

## ARTICLE

# The Role of Maturity in Artificial Habitat Selection by Female Red Snapper

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## Abstract

The Red Snapper *Lutjanus campechanus* is a reef-associated species found throughout the Gulf of Mexico that relies on artificial structures for habitat. In this study, we used Bayesian models to determine habitat selection by different sizes and ages of female Red Snapper and to identify whether there was a difference in habitat selection between immature and mature fish. Red Snapper ( $n = 693$ ) were sampled using vertical longlines from March or April through November of 2016–2018 off the coast of Mississippi at different artificial structure types (platforms, artificial reefs, and rigs-to-reef structures [hereafter, “rigs-to-reefs”]) and depths (shallow, <20 m; mid-depth, 20–49 m; and deep, 50–100 m). To adjust for the traditional occurrence of mature fish being larger and older than immature fish, only fish within the intersection of the FL ( $n = 616$ ) and age ( $n = 622$ ) ranges of immature and mature classes were used in these analyses. Fork length and age of immature and mature fish increased with increasing depth, but immature fish had a larger increase in FL per unit depth than mature fish. Immature fish on artificial reefs were found to be older than immature fish at platforms, while there was no age difference between the two structures for mature fish. There was no difference in FL or age between rigs-to-reefs and platforms or artificial reefs for immature fish, but FL and age of mature fish were greater at rigs-to-reefs than at platforms and artificial reefs. However, maturity did not play a role in how age increased with depth or with differences in FL between artificial reefs and platforms for mature fish. These differences in habitat use based on maturity should be considered along with FL and age to inform management regulations for Red Snapper.

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The Red Snapper *Lutjanus campechanus* is a reef-associated species found throughout the Gulf of Mexico (GOM; NOAA 2019) that relies on hard substrate for its habitat (Patterson et al. 2001; Ajemian et al. 2015). However, the majority of the GOM is comprised mostly of mud bottom (Shipp and Bortone 2009); therefore, Red Snapper exploit artificial structures for habitat (Downey et al. 2018). Oil and gas exploration in the GOM and the subsequent construction of platforms for oil and gas extraction beginning in the 1980s have provided structurally complex havens for these fish (Downey et al. 2018). Density assessments performed by Patterson et al. (2005) found that Red Snapper numbers were greatest in habitats that provide centimeters to meters of structure. Additionally, the creation of reefs from decommissioned platforms (i.e., rigs-to-reef structures [hereafter, “rigs-to-reefs”]), wrecks, and reef balls provides additional habitat for Red Snapper (Shipp and Bortone 2009; Syc and Szedlmayer 2012; Ajemian et al. 2015).

As with other lutjanid species, Red Snapper habitat preferences depend on fish size (Franks and VanderKooy 2000; Mikulas and Rooker 2008; Gallaway et al. 2009; Ajemian et al. 2015). As juveniles, these fish are most often present in low-relief habitat, such as individual pieces of debris and rubble patches (Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Workman et al. 2002). As they become larger and predation becomes less of a threat, Red Snapper are frequently found on structures that are meters in height with more complexity, such as oil and gas platforms, wrecks, and artificial reefs (Patterson et al. 2001; Workman et al. 2002; Wells 2007). While these types of structures make up a nominal amount of the high-relief habitat in the GOM, they tend to provide a safe environment for a high percentage of age-2–7 Red Snapper (Patterson et al. 2001; Gitschlag et al. 2003; Gallaway et al. 2009; Karnauskas et al. 2017). Finally, when Red Snapper reach around 8 years of age, they are often found over open habitat, as predation by other fish is less of an imminent threat (Gallaway et al. 2009).

Red Snapper have also shown preferences for different depths as they grow. Karnauskas et al. (2017) found that all ages of Red Snapper were most abundant at 50–90-m depth in the GOM, although smaller fish were usually found in waters shallower than 50 m (Gallaway et al. 2009). Stratification of Red Snapper populations on platforms results in smaller, younger fish being closer to the surface and larger, older fish occupying deeper water (Stanley and Wilson 2003; Wilson et al. 2006; Gallaway et al. 2009).

Previous studies have examined differences in Red Snapper artificial structure use throughout the GOM by using age and size as their metrics (Dance et al. 2011; Jaxion-Harm and Szedlmayer 2015; Karnauskas et al. 2017). Karnauskas et al. (2017) found older Red Snapper

on artificial reefs than on platforms, but their study did not differentiate the maturity status of those fish. The results of these studies have traditionally been extrapolated to infer that differences in habitat use between immature and mature Red Snapper exist because of size or age differences between maturity states. Indeed, recent data have shown that structure types are important for predicting the size of mature but not immature female Red Snapper (Leontiou et al. 2021).

We hypothesized that there is a difference in the use of artificial habitats between immature and mature female Red Snapper in the same size and age ranges. Therefore, the purpose of this study was to (1) examine the relationship of the FL and age of immature and mature female Red Snapper with depth and artificial structure types (habitat selection) and (2) determine whether these relationships differ by maturity status. Gulf of Mexico Red Snapper first reach sexual maturity between 2 and 3 years of age (Kulaw et al. 2017), and there is a large overlap in FL at age for 2–5-year-old Red Snapper (SEDAR 2018). Although it is a recognized fact that mature fish are usually larger and older than immature fish, there is a large overlap in both FL and age between immature and mature female Red Snapper in offshore Mississippi waters at all depths and artificial structure types. As such, for our analyses we only used data with overlapping FL and age between maturity classes to account for the observation that mature fish are not always larger or older than immature fish as traditionally thought.

