Importance of Depth and Artificial Structure as Predictors of Female Red Snapper Reproductive Parameters

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ARTICLE

Importance of Depth and Artificial Structure as Predictors of Female Red Snapper Reproductive Parameters

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Abstract

The Red Snapper *Lutjanus campechanus* is a structure-associated species occurring across a wide depth range in the northern Gulf of Mexico. We used the random forest machine learning algorithm to understand which habitat and individual fish characteristics could predict reproductive parameters of female Red Snapper. We evaluated fish captured from 2016 to 2018 on three artificial structure types with various structure heights at depths of 100 m or less. Overall, we found that depth and month were important predictors for most reproductive parameters, but the type of structure (artificial reefs, oil platforms, and rigs-to-reefs structures) was not important. Maturity was correctly classified in 88.9% of the cases when using the random forest ensemble model, with important predictors including FL, depth, structure height, and month of collection. Spawning seasonality (measured as gonadosomatic index [GSI]) was correctly classified in 59.5% of the cases when using histology reproductive phase, FL, month, and depth variables. Reproductively active or inactive females were correctly classified in 89.3% of the cases using GSI, month, FL, and depth, while females in the developing versus spawning capable phases were correctly classified in 82.2% of the cases using GSI, FL, month, and depth. Histological indicators that show potential spawning within a 36-h period were correctly classified 61.5% of the time, with the best predictors being depth, FL, GSI, and month. Stepwise regression indicated that month was the only factor that significantly predicted contrasts in relative batch fecundity, with significantly greater values in August compared to all other months. Our findings suggest that female Red Snapper reproductive effort is not consistently or well predicted by artificial structure type or height but that a combination of fish FL, month, and depth can predict reproductive characteristics of female Red Snapper.

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The Red Snapper *Lutjanus campechanus* is one of the most economically important species in the northern Gulf of Mexico (GOM), supporting large commercial and recreational fisheries. Due to overfishing, Red Snapper stocks began declining in the 1960s in the western GOM and were likely overfished in the eastern GOM by the 1950s, reaching an unsustainable level by 1990 (SEDAR 2018). Despite the implementation of a variety of regulations beginning in the 1990s (size limits, bag limits, seasonal fishing closures, gear restrictions, and establishment of an individual fishing quota program), the GOM Red Snapper stock was still considered overfished and to be undergoing overfishing in 2005 (SEDAR 2005). New, stricter regulations were enacted following Southeast Data, Assessment, and Review 7 (SEDAR 2005), resulting in the 2018 determination that the Red Snapper stock is recovering and, on a GOM-wide basis, is not overfished and not undergoing overfishing (SEDAR 2018). Despite this classification, stock recovery has not been uniform across the GOM; Red Snapper stocks in the eastern GOM are projected to decline due to lower recruitment and greater discard mortality relative to those occurring in the western GOM (SEDAR 2018).

Red Snapper are structure oriented, particularly during the first 8 years of their life (Galloway et al. 2009). The density of young fish is greater on artificial structures (i.e., artificial reefs [ARs] and/or oil and gas platforms) than on natural reefs (Karnauskas et al. 2017). Overall, Red Snapper are most abundant in the GOM in areas with the most oil and gas platforms and ARs (Gallaway et al. 2009), although historical catches indicate that Red Snapper were abundant in both the eastern and western GOM prior to the proliferation of artificial structures (Fitzhugh et al. 2020). The addition of AR structure to undifferentiated bottom in Alabama (USA) state waters transformed that region from one of low incidence to one of the highest for GOM Red Snapper (Shipp and Bortone 2009). Off the coasts of Texas and Louisiana, Red Snapper are most abundant on structures in depths ranging from 50 to 90 m, but off the coasts of Alabama and Florida they are more common in AR zones in a variety of depths (Karnauskas et al. 2017). Nearshore Mississippi waters contain 233 ARs, 17 rigs-to-reefs (R2R) structures, and 169 standing oil platforms (BOEM 2018; MDMR 2019) at depths ranging from 6 to 100 m, which potentially provide abundant but previously undocumented habitat for Red Snapper.

The reproductive biology of Red Snapper in the GOM has been well documented in the past 10 years, but only one study (Brown-Peterson et al. 2019) included data from Mississippi waters. Red Snapper have a reproductive season that lasts from April through September in the northern GOM, with peak spawning occurring from June through August (Brown-Peterson et al. 2019). Females are batch spawners with a mean spawning interval (SI; number of days between spawns) ranging from 3.2 to 6.6 d, although some females are capable of daily spawning (Brown-Peterson et al. 2019). Older, larger female Red Snapper spawn more frequently than smaller, younger individuals (Porch et al. 2015), and large females have a greater fecundity than smaller fish, although batch fecundity is variable (Lowerre-Barbieri et al. 2015).

Although ARs have been shown to provide reproductive habitat for Red Snapper in the GOM, previous studies generally have compared reproductive characteristics on ARs versus naturally occurring reefs (Glenn et al. 2017; Downey et al. 2018) or have discussed interannual differences (Kulaw et al. 2017; Brown-Peterson et. al. 2019). A study off Texas that focused on only ARs found no differences in Red Snapper reproductive capacity between nearshore and offshore reefs of similar materials at similar depths (Alexander 2015).

There is also a lack of information regarding Red Snapper reproduction on ARs at varying depths. In the Atlantic Ocean off the southeastern USA, the largest female Red Snapper with the longest spawning seasons and highest fecundities were found at depths greater than 60 m (Lowerre-Barbieri et al. 2015), but most of the locations sampled were natural reef structures. In the GOM, female Red Snapper were more reproductively active on deeper natural reefs compared to shallower ARs (Glenn et al. 2017). If contrasts in life history patterns are detected at varying depths of reef structures, this information may elucidate the role of ARs and natural reefs in the productivity patterns of the GOM Red Snapper stock.

The primary objective of this investigation was to understand the relationship of female Red Snapper reproductive characteristics to the habitat characteristics of depth and artificial structure in Mississippi's coastal waters. We hypothesized that contrasts in five reproductive parameters—maturity, duration of the spawning season, the percentage of reproductively active fish, frequency of spawning, and batch fecundity—would be influenced by habitat and biological characteristics. The results from our analyses of Red Snapper reproduction as it relates to depth and artificial structure from Mississippi waters are likely applicable to the entire GOM region that has many of these same structures.

