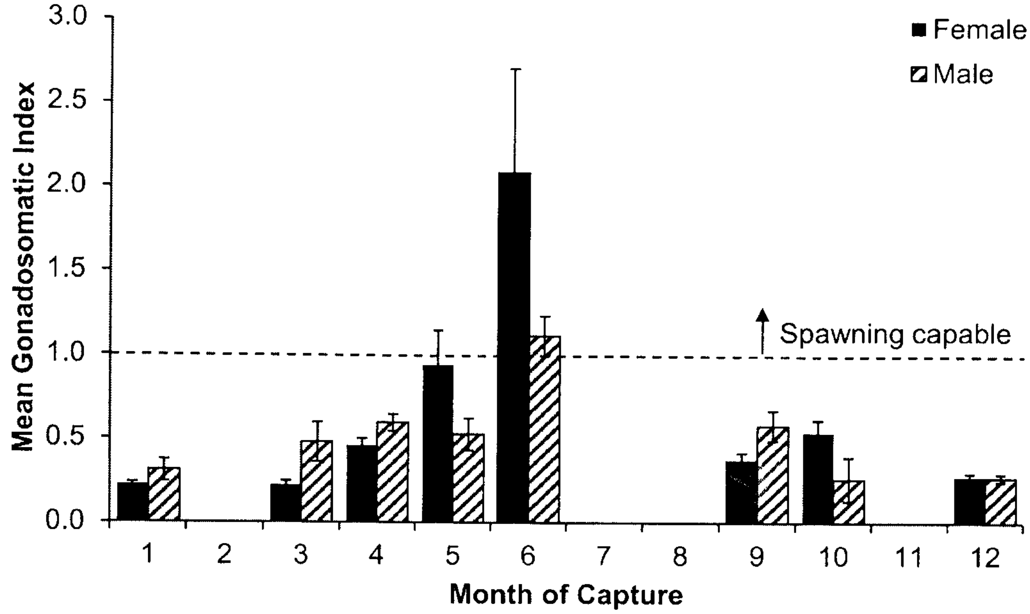


Figure 1. Mean gonadosomatic index (GSI) per month of female and male *Lutjanus campechanus* collected at artificial reefs in the northwestern Gulf of Mexico from December 2014 to December 2016. Individuals are considered spawning capable at a GSI > 1 (dashed line and arrow). Error bars are standard error. Note: no samples were collected in February, July, August, or November due to weather constraints. Females, n = 184, and males, n = 205.

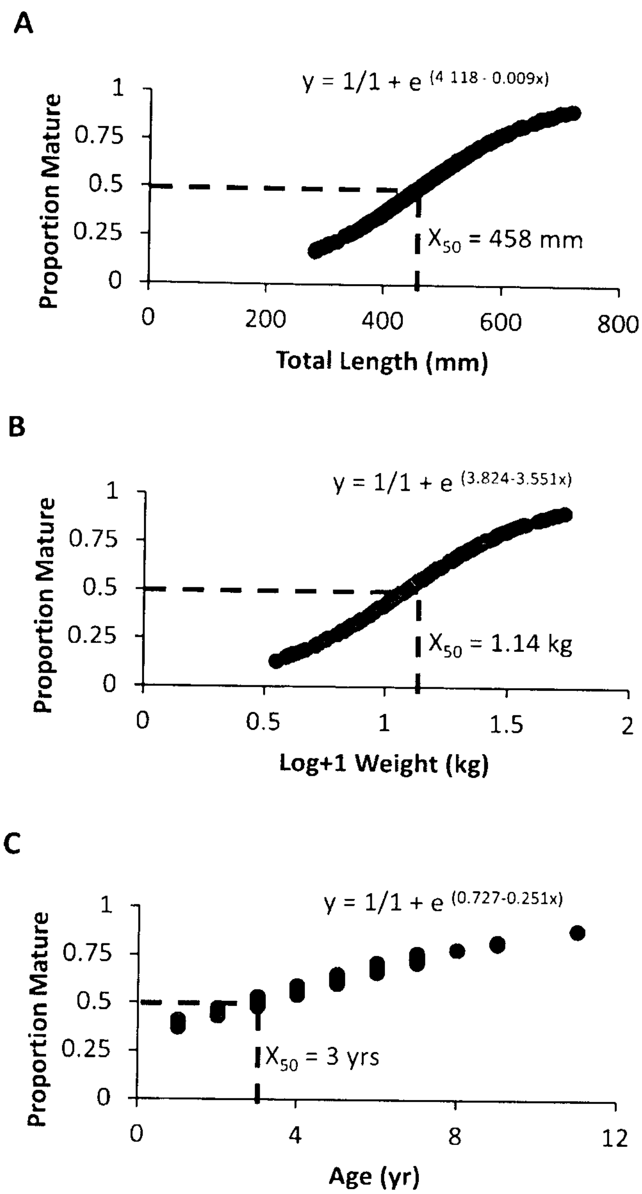


Figure 2. Estimated proportion maturity from binary logistic regressions (equations embedded) as a function of A) total length (mm), B) Log+1 weight (kg), and C) age (yrs) of female *Lutjanus campechanus* collected from artificial reefs in the northwestern Gulf of Mexico. Dashed lines represent values at which 50% of females (X_{50}) were identified as mature; n = 184.