## METHODS

*Study area and sample collection.*—Samples for this study were collected in the north-central GOM during the spring–fall reproductive season in 2016, 2017, and 2018 (March/April–October/November; Figure 1). Samples were collected from three different structure types: active petroleum platforms, artificial reefs, and former platforms with their tops cut off and toppled (i.e., rigs-to-reefs). These structures were contained within three depth strata (shallow, <20 m; mid-depth, 20–49 m; and deep, 50–100 m). Artificial reefs (consisting of rubble, reef balls, submerged vessels, and concrete culverts) were sampled in the shallow and mid-depth strata. Platforms were sampled at all three depth strata, and rigs-to-reefs only occurred in deep depths. Seventeen randomly stratified stations were sampled each month, resulting in 374 stations sampled over the course of the study. The 17 monthly stations included three in one reef zone from both shallow and mid-depth strata (6 stations), one station at two rigs-to-reefs in deep water (2 stations), and a station at three separate platforms per depth zone (9 stations). For each station, depth (m), latitude and longitude, and environmental data were collected and recorded. At each sampling station, three

vertical longlines with 10 baited hooks each (sizes 8/0, 11/0, and 15/0) were simultaneously deployed and fished for 5 min at a time within 1 m above each structure type. Any captured fish were immediately tagged and put on ice.

All fish sampled were processed within 24 h of capture. For each Red Snapper, the SL (mm), FL (mm), TL (mm), weight (0.01 kg), and sex were recorded, and otoliths and gonads were removed.

**Sample analysis.**—Total gonad weight was recorded (0.01 g) and a small (0.1-cm<sup>3</sup>) portion of ovarian tissue was preserved for 7 d in 10% neutral buffered formalin for histological analysis. Tissues were dehydrated, embedded in paraffin, sectioned at 4 μm, and stained with

hematoxylin and eosin via standard techniques. Microscopic determination of ovarian reproductive phases followed Brown-Peterson et al. (2011). If cortical alveolar or vitellogenic oocytes were the leading oocyte stage or if there were indications of previous spawning activity, the fish were considered sexually mature.

Sectioned otoliths were analyzed according to VanderKooij (2009) to determine fish age. Opaque bands were counted as annuli, and the area between the last annulus and otolith edge (i.e., the margin) was measured. For each fish, three independent readers determined both the age and margin code. Any discrepancies were corrected during a joint reading session. Once age was determined, it was

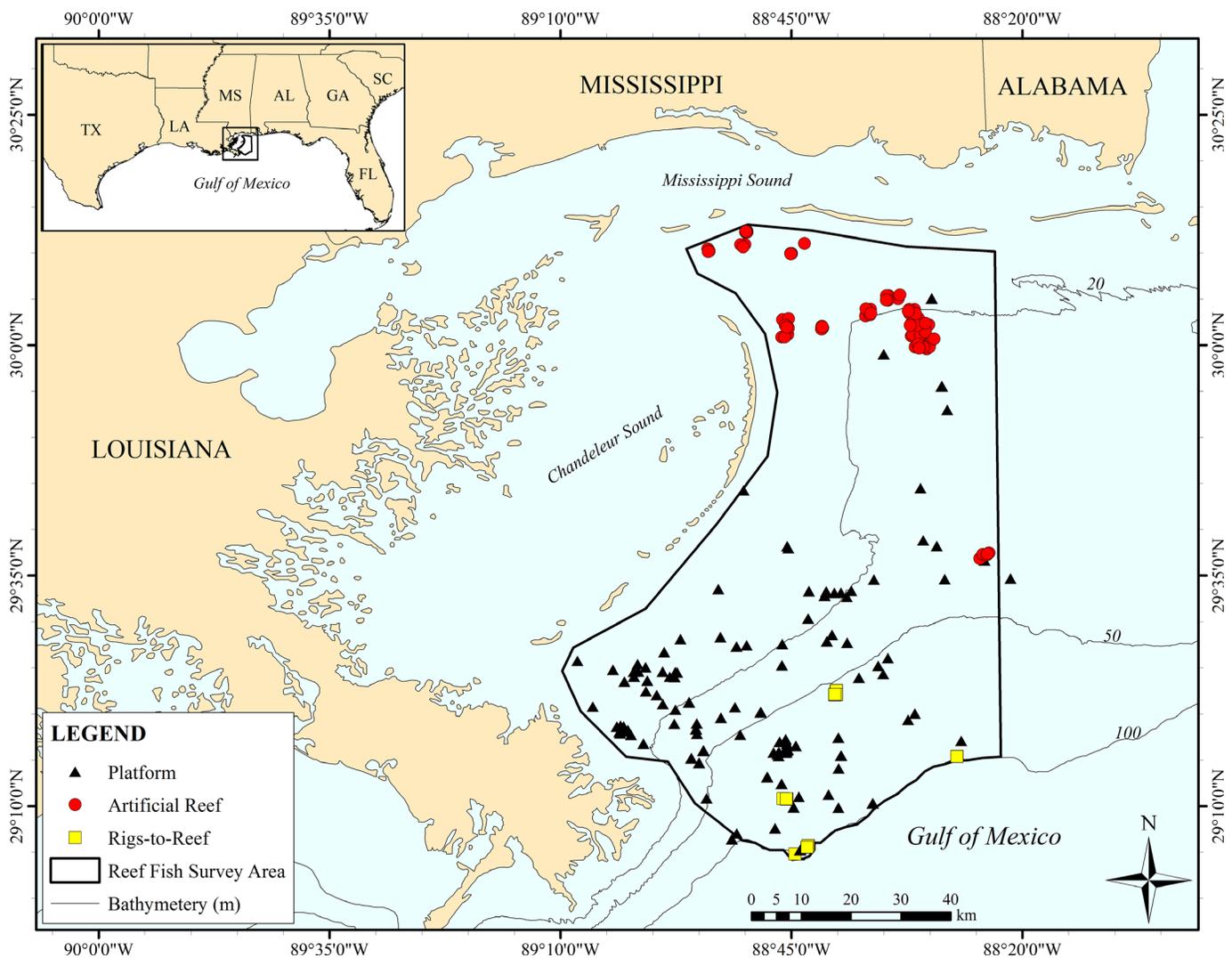


FIGURE 1. Artificial structure stations sampled for female Red Snapper in Mississippi waters of the Gulf of Mexico during 2016–2018. Monthly sampling was randomly stratified and occurred in three depth strata (<20, 21–49, and 50–100 m) and on three different structure types (oil and gas platforms, artificial reefs, and retired platforms with tops cut off and toppled [“rigs-to-reefs”]) for a total of 17 stations/month and 374 stations overall. Some stations were sampled multiple times during the 3 years of the project. (Figure adapted from Brown-Peterson et al. 2021).

converted to biological age (based on annulus count, date of collection, and mean timing of annulus formation) using a June 1 birthdate (VanderKooy 2009).