METHODS

Sampling Sites

A total of 374 randomly allocated stations containing artificial structures were sampled in Mississippi waters from 2016 to 2018 (Figure 1). Red Snapper were collected using a stratified random sample allocation from three depth strata (shallow: <20 m; mid-depth: 20–49 m; deep:

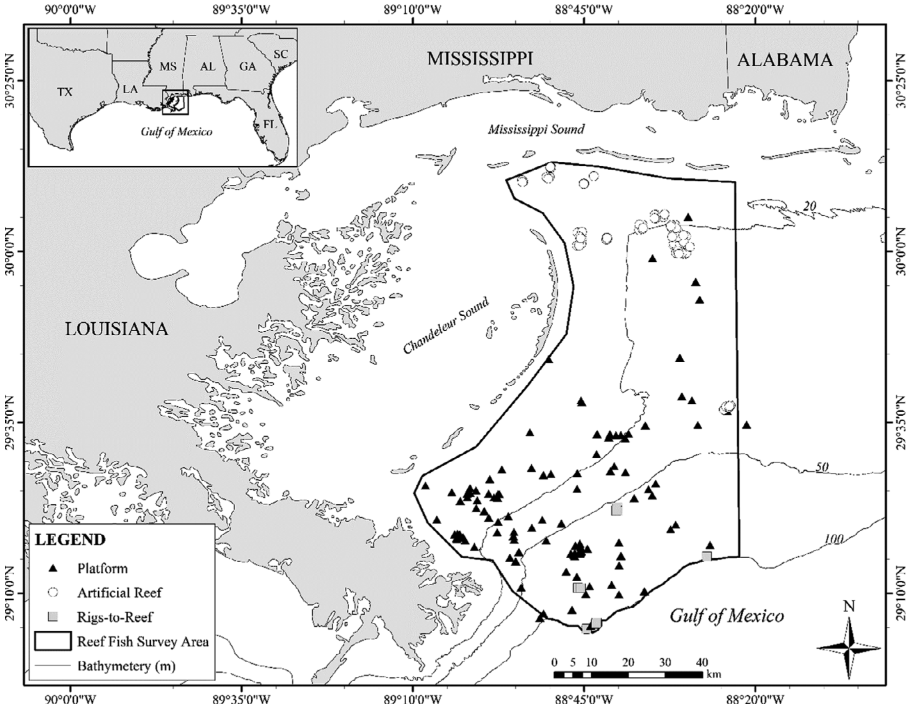

FIGURE 1. Artificial structure stations sampled for female Red Snapper in Mississippi waters of the Gulf of Mexico, 2016–2018. Monthly sampling occurred in three depth strata for a total of 17 stations/month. Some stations were sampled multiple times during the 3 years of the study.

50–100 m) and three artificial structure types. Structure types included ARs (rubble, concrete culverts, concrete pyramids, bay balls, and/or sunken vessels), oil and gas platforms (hereafter, platforms), and R2Rs (decommissioned platforms with the upper structure cut off and then toppled). Platforms occurred in all depth strata, ARs were located in the shallow and mid-depth strata, and R2Rs were only located in the deep stratum. The depth at each station (m) was determined with an onboard down-scan depth sounder (Garmin GPSmap 7610xsv).

The vertical height (m) of ARs at shallow and mid-depths was determined from images taken using side-scan sonar and cross-section views of each structure (MDMR 2016). The height of R2R structures was determined onsite by subtracting the depth at the top of the structure from the total depth of the site using the down-scan depth sounder. The height of platforms was equivalent to the depth of the water at that site as measured using the onboard down-scan depth sounder.

Fish Sampling

Red Snapper were collected each month from April to November 2016, April to October 2017, and March to October 2018 during daylight hours using vertical longlines baited with Atlantic Mackerel *Scomber scombrus*. Sampling gear consisted of three electric bandit reels rigged with an 8-m vertical mainline outfitted with ten 45.7-cm leaders spaced 0.67 m apart and a 4.5-kg weight at the terminal end. Every leader on the line was rigged with one hook size (8/0, 11/0, or 15/0 circle hooks with zero offset). Lines were fished just off the bottom for 5-min sets. During each sampling event, three 5-min sets were made at platform and AR sites at each depth stratum and two 5-min sets were made at R2R sites, resulting in a total of 17 stations/month.

Immediately upon capture, fish were stored on ice until after the completion of daily sampling when measurements (FL; mm) and weight (0.01 kg) were taken. Gonadal tissue was removed, weighed (0.01 g), and macroscopically assessed for reproductive phase (Brown-Peterson et al. 2011). Within 15 h of capture, a mid-section from the right ovary of each female was preserved in 10% neutral buffered formalin for histological analysis. Preserved ovarian tissues were rinsed overnight in running tap water, dehydrated, cleared, embedded in paraffin, sectioned at 4 μm, and stained with hematoxylin and eosin following standard histological techniques. Reproductive phases were defined microscopically in accordance with Brown-Peterson et al. (2011). A 1–4-g portion of the ovary of all females that were macroscopically identified to be in the actively spawning subphase was weighed (0.01 g) and preserved for a minimum of 3 months in Gilson's solution for later fecundity analysis. For fish that were histologically verified to be in the actively spawning subphase, batch fecundity was determined volumetrically for six subsamples/individual (Bagenal and Braum 1971).

Reproductive Parameters

Reproductive seasonality was assessed using the gonadosomatic index (GSI), where GSI = (gonad weight/gonad-free weight) × 100. Only mature fish were included in GSI analyses. Ovarian development was assessed histologically. Females were considered sexually mature if cortical alveolar oocytes were present in the ovary (Lowerre-Barbieri et al. 2011) or if inactive ovaries showed signs of previous spawning (i.e., oocyte atresia, thick ovarian wall, blood vessels, muscle bundles, and a high percentage of perinucleolar oocytes). Fish were considered reproductively active if they were in the developing, spawning capable, and actively spawning phases; fish were considered reproductively inactive if they were in the immature, early developing, regressing, and regenerating phases.

Spawning indicators were defined as any stage of oocyte maturation (OM), including hydrated oocytes (Lowerre-Barbieri et al. 2011), and/or the presence of postovulatory follicle (POF) complex ≤24 h. These spawning indicators represent a 36-h period of spawning activity in Red Snapper (Glenn et al. 2017). Spawning interval (SI; number of days between spawns) was calculated as SI = (number of fish in spawning capable + actively spawning phases)/[(number of fish undergoing OM or with POFs) × 0.5]. Since batch fecundity is positively correlated to fish size (Lowerre-Barbieri et al. 2015), relative batch fecundity (RBF) was used in all analyses and calculated as RBF = (batch fecundity)/(ovary-free body weight).

Data Analyses

Maturity ogive.— We modeled the probability of maturity at length of females by using logistic regression. Individuals were assigned to a maturity phase and coded as immature (0) or mature (1). The probability of maturity at length (P_L) was estimated using a two-parameter logistic model:

$$P_L = \frac{1}{1 + e^{-r(\mathrm{FL} - \mathrm{FL}_{50})}}.$$

The model parameter r is the instantaneous rate of change, and the parameter FL_{50} is the FL at 50% maturity. Parameter values were estimated by minimizing the sum of squared residual values. The 95% CIs of the point estimates were determined using a bootstrap procedure. The maturity and FL data were sampled, with replacement, 1,000 times. From each bootstrap sample, we used the two-parameter logistic model to determine the mean P_L. From the iterative fitting of the model to the bootstrapped data, we extracted the 2.5% and 97.5% percentiles of FL_{50} (mm).