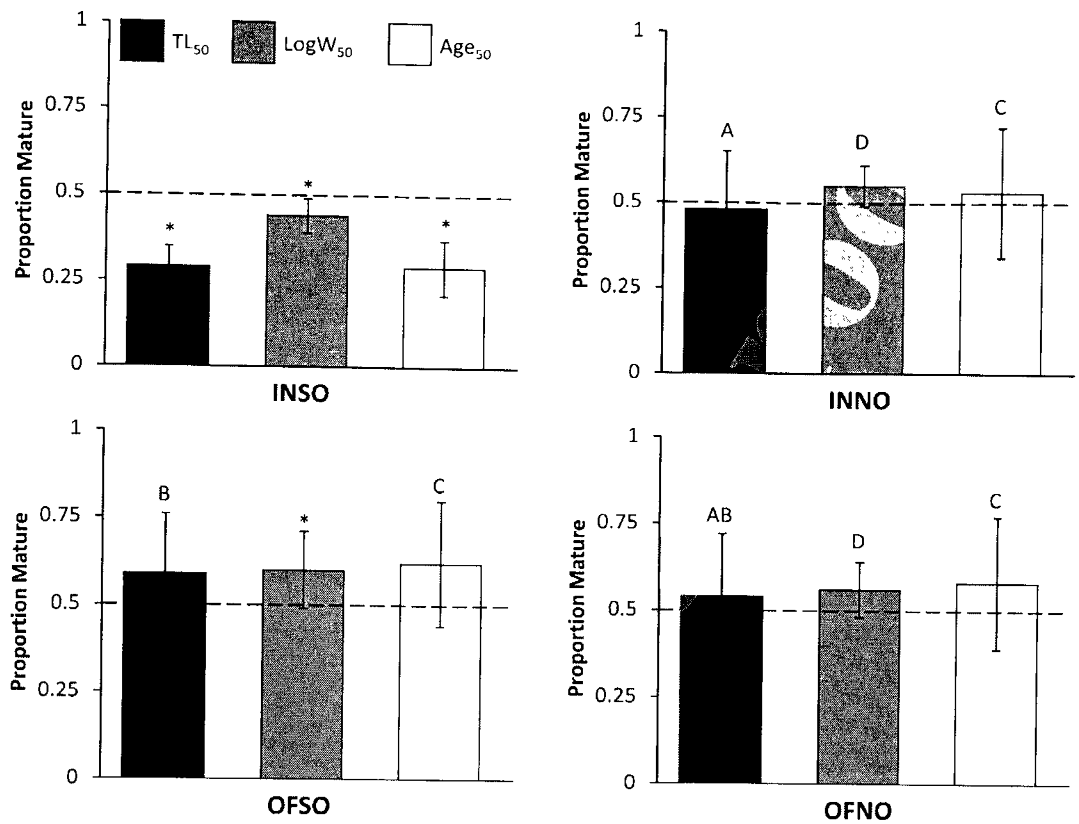


Figure 3. Mean proportion mature ± standard deviation (SD, bars) by site and location of female *Lutjanus campechanus* as determined by total length (mm, TL_{50}), log_{10}+1 weight (kg, $LogW_{50}$), and age (yrs, Age_{50}) among four artificial reef sites in the northwestern Gulf of Mexico. Dashed lines represent values at which 50% of females (X_{50}) were identified as mature. Asterisks above bars indicate difference from all other means among sites, while different letters highlight means that are significantly different among sites. Site abbreviations and sample sizes are: INSO = inshore south, n = 13; INNO = inshore north, n = 4; OFSO = offshore south, n = 67; and OFNO = offshore north, n = 61.

Author Statement

Catheline Y.M. Froehlich[a,b]
Adam M. Lee[c]
Ramiro Oquita[c]
Carlos E. Cintra-Buenrostro[c]
J. Dale Shively[d]

[a]School of Earth, Environmental, and Marine Sciences (SEEMS)
University of Texas Rio Grande Valley (UTRGV)
One West University Blvd.; Brownsville; Texas 78520 USA

[b]School of Earth, Atmospheric, and Life Sciences
University of Wollongong
Northfields Ave.; Wollongong, NSW; 2500 Australia

[c]Ocean, Coastal Environmental and Ecological Assessment Lab.
SEEMS
UTRGV
One West University Blvd.; Brownsville; Texas 78520 USA

[d]Texas Parks and Wildlife Department
Artificial Reef Program
4200 Smith School Rd.; Austin; Texas 78744 USA

May 25, 2021

Dear Kenneth Mei Yee Leung
Editor in Chief
Regional Studies in Marine Science

Thank you for the manuscript status as acceptable with minor revisions. Our manuscript has been revised accordingly for publication in *Regional Studies in Marine Science* as a research article. We have addressed and acknowledge the provided feedback by the reviewer that has improved our manuscript. The manuscript presents a comparison of the reproductive activity of *L. campechanus* among state (inshore) and federal (offshore) jurisdictions, and assess their spawning potential on artificial reefs (ARs), individuals were collected in the northwestern Gulf of Mexico from four ARs on a quarterly basis for 2 yrs. Noteworthy, the management of the fishery differs on a regional basis with state and federal jurisdictions, yet reproductive differences among regions have recently been investigated; which provides a novel approach particularly in the area of study - south Texas - that tends to be neglected in research endeavors compared to other regions of the United States of America. Reviewer 1 concurs that the manuscript "is interesting and gives some useful information regarding maturity of *L. campechanus* in AR's". We declare none of us have a conflict of interest, and all listed authors have read and approved the suggested modifications by the reviewers as addressed in our response to reviewers.

On behalf of Catheline Y.M. Froehlich, Adam M. Lee, Ramiro Oquita, and J. Dale Shively

thanks in advance for your consideration,

Carlos E. Cintra Buenrostro, Ph.D.

Professor

University of Texas Rio Grande Valley

School of Earth, Environmental, and Marine Sciences

Ocean, Coastal Environmental and Ecological Assessment Lab.

Conflict of Interest

We declare none of us have a conflict of interest.