*Statistical analyses.*— Our analyses only used fish with FL and age between those of the smallest and youngest mature fish and the largest and oldest immature fish in order to control for the natural size bias that occurs between immature and mature fish. This strategy still allowed us to use the majority of the data collected during the study (90% for FL,  $n = 616$ ; 93% for age,  $n = 622$ ).

Bayesian inference has the advantage of readily quantifying uncertainties related to parameters and predictions through credible intervals (CrIs) of posteriors. Here, we applied hierarchical Bayesian models and model comparisons to predict how FL and age related to depth and structure types and to draw inferences on whether these relationships differed between mature and immature fish. To describe how the models were developed, we use one FL model as an example (Figure 2). We assumed FL for fish individual  $i$  in the maturity category  $j$  (mature or immature;  $FL_{ji}$ ) followed a normal distribution ( $\sim N$ ) with a mean of  $FL_{ji,\mu}$  and a variance of  $\sigma^2$  at the individual scale,

$$FL_{ji} \sim N(FL_{ji,\mu}, \sigma^2). \quad (1)$$

We modeled the mean of FL ( $FL_{ji,\mu}$ ) as a function of depth ( $D$ ) and factor variables that represented the

artificial reefs ( $A$ ) and the rigs-to-reefs ( $R$ ). Zeros for both of the two variables represented the platform structure:

$$FL_{ji,\mu} = f(\beta_0_j, \beta_1_j, \beta_2_j, \beta_3_j) = \beta_0_j + \beta_1_j \times D_{ji} + \beta_2_j \times A_{ji} + \beta_3_j \times R_{ji}, \quad (2)$$

where  $\beta_0_j$  represents the intercept (i.e., platforms); and  $\beta_1_j$ ,  $\beta_2_j$ , and  $\beta_3_j$  represent the coefficients for depth, artificial reefs, and rigs-to-reefs, respectively. If we do not consider the effect of depth (depth = 0 m),  $\beta_0_j$  represents the mean of FL at platforms, while  $\beta_2_j$  represents the mean difference in FL between artificial reefs and platforms and  $\beta_3_j$  represents the mean difference in FL between rigs-to-reefs and platforms. Furthermore, the difference between  $\beta_3_j$  and  $\beta_2_j$  represents the mean difference in FL between rigs-to-reefs and artificial reefs without the effect of depth.

Therefore, we modeled FL for both mature and immature fish and  $I_j$  individuals at each maturity category ( $j$ ) as

$$p(FL|\beta_0_j, \beta_1_j, \beta_2_j, \beta_3_j), \quad (3)$$

$$\propto \prod_{j=1}^2 \prod_{i=1}^{I_j} N[FL_{ji}|f(\beta_0_j, \beta_1_j, \beta_2_j, \beta_3_j), \sigma^2]$$

We assumed that the effect of the intercept and the coefficients of depth and structure types on FL varied by maturity ( $j$ ). We sampled  $\beta_0_j, \dots, \beta_3_j$  from the parameters at

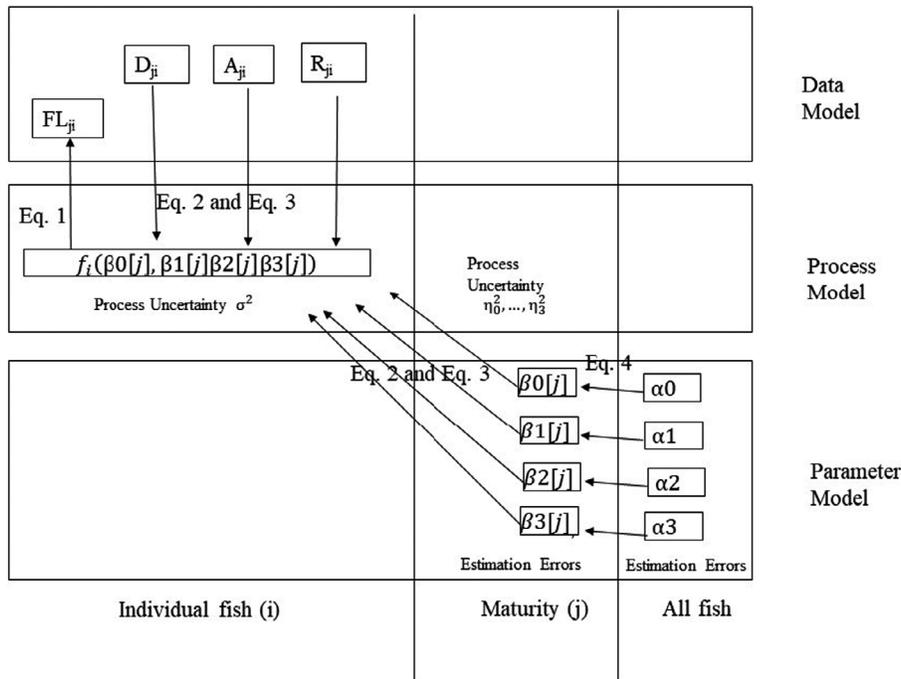


FIGURE 2. Conceptual model to illustrate the hierarchical structure, with complexity decomposed into stages of data, process and parameters (vertical direction), and the association of different spatial scales (horizontal direction; adapted from Wu et al. 2018). Equations (1)–(4) refer to where each of the equations shown in Methods fits into the overall model. The symbols  $\alpha$ ,  $\beta$ ,  $\sigma$ , and  $\eta$  represent the parameters in the model;  $D$  denotes depth,  $A$  denotes artificial reefs, and  $R$  denotes rigs-to-reefs. (Figure generated in Microsoft PowerPoint.)