Random forest prediction and classification.— Categorical reproductive characteristics (maturity, histological phase, reproductively active/inactive, reproductively active phases, and presence/absence of spawning indicators) and one continuous reproductive characteristic (GSI) were the response variables evaluated using random forest machine learning algorithms. Explanatory variables used for these analyses included depth (m), structure type, structure height (m), FL, GSI, and histological phase (Table 1). Our preliminary analysis did not indicate that there was interannual variation or representation in the response variables, and we aggregated the data for all years of collection and thus were not able to explore annual contrasts in reproductive characteristics. The random forest algorithm was implemented using R package randomForest (Liaw and Wiener 2002). Random forest is an ensemble, black box approach for prediction and classification using multiple realizations of "decision" trees. Individual decision trees in the forest are created by (1) random selection of a subset of candidate predictors and records; (2) evaluation of each predictor, using the subset of data, to understand which explanatory variable and what value of that variable result in the greatest contrast in the response variable; (3) establishment of a node (a split), where each node provides reject-or-accept criteria regarding the value of an input variable; and (4) repetition of the creation of subsequent nodes for all other explanatory variables. For each random forest model, we specified the construction of 500 decision trees. Our preliminary analysis indicated that this was a sufficient number of decision trees to stabilize the out-of-bag (OOB) error estimate.

Three indicators of the quality of the classification models were evaluated: the OOB error estimate, the resulting confusion matrix, and the percentage of variance explained by the model. For the classification model, the OOB error estimate and confusion matrix were evaluated. The OOB estimate is calculated using the OOB observations of each tree. During construction of a single tree, only a subset of observations (~2/3) is used to fit the model. The remaining data are OOB samples that are used to calculate the classification error of the tree. The OOB estimate reported for each random forest here is the grand mean error rate for all trees. The second indicator of classification model performance is the confusion matrix, a table that reports how well the model classifies observations. For the random forest regression model that predicted the continuous variable GSI, the percentage of variance explained by the model was calculated.

We used multi-way importance plots (Paluszynska et al. 2019) to derive three measures of variable importance: the mean depth of the first split of the variable, the number of trees in which the root (the first node) is split on the variable, and the number of nodes in the forest (the suite of 500 trees) that split on the variable (see Appendix Figure A.1 for an example of a classification tree). Mean tree depth is informative because variables

TABLE 1. Summary of response and explanatory variables used in the six random forest models of Red Snapper reproductive characteristics. An "X" indicates that the explanatory variable was used in the given model (GSI = gonadosomatic index).

	Explanatory variable						
Response variable	Depth	FL	GSI	Month	Structure height	Structure type	Histological phase
Maturity	X	X		X	X	X	
Spawning indicator	X	X	X	X	X	X	
Histological phase	X	X	X	X	X	X	
GSI	X	X		X	X	X	X
Developing versus spawning capable	X	X	X	X	X	X	
Reproductively active	X	X	X	X	X	X	

that have a large impact on prediction occur more frequently at an early split, where they partition large samples of the data (Ehrlinger 2016). Similarly, independent variables that split the response variable at the root node are at the first split. The mean tree depth indicates the mean location of the node, with a smaller mean tree depth indicating a more important variable for prediction. Similarly, the inclusion of a variable in the tree, regardless of the placement in the node position, indicates that the variable adds predictive power to the tree. The number of nodes can vary in each decision tree because of the resampling nature of the tree construction, where each tree uses a subset of the data and a subset of the independent variables. Additionally, trees based on continuous data have more nodes than those based on ordinal data.

RESULTS

Fish Sampling

A total of 693 female Red Snapper ranging in size from 168 to 795 mm FL were captured during the course of this study; of those females, 84.2% were sexually mature. The most fish were captured on ARs in the mid-depth stratum, and the fewest were captured on R2Rs in the deep stratum (Table 2). Artificial structure height increased with increasing depth stratum; ARs were 0.27–2.9 m high (mean ± SE = 1.70 ± 0.12 m) in shallow water and 0.33–8.9 m high (2.19 ± 0.13 m) at mid-depths. In deep water, R2Rs were 6.1–71.6 m high (13.27 ± 2.39 m). Platform heights were 9.7–19.8 m (16.08 ± 0.23 m) in the shallow stratum, 20.1–49.1 m (31.40 ± 0.62 m) in the mid-depth stratum, and 53.3–90.5 m (69.63 ± 1.06 m) in the deep stratum.

TABLE 2. Number of female Red Snapper captured at various depths and artificial structure types in waters off Mississippi from 2016 to 2018 (platforms = oil and gas platforms; ARs = artificial reefs; R2Rs = rigs-to-reefs structures).

Depth stratum	Platforms	ARs	R2Rs	Total
Shallow (<20 m)	137	45	0	182
Mid-depth (20–50 m)	188	205	0	393
Deep (50–100 m)	93	0	30	123
Total	418	250	30	698

Maturity

Evaluation of the probability of maturity at length (Figure A.2) indicated that immature females ranged in FL from 168 to 525 mm (n = 120) and mature females ranged in FL from 232 to 795 mm (n = 573). Using least-squares model fitting, we found that r was 0.025 per millimeter (95% CI = 0.020–0.032) and FL_{50} was 274.0 mm (95% CI = 263.4–282.4 mm).

Our evaluation of the predictors that determine contrast in maturity classification indicated that FL, depth, structure height, and month had predictive ability (Figure 2). In the 500 trees, each of these variables occurred as a root 80–192 times, and the mean tree depth of these predictors was 0.95–1.62. Fork length appeared in 8,477 nodes, whereas structure type appeared in only 977 nodes (11.5% of the maximum occurrence). Structure type was not an important predictor; the mean tree depth of this variable in the suite of random forest trees was 4.20, and it had no occurrences as a root node. In contrast, the mean tree depth of structure height was 1.54, with 96 occurrences as a root node, suggesting that structure height was more important than structure type when predicting female Red Snapper maturity. The OOB error rate was 11.13%. Given the ensemble of trees, immature females were correctly classified 57.0% of the time and mature females were correctly classified 95.8% of the time (Appendix Table A.1).

Spawning Seasonality

Aggregated GSI values (by year, depth, and structure type) began to increase in April, peaked in May, and

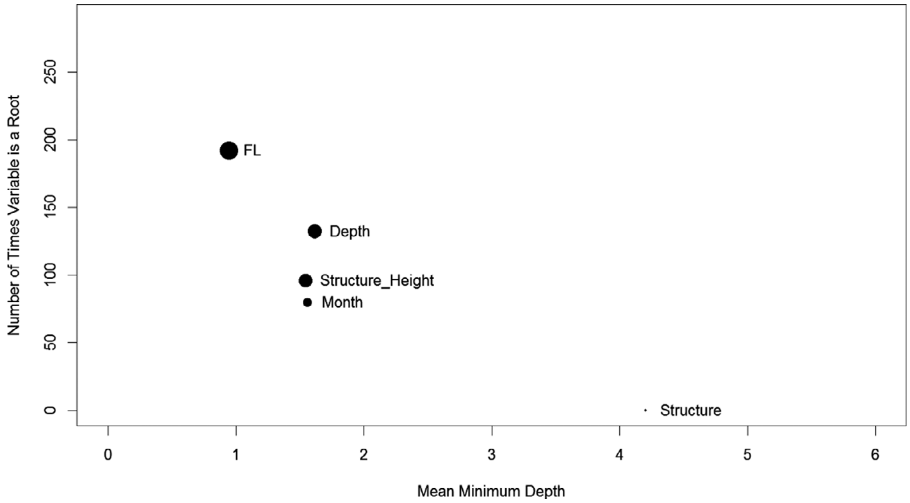

FIGURE 2. Random forest model predictions of explanatory variables predicting maturity status of female Red Snapper captured at various depths and artificial structures in the north-central Gulf of Mexico during 2016–2018. The variable importance plot represents the aggregated results from 500 tree models. Mean minimum depth refers to the depth of the regression tree. The number of times the variable is a root is the frequency of the trees that had the variable as the first split (the first node of a regression tree). The size of the circle indicates the relative number of times each variable was included in a regression tree, with larger circles indicating greater representation.