the “all fish” scale (Figure 2) by using normal distributions,

$$\begin{aligned}\beta_{0j} &\sim N(\alpha_0, \eta_0^2), \\ \beta_{1j} &\sim N(\alpha_1, \eta_1^2), \\ \beta_{2j} &\sim N(\alpha_2, \eta_2^2),\end{aligned}\quad (4)$$

and

$$\beta_{3j} \sim N(\alpha_3, \eta_3^2),$$

where  $\alpha_0$ – $\alpha_3$  represent the means of the parameters at the all-fish scale and  $\eta_0^2$ – $\eta_3^2$  represent the variances across maturity for these parameters. To complete the Bayesian model, we defined vague prior probability distributions for unknown parameters ( $\alpha$ ,  $\sigma^2$ , and  $\eta^2$  parameters), as we had limited information on them (Lambert et al. 2005). We used normal distributions with a large variance as priors for the  $\alpha$  parameters, and uniform distributions with large intervals were used as priors for the SDs ( $\sigma$  and  $\eta$  parameters).

We also explored models in which the parameters at the individual scale did not vary by maturity (i.e., maturity was not a random factor). We compared the models based on predictive posterior loss (PPL) and the deviance information criterion (DIC; Hooten and Hobbs 2015; Wu et al. 2018). The lower the PPL or DIC, the better the model predicts. We applied the algorithm of Markov chain–Monte Carlo simulations (Gelfand and Smith 1990) to derive posteriors in JAGS through the R package rjags (R Core Team 2015; Plummer 2019; for the codes, see Supplements A and B available separately online). We simulated three Markov chain–Monte Carlo chains that used three different sets of initial values for the parameters in order to evaluate model convergence. The simulated posteriors identified the effects of depth and structure types on FL or age and whether the effects differed by maturity. When we inspected the results from the Bayesian models, we focused on two statistics commonly used to summarize posteriors: medians and/or means and CrIs. The medians/means of the posteriors represent the central tendency of the corresponding parameters, while CrIs represent intervals within which the parameters fall with a particular probability. Our figures show medians, 95% CrIs, and 50% CrIs, but in the text we only focus on describing 95% CrIs (i.e., the intervals in which the parameter estimates occur with a 95% probability).

## RESULTS

Our analyses used 616 female Red Snapper (110 immature, 506 mature) that ranged in size from 232 to 525 mm FL and 622 fish (116 immature, 506 mature) that ranged in age from 0.9 to 5.3 years. Sample sizes differed due to differences in the overlap ranges between FL and age. The ranges of immature and mature fish were the same for size

and age, but the distribution within those ranges differed between immature and mature individuals (Figure 3). However, for both mature and immature fish, the largest numbers of fish were represented in the 300–400-mm FL and 1.8–2.8-year intervals.

The best model for FL based on a combination of PPL and DIC was model 8 (Table 1), which was also more parsimonious than FL model 1, although the difference in DIC ( $\Delta$ DIC) was less than 2. In FL model 8, the coefficient for artificial reef did not vary by maturity, while the intercept and coefficients for depth and rigs-to-reefs varied by maturity (Table 1). This indicates that maturity did not play a role in the FL difference between the artificial reefs and platforms (coefficient for artificial reef), but maturity needed to be accounted for in explaining FL at the platforms (intercept), the difference in FL between the rigs-to-reefs and platforms (coefficient for rigs-to-reefs), and the relationship between FL and depth (coefficient for depth). The best model for age was model 9, in which the coefficient for depth did not vary by maturity, while the intercept and coefficients for artificial reefs and rigs-to-reefs varied by maturity (Table 1). This indicates that the relationship between age and depth did not differ by maturity, whereas maturity played a role in explaining age at the platforms (intercept), the age difference between the artificial reefs and platforms (coefficient for artificial reefs), and the age difference between the rigs-to-reefs and platforms (coefficient for rigs-to-reefs).

At platform and artificial reef structures, the predicted medians of FL and age were smaller for immature fish, but the 95% CrIs of the predictions overlapped between mature and immature fish (Figure 4). Few immature fish were captured at the rigs-to-reefs, but their predicted medians of FL and age were smaller than those of mature fish. The large overlaps were due to the large individual variance. Nevertheless, the different slopes of FL versus depth for immature and mature fish indicated the greater increase in FL needed for immature fish to utilize deeper habitat at both platforms and artificial reefs compared to mature fish (Figure 4). Age was greater in the deeper depths for both mature and immature fish, but there was no difference in the slopes of age versus depth between immature and mature fish for either platforms or artificial reefs (Figure 4), suggesting that the increase in age for depth utilization was similar for both maturity types.

To further investigate how the means of FL and age responded to depth and structure types (without accounting for individual-scale variances  $\sigma^2$  in equations 1 and 3), we studied the posteriors of the coefficients for depth and structure types (equation 2). The FL and age increased with depth for both mature and immature fish (Figure 5A2, B2). The increase of FL per unit depth in immature fish was larger than that in mature fish (Figure 5A2; negative 95% CrI for mature versus immature), while the

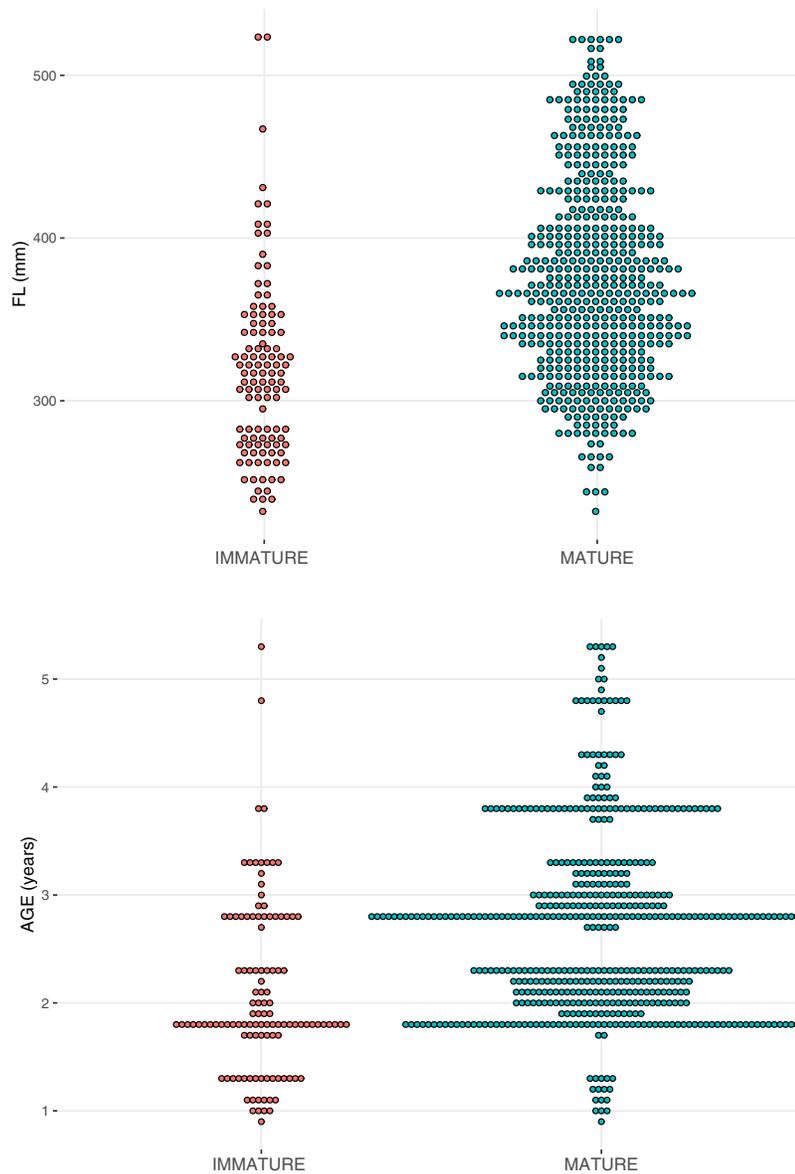


FIGURE 3. Overlap in size (FL; top panel) and age (bottom panel) of immature and mature female Red Snapper used in the analyses. (Figure generated in ggplot2 [Wickham 2016].)

increase of age per unit depth was similar for both immature and mature fish (Figure 5B2). This shows that immature fish needed to grow much longer per unit depth in order to utilize deeper habitats compared to mature fish but that there was no difference in age increase by depth between fish of differing maturity status.

The effect of structure types on FL or age was more complicated. The FLs were similar between artificial reefs and platforms for both immature and mature fish (Figure 5A3), with both the 50% CrI and the 95% CrI of the coefficient for artificial reefs overlapping zero. Ages were similar between the artificial reefs and platforms for mature fish (Figure 5B3; 95% CrI overlapped zero), while

immature fish at the artificial reefs were older than those at the platforms (Figure 5B3; positive 95% CrI). Furthermore, the age difference between mature fish at artificial reefs and those at platforms was smaller than the age difference in immature fish (Figure 5B3; negative 95% CrI for mature versus immature).

The FLs or ages for immature fish were similar between rigs-to-reefs and platforms (Figure 5A4, B4) and between rigs-to-reefs and artificial reefs (Figure 5A5, B5), since the analysis showed that the 95% CrIs of the coefficients of rigs-to-reefs and the difference between rigs-to-reefs and artificial reefs for immature fish contained zero. In contrast, the mature fish at rigs-to-reefs were larger and

TABLE 1. Comparisons of hierarchical Bayesian models predicting habitat utilization by mature and immature female Red Snapper based on FL and age. The “x” indicates that the specified parameter varied by maturity. Models presented in bold are the best models selected for FL and age based on predictive posterior loss (PPL) and the deviance information criterion (DIC;  $\beta_0$  = intercept, also representing FL or age at platforms without accounting for depth;  $\beta_1$  = coefficient for depth;  $\beta_2$  = coefficient for artificial reefs, representing the difference in FL or age between artificial reefs and platforms;  $\beta_3$  = coefficient for rigs-to-reefs, representing the difference in FL or age between rigs-to-reefs and platforms).

Model number	$\beta_0$	$\beta_1$	$\beta_2$	$\beta_3$	DIC	PPL
<b>FL models</b>						
1	x	x	x	x	6,688	3,695,901
2					6,767	4,225,839
3	x				6,692	3,733,999
4		x			6,720	3,907,700
5			x		6,743	4,061,086
6				x	6,761	4,174,803
7	x	x	x		6,692	3,727,085
<b>8</b>	<b>x</b>	<b>x</b>		<b>x</b>	<b>6,687</b>	<b>3,692,563</b>
9	x		x	x	6,692	3,723,338
10		x	x	x	6,721	3,904,711
11	x	x			6,691	3,723,488
12	x		x		6,693	3,738,475
13	x			x	6,690	3,718,621
14		x	x		6,721	3,912,543
15		x		x	6,720	3,903,986
16			x	x	6,737	4,010,016
<b>Age models</b>						
1	x	x	x	x	1,441	728.1477
2					1,481	782.6005
3	x				1,446	737.7851
4		x			1,454	747.1644
5			x		1,479	778.6424
6				x	1,473	770.9214
7	x	x	x		1,444	732.8323
8	x	x		x	1,443	731.6640
<b>9</b>	<b>x</b>		<b>x</b>	<b>x</b>	<b>1,439</b>	<b>727.4169</b>
10		x	x	x	1,451	742.6053
11	x	x			1,448	739.1829
12	x		x		1,442	731.4386
13	x			x	1,442	731.6420
14		x	x		1,452	743.8338
15		x		x	1,452	743.6110
16			x	x	1,471	766.7888

older than those at platforms (Figure 5A4, B4) or at artificial reefs (Figure 5A5, B5) on average. The difference in FL or age was larger for the mature fish than for the immature fish between rigs-to-reefs and platforms (Figure 5A4, B4; positive 95% CrIs for mature versus immature) and between rigs-to-reefs and artificial reefs

(Figure 5A5, B5; positive 95% CrIs for mature versus immature).