remained elevated through September (Figure A.3). Our evaluation of the explanatory predictors that determined contrast in GSI indicated that histology phase, month, and FL were important variables with predictive ability for spawning seasonality (Figure 3). Each of these variables occurred in the 500 trees from 123 to 139 times as a root, and the mean tree depth of these predictors was 1.28–1.39. Fork length appeared in 18,848 nodes, and structure type appeared in only 3,718 nodes (19.7% of the maximum occurrence). The variables depth, structure height, and structure type were less important predictors; the range of mean tree depth for these variables in the suite of random forest trees was 2.05–2.77, and they occurred from 26 to 44 times as a root node. Although depth did appear often in the trees as the second most frequent node, on average it was at the second node and therefore was not included as an important predictor. The mean of the squared residuals was 0.484, and the model, which included all of the predictors, explained 59.2% of the variation in GSI.

Ovarian Development

The best predictors of histological phase were GSI, month, FL, and depth. Each of these variables occurred

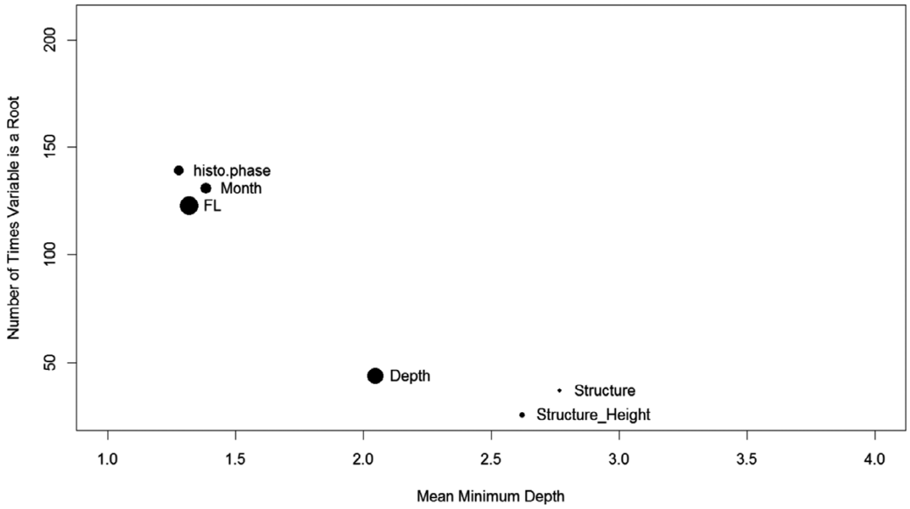

FIGURE 3. Random forest model predictions of explanatory variables predicting the gonadosomatic index of female Red Snapper in the north-central Gulf of Mexico during 2016–2018. See Figure 2 caption for details of the variable importance plot (histo.phase = histological phase).

in the 500 trees from 68 to 169 times as a root (Figure 4A), and the mean tree depth of these predictors was 1.08–1.82. The GSI appeared in 19,390 nodes, and structure type appeared in only 2,766 nodes (14.2% of the maximum occurrence). Neither structure height nor structure type was an important predictor of histological phase; the range of mean tree depth of these variables in the suite of random forest trees was 2.75–3.32, and they occurred from 20 to 28 times as a root node. The OOB estimate of error rate was 46.39% (Table 3). Correct prediction of histological phase varied by phase; classification error was greatest for the actively spawning phase and lowest for the spawning capable phase (Table 3).

To improve the classification of histological phase, fish were grouped into reproductively active (ovaries containing vitellogenic oocytes in the developing, spawning capable, and actively spawning phases) and reproductively inactive (immature, early developing, regressing, and regenerating phases) response variables, and the random forest was rerun. Collapsing the phases to these broader

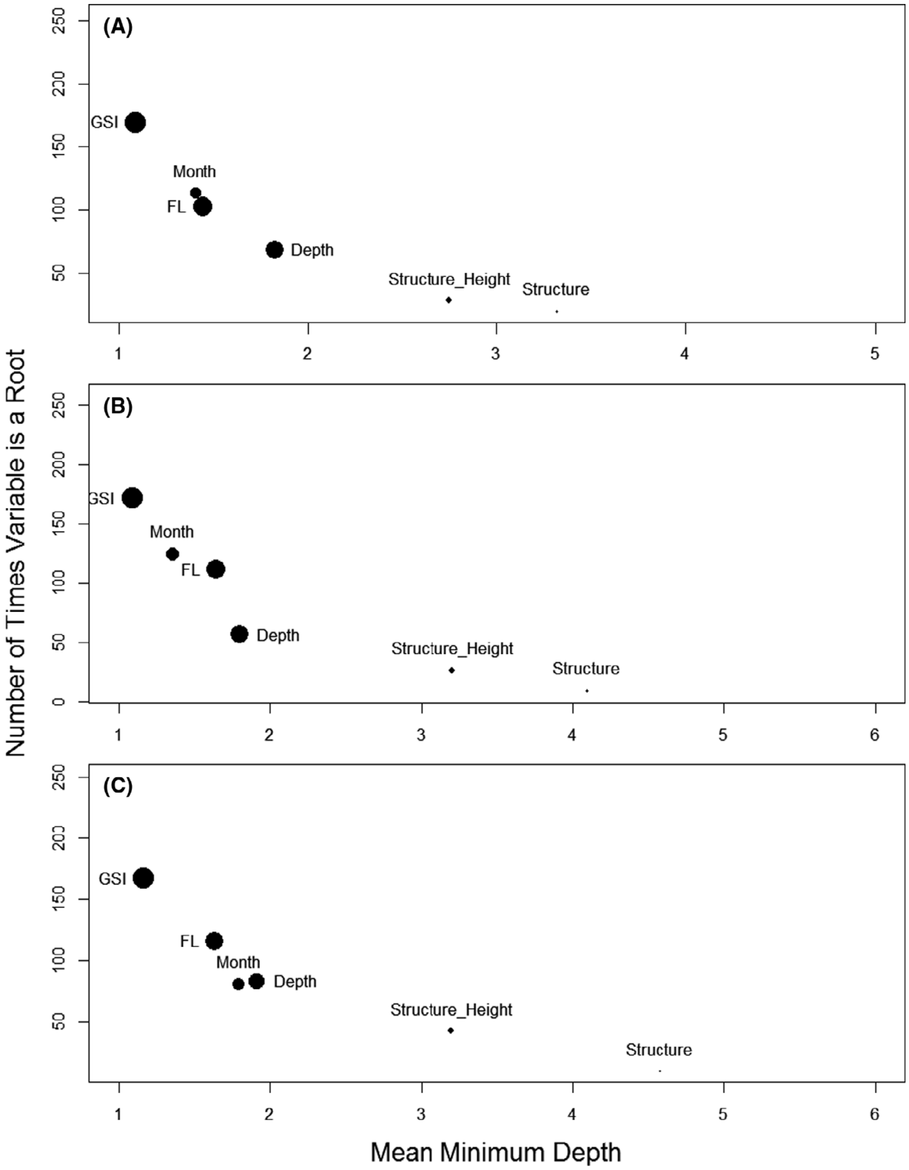

FIGURE 4. Variable importance plots for the aggregated results from 500 classification tree models for ovarian development of female Red Snapper captured at various depths and artificial structures in the north-central Gulf of Mexico during 2016–2018: **(A)** histological phase; **(B)** phases combined into reproductively active (developing, spawning capable, and actively spawning) versus reproductively inactive (immature, early developing, regressing, and regenerating); and **(C)** comparison of reproductively active phases only (developing versus spawning capable). See Figure 2 caption for details of the variable importance plots (GSI = gonadosomatic index).