In more detail, without accounting for individual variances ( $\sigma^2$  in equations 2 and 3) or the effect of depth, there was a 95% probability that the mean FL for immature fish at the platforms ranged from 234.28 to 283.87 mm, while the mean FL for mature fish at the platforms ranged from 325.20 to 348.33 mm (Table 2). As such, there was a 95% probability that mature fish were 50.11–105.30 mm longer than immature fish at the platforms. For both mature and immature fish on the artificial reefs, there was a 95% probability that the mean FL difference between artificial reefs and platforms was 9.84 mm shorter to 8.98 mm longer (Table 2). Since the 95% CrI overlapped zero (Figure 5A3), FLs were not considered to differ between the platforms and artificial reefs. Furthermore, the mean FL for immature fish at the rigs-to-reefs likely did not differ from the mean FL at the platforms (Figure 5A4), while the mean FL for mature fish was 42.65–99.72 mm longer at the rigs-to-reefs than at the platforms (Table 2). Similarly, there was a 95% probability that the difference in mean FL of mature fish between rigs-to-reefs and platforms was 8.19–178.73 mm greater than the difference in mean FL of immature fish between these two structure types (Table 2). Comparing rigs-to-reefs with artificial reefs, the mean FL for immature fish likely did not differ (Figure 5A5), while the mean FL for mature fish was 42.02–101.19 mm longer at the rigs-to-reefs than at the artificial reefs (Table 2). Therefore, the difference in mean FL between rigs-to-reefs and artificial reefs was much larger for the mature fish than for the immature fish. The 95% CrI for the depth parameter for immature fish was 1.30–3.05 mm, while the 95% CrI for mature fish was smaller than that (Table 2). Indeed, the increase in FL per unit of depth was 0.0749–1.952 mm lower for mature fish than for immature fish, indicating that immature fish need to grow more or faster in order to utilize deeper habitats compared to mature conspecifics.

Similarly, we also used posteriors to examine habitat selection in detail based on age between mature and immature fish. Without accounting for individual-scale variance or depth, there was a 95% probability that the mean age for immature fish on the platforms ranged from 1.24 to 1.65 years, while the mean age for mature fish on the platforms ranged from 1.89 to 2.20 years, with a 95% probability that mature fish were 0.396–0.813 years older than immature fish on the platforms (Table 3). There was a 95% probability that immature fish on the artificial reefs were 0.169–0.758 years older than immatures at the platforms (Table 3), whereas age was unlikely to differ for mature fish between artificial reefs and platforms (Figure 5B3). Furthermore, the mean age for immature fish at the rigs-to-reefs likely did not differ from mean age at the platforms (Figure 5B4), while mature fish at the rigs-to-reefs were 0.432–1.44 years older than those at the platforms on average (Table 3).