TABLE 3. Confusion table showing the classification error (Error, %) for female Red Snapper in each histological phase (Imm = immature; EDev = early developing; Dev = developing; SC = spawning capable; AS = actively spawning; Rgs = regressing; Rgn = regenerating). The overall mean out-of-bag error for the classification was 46.39%. Values represent the numbers of fish in each phase based on the actual classification (rows) versus the predicted classification (columns).

	Predicted classification							
Actual classification	Imm	EDev	Dev	SC	AS	Rgs	Rgn	Error (%)
Imm	60	11	6	2	0	2	6	31.0
EDev	18	30	4	2	1	2	9	54.5
Dev	5	8	14	5	3	1	5	65.9
SC	2	2	2	93	24	1	4	27.3
AS	0	2	4	50	20	1	1	74.0
Rgs	2	4	0	0	2	16	7	48.4
Rgn	13	4	4	2	9	5	27	50.9

categories resulted in an OOB error rate estimate of 10.72% (Table A.2). The predictors GSI, month, FL, and depth were informative variables for predicting reproductive activity (Figure 4B). Each of these variables occurred in the 500 trees from 56 to 172 times as a root, and the mean tree depth of these predictors was 1.08–1.80. Gonadosomatic index appeared in 7,073 nodes, and structure type appeared in only 1,024 nodes (14.5% of the maximum occurrence). Neither structure height nor structure type was a good predictor of reproductive activity; the range of mean tree depth of these variables in the suite of random forest trees was 3.21–4.09, and they occurred from 9 to 26 times as a root node. Reproductively active females were incorrectly classified 12.1% of the time in this random forest classification (Table A.2).

Finally, we investigated the classification of different phases within the reproductively active response variable to determine whether there was a difference between spawning (spawning capable and actively spawning phases) and nonspawning (developing phase) female Red Snapper. The best predictors of spawning versus nonspawning fish were GSI, FL, month, and depth (Figure 4C). Each of these variables occurred in the 500 trees from 81 to 167 times as a root, and the mean tree depth of these predictors was 1.16–1.91. The GSI appeared in 3,753 nodes, and structure type appeared in only 468 nodes (12.5% of the maximum occurrence). The OOB error rate was 17.84%. Depth occurred more often as a root node and month occurred less often when predicting the presence of spawning fish, in contrast to previous trees that included both reproductively active and inactive females (Figure 4A, B). Furthermore, FL was a more important predictor than month for reproductively active fish, in contrast to classifications using all reproductive phases (Figure 4A) or active versus inactive fish (Figure 4B). Overall, the confusion matrix indicated that fish in the developing phase were incorrectly classified 51% of the time, whereas spawning fish were incorrectly classified only 8.9% of the time (Table A.3).

Spawning Indicators

Only Red Snapper in the spawning capable or actively spawning phases ($n = 285$) were analyzed for spawning indicator predictions. Overall, the SI of all females from 2016 to 2018 was 2.86 d. Additionally, 23.7% of the actively spawning females captured showed histological evidence of daily spawning (i.e., presence of POFs ≤24 h in ovaries undergoing OM).

Our evaluation of the explanatory predictors that determined contrast in spawning indicators suggested that depth, FL, GSI, and month were important variables with predictive ability, and the OOB error rate was 38.58%. Each of these variables occurred in the 500 trees from 69 to 154 times as a root (Figure 5), and the mean tree depth of these predictors was 1.24–1.72. The variable depth appeared in 4,900 nodes, and structure type occurred in only 879 nodes (17.9% of the maximum occurrence). Structure height and structure type were not considered important predictive variables; the range of mean tree depth for these variables in the suite of random forest trees was 2.96–3.50, and they occurred from 22 to 33 times as a root node. Depth was the best predictor of spawning indicators, in contrast to analyses of all other reproductive characteristics. However, the classification error of nonspawning indicators was relatively high (60%; Table A.4), indicating the instability of this model.

Fecundity

Fecundity estimates were made from 75 actively spawning Red Snapper during the course of this study. Batch fecundity ranged from 630 to 321,872 eggs/female, and there was a significant positive relationship between batch fecundity and FL ($F_{1,\ 73} = 14.91$, $P = 2.4 \times 10^{-4}$, $r^2 = 0.170$; Figure A.4 [top]) despite the large variation in

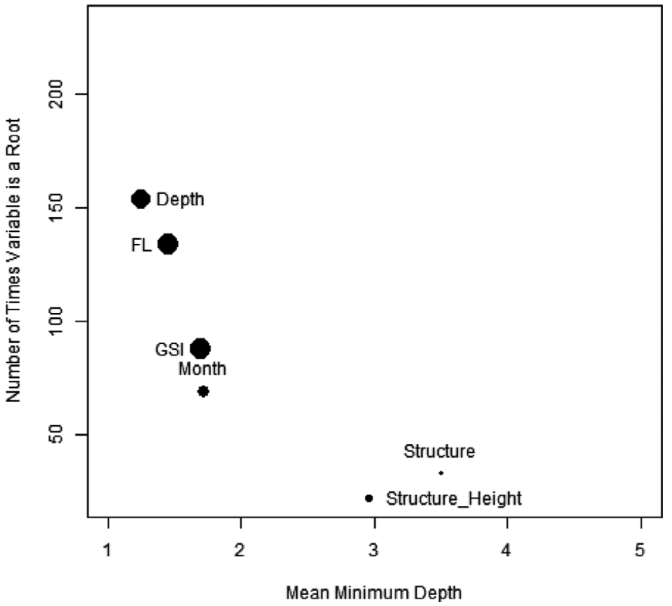

FIGURE 5. Random forest regression tree results for independent variables explaining variation in spawning indicators of female Red Snapper captured at various depths and artificial structures in the north-central Gulf of Mexico during 2016–2018. Fish with spawning indicators include females undergoing oocyte maturation and those with postovulatory follicles ≤24 h, representing a potential spawning event within 36 h. See Figure 2 caption for details of the variable importance plot (GSI = gonadosomatic index).

fecundity numbers. Relative batch fecundity ranged from 1.24 to 714.16 eggs/g of ovary-free body weight, with an overall mean RBF (±SE) of 80.46 ± 15.72 eggs/g ovary-free body weight, and there was no relationship between RBF and FL (P = 0.472; Figure A.4 [bottom]). Therefore, RBF was predicted using a stepwise regression that included month, depth, structure type, structure height, and age as variables. Only month entered significantly into the regression ($F_{5,\ 69} = 3.149$, $P = 0.0128$, $r^2 = 0.1268$), with RBF being highest in August and lowest in April (Figure 6).