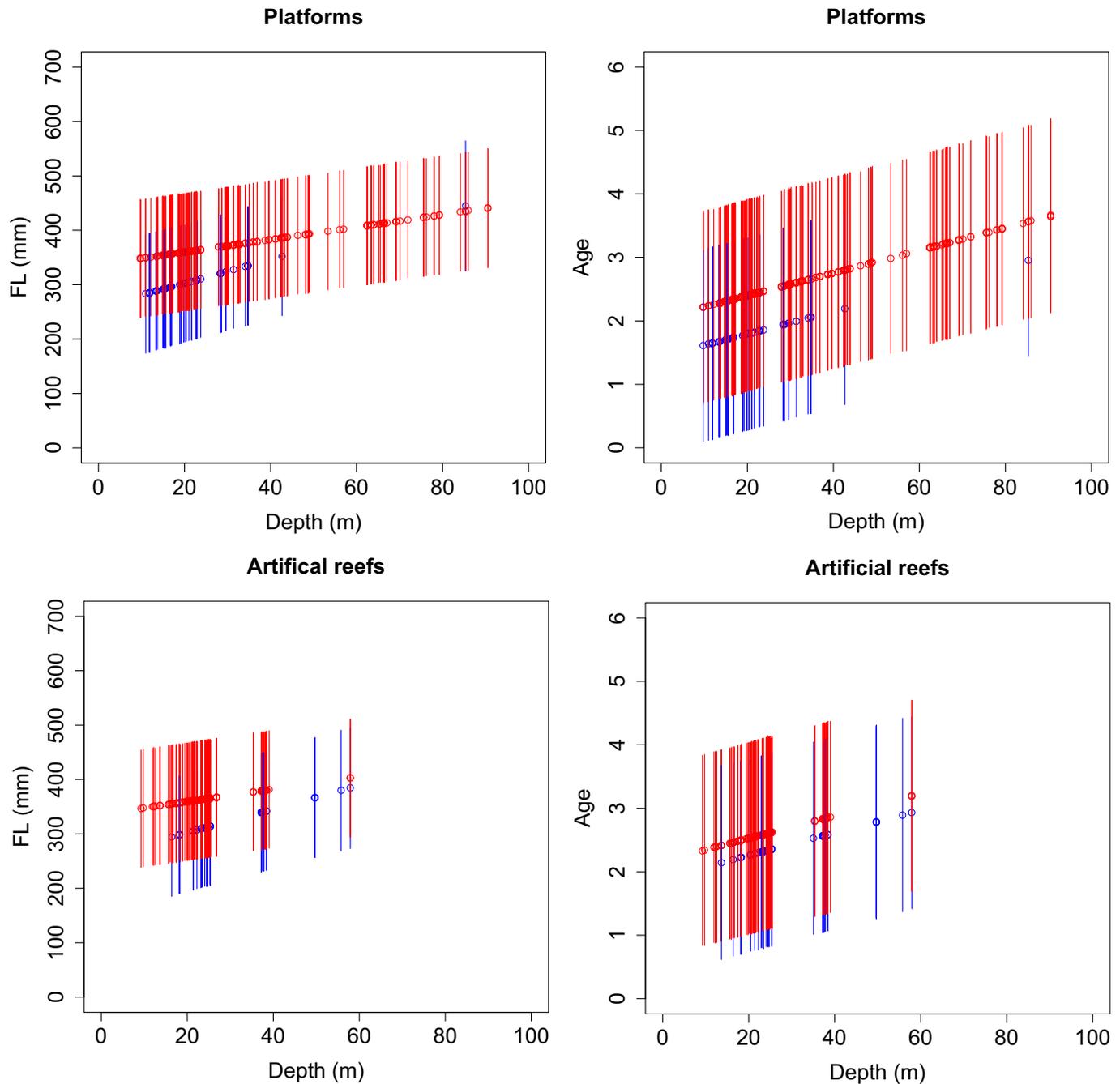


FIGURE 4. Plots of Red Snapper FL (mm) versus depth (m; left panels) and age (years) versus depth (right panels) at platforms and artificial reefs. The lines show 95% CrIs of predicted FL or age for immature (blue) and mature (red) females. The dots denote the medians of the predictive posteriors of FL or age for immature (blue) and mature (red) females. (Figure generated in the R base package.)

Comparing rigs-to-reefs with artificial reefs, the mean age for immature fish likely did not differ (Figure 5B5), while the mean age for mature fish was 0.293–1.255 years greater at the rigs-to-reefs than at artificial reefs (Table 3). Therefore, the difference in mean age between rigs-to-reefs and artificial reefs was greater for the mature fish than for immature fish. The 95% CrI for the parameter of depth for

both immature fish and mature fish was 0.0141–0.0215 year (Table 3), indicating that both immature and mature fish needed to attain a similar age per depth in order to utilize deeper habitats.

In summary, the relationship to FL for both depth and rigs-to-reefs differed between mature and immature fish, whereas the relationships of all three structure types to

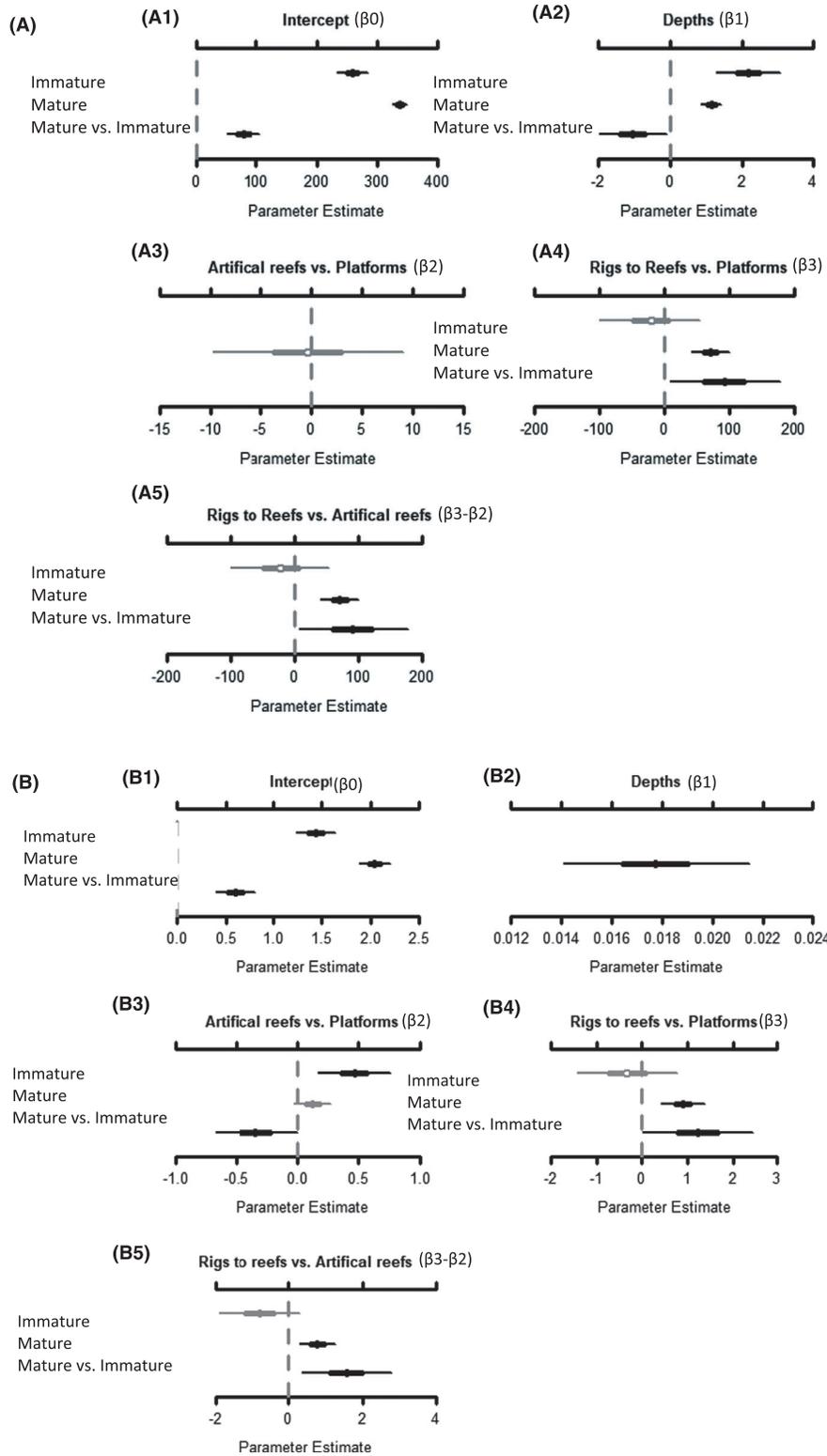


FIGURE 5. Credible intervals (CrIs) for the parameters in (A) the best FL model (FL model 8 in Table 1) and (B) the best age model (age model 9 in Table 1) for female Red Snapper.  $\beta_0$  denotes the intercept,  $\beta_1$  denotes the coefficient for depth,  $\beta_2$  denotes the coefficient for artificial reefs (representing the difference in FL or age between artificial reefs and platforms),  $\beta_3$  denotes the coefficient for rigs-to-reefs (representing the difference in FL or age between rigs-to-reefs and platforms), and “ $\beta_3-\beta_2$ ” denotes the difference in FL or age between rigs-to-reefs and artificial reefs. The thin line shows the 95% CrI, and the thick line shows the 50% CrI. The gray line with an open dot indicates that both the 50% CrI and the 95% CrI contain zero, the gray line with a solid gray dot indicates that the 50% CrI does not contain zero while the 95% CrI does, and the black line with a solid black dot indicates that neither the 50% CrI nor the 95% CrI contains zero. (Plot generated using the MCMCvis package [Youngflesh 2018].)