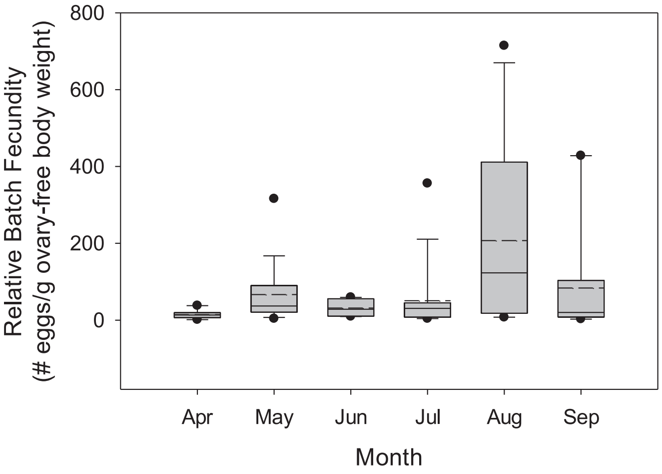

FIGURE 6. Monthly relative batch fecundity of actively spawning female Red Snapper captured at various depths and artificial structures in the north-central Gulf of Mexico during 2016–2018. The solid horizontal line represents the median, the dashed horizontal line represents the mean, the box represents the interquartile range, the whiskers are the 5% and 95% quartiles, and the black dots are the outliers. Stepwise regression showed significant differences among months (P = 0.0128).

DISCUSSION

Many aspects of the reproductive biology of female Red Snapper in the GOM have previously been described (Collins et al. 1996; Jackson et al. 2006; Porch et al. 2015; Kulaw et al. 2017; Brown-Peterson et al. 2019). Those studies focused on identifying seasonal and annual reproductive parameters throughout the region. Our analyses focused on describing the biological and habitat variables that enable prediction and classification of a suite of reproductive characteristics. In particular, we were interested in describing the interaction between depth and ARs because the Red Snapper is a structure-oriented species and previous studies have documented reproductively active females on ARs (Alexander 2015; Glenn et al. 2017; Downey et al. 2018). Our results indicate that depth is a useful predictor of maturity status, ovarian development, and the presence of spawning indicators. In contrast, the type of artificial structure (platforms, ARs, or R2Rs) was not a suitable predictor of any of the reproductive characteristics that we examined. Although the data used in these analyses were characterized by an incomplete representation of all structure types in all depth strata, the overall low occurrence of structure type as a root in each analysis indicates that structure type has relatively low importance. Overall, biological (FL) and seasonal (month) variables most consistently predicted reproductive characteristics. For instance, FL was the most important predictor of maturity status and was useful in predicting spawning seasonality (e.g., GSI), ovarian development, and spawning indicators. Month was an important predictor for all reproductive characteristics examined and was the only variable that was useful for predicting RBF.

Random forest algorithms are an ensemble and black box approach for classification and prediction. The method is fundamentally different from other types of statistical parameter estimation procedures because those methods do not involve fitting statistical models to data (Bzdok et al. 2018) and thus do not allow the discovery of the underlying mechanisms that determine prediction and classification. Random forest has been evaluated using simulation, and the performance of logistic regression is generally preferred for its greater accuracy (Kirasich et al.

2018). Despite this, some aspects of ecological investigation make the use of random forest regression and classification appropriate. Random forest models, unlike logistic regression, allow the inclusion of high-dimensional, multicollinear predictive variables (Zhu et al. 2019). However, models produced from these data may not exhibit generalizability (Zhu et al. 2019) because the distribution of the data used for training the model is different from the distribution of the data used to test the model (Khalilia et al. 2011). A model that is not generalizable is an "overfitted" model that will have low predictive power for the correct classification and prediction of new cases. We observed this reduced ability to make predictions and classification for some of the models presented here due to the imbalance of representation (in this case, nonrepresentation) of structure types among depth strata. One approach to handling extremely unbalanced data prior to modeling is to subsample the data and use those data that comprise complete cases. Alternatively, computational approaches have been derived that assign different weights for each variable (Lee et al. 2015). However, the nature of the distribution of habitat types among depth strata (e.g., R2Rs occurred in only one depth stratum, and ARs were represented in only two depth strata) in nearshore Mississippi waters does not allow this. Similarly, we note that the variables depth and age exhibit multicollinearity because Red Snapper depth and FL were positively correlated (larger and older fish were found at deeper depths). This impacts the interpretation of the variable importance patterns that we describe and to some extent confounds the interpretation of these variables singly. A reasonable conclusion from our work is that the variable importance patterns we have derived and presented here should be considered as testable hypotheses if (and likely when) there is an expansion of the construction of habitat types among depth strata.

The estimated FL_{50} (274 mm) for our samples was similar to or slightly smaller than the 50% maturity values reported previously for GOM Red Snapper (280–290 mm FL: Render 1995; 275 mm FL: Woods et al. 2003; 323 mm FL: Alexander 2015; 323–368 mm FL: Glenn et al. 2017); therefore, our predictions for maturity status of Mississippi Red Snapper would likely apply across the GOM. Maturity status was better predicted than all of the other reproductive characteristics we examined, with an OOB error rate of only 11.13%. Not surprisingly, FL was the most important predictor for distinguishing between mature and immature Red Snapper. It is noteworthy that depth and artificial structure height were also important variables for predicting maturity status, whereas month was least important. Given their extended spawning season, all Red Snapper are unlikely to first attain maturity during the same month, which likely accounts for the lack of importance of month as a predictor of maturity status. Larger, mature Red Snapper have previously been shown to occur at deeper depths throughout the GOM (Stanley and Wilson 2000; Patterson et al. 2005; Galloway et al. 2009; Karnauskas et al. 2017), lending support to the accuracy of our predictions. Indeed, linear mixed-effects models predicted that FL increased with depth in both mature and immature female Red Snapper (A. J. Leontiou, W. Wei, and N. J. Brown-Peterson, unpublished data).

Female Red Snapper in Mississippi waters have elevated GSI values from April through September, with a peak in May. Traditionally, peak GSI values for female Red Snapper have been reported as occurring from June through August (Render 1995; Collins et al. 1996; Fitzhugh et al. 2004), although a recent meta-analysis found that May can also be a peak spawning month for Red Snapper (Brown-Peterson et al. 2019). Histology phase was the most important predictor of spawning seasonality, followed closely by month and FL, despite these trees having a high OOB error rate (40.8%), which suggests relatively low confidence in spawning seasonality prediction with the variables used in our analysis. Although the GSI is a ratio that takes fish size into account, we found that FL is still an important variable for predicting spawning seasonality. None of the habitat variables (depth, structure type, or structure height) was found to be a useful predictor of GSI. Similarly, Downey et al. (2018) and Lowerre-Barbieri et al. (2015) reported that Red Snapper GSI did not differ between platforms and R2Rs at similar depths in south Texas or at different depths on hard-bottom reefs in Florida, respectively. In contrast, Alexander (2015) found higher GSI values at shallower nearshore ARs in Texas—despite the presence of smaller females—compared to deeper offshore ARs, suggesting that depth is important in that system.

Our results showed that GSI was the best predictor of ovarian development regardless of the histology metric used (i.e., all reproductive phases, reproductively active versus inactive females, or active females only). The GSI has been shown to accurately reflect ovarian development in a number of species (Ganias et al. 2007; McPherson et al. 2011; Flores et al. 2019), thus validating the predictive power of GSI. However, prediction of ovarian development, as measured by reproductive phase, had the highest error rate among the reproductive characteristics we examined (OOB error = 46.39%), indicating that the combination of variables in our models was not effective for predicting reproductive phase. Conversely, the best predictions of ovarian development were seen for reproductively active versus inactive females, with OOB error of only 10.72%, implying that a combination of GSI, month, FL, and depth can accurately distinguish reproductive activity. Our model supports previous work, which has suggested that simply assigning an active or inactive classification to fish can aid managers in identifying spawning seasonality or even spawning location (e.g., Lowerre-Barbieri et al. 2015; Brown-Peterson et al. 2017; Costa 2019). Finally, month became less important than FL when predicting the spawning activity of reproductively active fish. The decreased importance of month in the prediction of reproductively active fish is likely attributable to the Red Snapper's extended spawning season. Depth increased in importance when we only examined reproductively active females compared to the two other models predicting ovarian development. The increased importance of depth in predicting spawning activity is supported by Glenn et al. (2017), who found more reproductively active females at deep natural reefs versus shallow ARs in the GOM.

Depth and FL were important predictors of spawning indicators, although overall these predictors only classified 61.4% of the variation in this reproductive metric. Month occurred as a predictor variable much less frequently than either depth or FL. These results contrast with previous modeling of GOM Red Snapper spawning markers, which showed that time of year (i.e., month) and, to a lesser extent, fish size explained the most variation in spawning fraction across the GOM (Porch et al. 2015). Although the Porch et al. (2015) models did suggest evidence for a strong depth or regional effect, those variables did not explain a substantial amount of the variance in spawning indicators in their models. Our model also contrasts with results from Lowerre-Barbieri et al. (2015), who found that the proportion of females with spawning indicators differed significantly by month and that size did not significantly impact the temporal pattern of spawning. The lesser importance of month in our model compared to previous work is likely related to pooling 3 years of observations. This serves to dampen interannual variability as compared to evaluating only a single year of observations as in the Porch et al. (2015) and Lowerre-Barbieri et al. (2015) studies. Our approach using pooled years allows identification of factors other than month that are important in predicting spawning indicators.

Because our analyses show that the type of artificial structure is not an important predictor of Red Snapper reproductive characteristics, managers could deploy a variety of artificial structures equally effectively. These structures will likely serve to attract Red Snapper, but our study indicates that they will not impact the reproductive characteristics we measured. However, the depth at which those structures are deployed may be of more consequence based on the results of our analyses.

Although this study was not designed to include natural reefs in the analyses, natural reefs have been shown to be important habitat for Red Snapper reproduction (Brulé et al. 2010; Lowerre-Barbieri et al. 2015; Glenn et al. 2017). Indeed, Glenn et al. (2017) found more reproductively active female Red Snapper on natural reefs compared to artificial structures off the Louisiana coast, but their study was confounded by the natural reefs being at greater depths than the artificial structures. In contrast, Downey et al. (2018) found no differences in female Red Snapper reproductive potential at natural reefs versus ARs sampled at 60–90 m off the Texas coast. In a preliminary study designed to evaluate vertical line fishing gear over natural reefs and ARs at deep depths (60–92 m) off the Mississippi coast, 98% of the Red Snapper sampled were captured from artificial structures (Center for Fisheries and Research Development, University of Southern Mississippi [USM], unpublished data). The tested gear targeted Red Snapper age 9 and younger, and the results suggested that smaller adults were not using the low-relief natural reefs for reproduction in deep waters, in contrast to the findings from Downey et al. (2018) at similar depths.

Artificial reefs may offer both an attraction and production benefit to Red Snapper (Bortone 2020), but there has been limited research delineating how artificial structures impact Red Snapper populations. Inclusion of depth- and structure-specific reproductive data would allow a better understanding of the attraction versus production question regarding artificial habitats and Red Snapper, which would provide better inputs for the management of this important GOM species.

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Appendix: Additional Tables and Figures

TABLE A.1. Confusion matrix showing classification error (Error, %) for immature versus mature female Red Snapper. The overall mean out-of-bag error for the classification was 11.13%. Values represent the numbers of fish in each group based on the actual classification (rows) versus the predicted classification (columns).

	Predicted classification		
Actual classification	Immature	Mature	Error (%)
Immature	49	37	43.02
Mature	17	382	4.26

TABLE A.2. Confusion matrix showing classification error (Error, %) for reproductively active versus inactive female Red Snapper. The overall mean out-of-bag error for the classification was 10.72%. Values represent the numbers of fish in each group based on the actual classification (rows) versus the predicted classification (columns). Active fish were those with vitellogenic oocytes in the developing, spawning capable, and actively spawning phases; inactive fish were those in the immature, early developing, regressing, and regenerating phases.

	Predicted classification		
Actual classification	Inactive	Active	Error (%)
Inactive	216	22	9.2
Active	30	217	12.1

TABLE A.3. Confusion matrix showing classification error (Error, %) for reproductively active female Red Snapper. Fish are separated by spawning (i.e., in the spawning capable or actively spawning phase) or nonspawning (i.e., in the developing phase). The overall mean out-of-bag error for the classification was 17.84%. Values represent the numbers of fish in each group based on the actual classification (rows) versus the predicted classification (columns).

	Predicted classification		
Actual classification	Nonspawning	Spawning	Error (%)
Nonspawning	25	26	51.0
Spawning	17	173	8.9

TABLE A.4. Confusion matrix showing classification error (Error, %) for spawning indicators of female Red Snapper. Fish with spawning indicators include females undergoing oocyte maturation and those with postovulatory follicles ≤24 h,fspawning indicators of female Red Snapper. Fish with spawning indicators representing a potential spawning event within 36 h. The overall mean out-of-bag error for the classification was 38.58%. Values represent the numbers of fish in each group based on the actual classification (rows) versus the predicted classification (columns).

	Predicted classification		
Actual classification	No indicator	Indicator	Error (%)
No indicator	30	45	60.0
Indicator	31	91	25.4

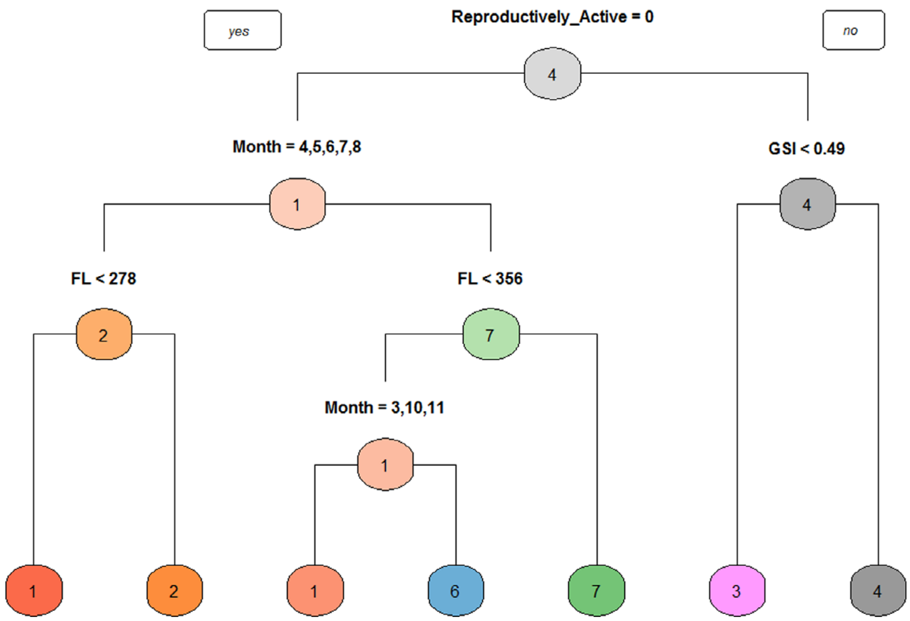

FIGURE A.1. Example of a classification tree produced in the random forest ensemble predicting histological classification (class 1, 2, 3, 4, 6, or 7) of Red Snapper. Each node (circle) in the tree represents an accept-or-reject proposition, where acceptance leads to the left branch and rejection leads to the right branch. The nodes are determined by the values of the predictor variables (GSI = gonadosomatic index). Tree depth refers to the numbers of nodes to reach a given classification, with the FL (mm) variables in this example occupying a depth of 3. The depth of this tree is 4. Month is the deepest node.

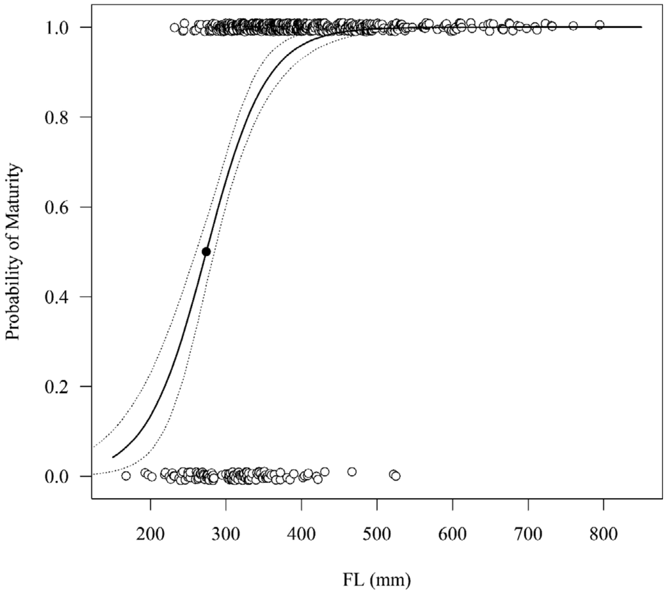

FIGURE A.2. Female FL-specific maturity based on predictions from a two-parameter logistic model describing the maturity at length for Red Snapper captured at various depths and artificial structures in the north-central Gulf of Mexico during 2016–2018 (n = 693). The inflection point (filled circle) is the mean parameter estimate of the FL at 50% maturity. The dotted lines indicate the predicted 95% CI of the mean probability of maturity at length based on fitting the two-parameter logistic model to 1,000 bootstrapped samples. Note that a small jitter is applied to the points for improved visualization.

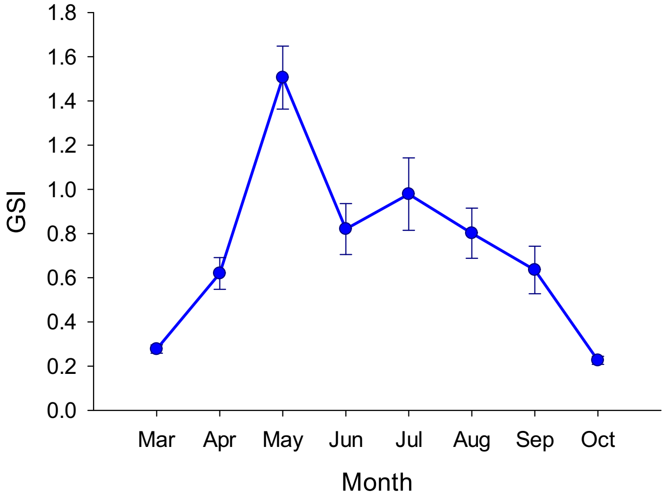

FIGURE A.3. Mean (±SE) monthly gonadosomatic index (GSI) of female Red Snapper captured at various depths and artificial structures in the north-central Gulf of Mexico during 2016–2018.

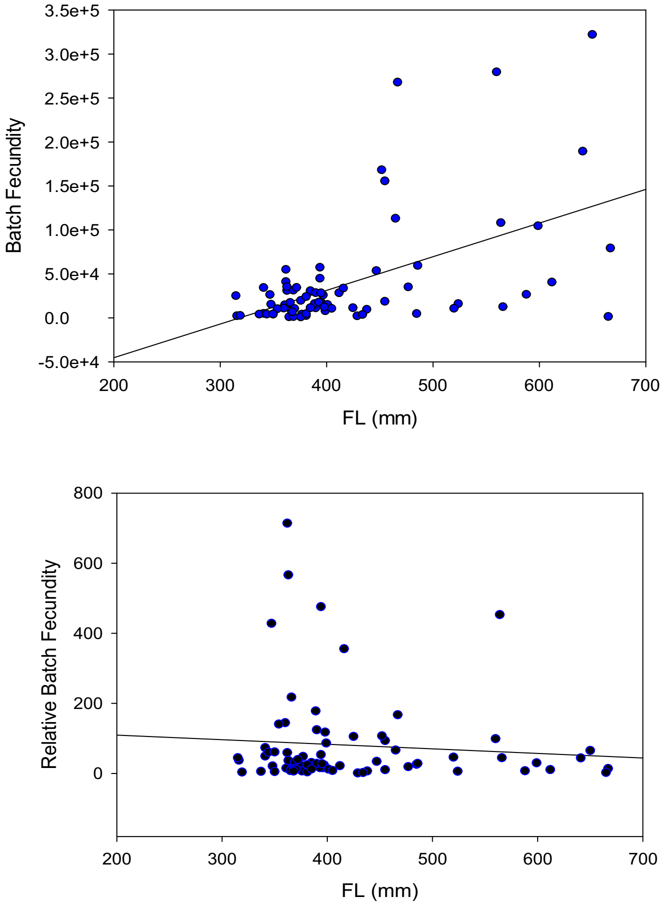

FIGURE A.4. Relationship between fecundity and FL for actively spawning female Red Snapper captured at various depths and artificial structures in the north-central Gulf of Mexico during 2016–2018: (top) batch fecundity (number of eggs) and (bottom) relative batch fecundity (number of eggs/g of ovary-free body weight).