TABLE 2. Summary of posteriors of the parameters for a hierarchical Bayesian FL model (FL model 8 in Table 1) predicting habitat utilization by mature and immature female Red Snapper ( $\beta_0$  = intercept, also representing mean FL at platforms without accounting for depth;  $\beta_1$  = coefficient for depth;  $\beta_2$  = coefficient for artificial reefs, representing the difference in FL between artificial reefs and platforms;  $\beta_3$  = coefficient for rigs-to-reefs, representing the difference in FL between rigs-to-reefs and platforms). The numbers in brackets represent immature fish ([1]) or mature fish ([2]). If there is no index for a particular coefficient, then that coefficient does not vary by maturity status.

Parameter	Mean	Median	2.5% quantile	97.5% quantile
Platform [immature] ( $\beta_0$ [1])	259.06	259.06	234.28	283.87
Platform [mature] ( $\beta_0$ [2])	336.77	336.80	325.20	348.33
Platform, mature vs. immature	77.71	77.76	50.11	105.30
Depth [immature] ( $\beta_1$ [1])	2.18	2.18	1.30	3.05
Depth [mature] ( $\beta_1$ [2])	1.15	1.15	0.860	1.43
Depth, mature vs. immature	-1.03	-1.03	-1.96	-0.0749
Artificial reef vs. platform ( $\beta_2$ )	-0.43	-0.43	-9.84	8.98
Rigs-to-reef vs. platform [immature] ( $\beta_3$ [1])	-21.69	-21.22	-101.24	55.07
Rigs-to-reef vs. platform [mature] ( $\beta_3$ [2])	71.11	71.13	42.65	99.72
Rigs-to-reef vs. platform, mature vs. immature	92.80	92.43	8.19	178.73
Rigs-to-reef vs. artificial reef [immature] ( $\beta_3$ [1]- $\beta_2$ )	-21.26	-20.80	-100.88	50.08
Rigs-to-reef vs. artificial reef [mature] ( $\beta_3$ [2]- $\beta_2$ )	71.54	71.57	42.02	101.19
Rigs-to-reef vs. artificial reef, mature vs. immature	92.80	92.43	8.19	178.73

TABLE 3. Summary of posteriors of the parameters for a hierarchical Bayesian age model (age model 9 in Table 1) predicting habitat utilization by mature and immature female Red Snapper ( $\beta_0$  = intercept, also representing mean age at platforms without accounting for depth;  $\beta_1$  = coefficient for depth;  $\beta_2$  = coefficient for artificial reefs, representing the difference in age between artificial reefs and platforms;  $\beta_3$  = coefficient for rigs-to-reefs, representing the difference in age between rigs-to-reefs and platforms). The numbers in brackets represent immature fish ([1]) or mature fish ([2]). If there is no index for a particular coefficient, then that coefficient does not vary by maturity status.

Parameter	Mean	Median	2.5% quantile	97.5% quantile
Platform [immature] ( $\beta_0$ [1])	1.14	1.44	1.24	1.64
Platform [mature] ( $\beta_0$ [2])	2.04	2.04	1.89	2.20
Platform, mature vs. immature	0.61	0.605	0.396	0.813
Depth ( $\beta_1$ )	0.0178	0.0178	0.0141	0.0215
Artificial reef vs. platform [immature] ( $\beta_2$ [1])	0.464	0.465	0.169	0.758
Artificial reef vs. platform [mature] ( $\beta_2$ [2])	0.127	0.128	-0.0209	0.275
Artificial reef vs. platform, mature vs. immature	-0.337	-0.337	-0.672	-0.00168
Rigs-to-reef vs. platform [immature] ( $\beta_3$ [1])	-0.333	-0.337	-1.44	0.774
Rigs-to-reef vs. platform [mature] ( $\beta_3$ [2])	0.901	0.902	0.432	1.37
Rigs-to-reef vs. platform, mature vs. immature	1.23	1.24	0.0238	2.44
Rigs-to-reef vs. artificial reef [immature] ( $\beta_3$ [1]- $\beta_2$ [1])	-0.797	-0.800	-1.91	0.307
Rigs-to-reef vs. artificial reef [mature] ( $\beta_3$ [2]- $\beta_2$ [2])	0.774	0.774	0.293	1.26
Rigs-to-reef vs. artificial reef, mature vs. immature	1.57	1.58	0.362	2.78

age differed by maturity. Maturity did not play a role in how age increased with depth and FL differences (or a lack of differences) between artificial reefs and platforms. Overall, there were no consistent responses to depth and/or artificial reef type based on age or FL for either immature or mature fish. However, immature fish apparently needed to grow faster than mature fish to take advantage of deeper habitats, although these larger immature fish were not older than the mature fish.

## DISCUSSION

Ascertaining the differences in how immature and mature Red Snapper use habitat facilitates an understanding of whether reproductive capability determines how these fish interact with their environment. This information can provide guidance for future management of GOM Red Snapper stocks related to reproductive potential, which is important since there is a large overlap in FL and age between immature and mature fish in the

north-central GOM. Differences in maturity status could help to explain habitat use beyond simply looking at fish size and age.

We hypothesized that there would be a difference in the way immature and mature fish use artificial habitat when they are of similar age and size, and our analyses showed that this is true depending on the habitat and depth. Although previous studies have established that length and age are factors in Red Snapper habitat use (Franks and VanderKoooy 2000; Mikulas and Rooker 2008; Gallaway et al. 2009; Ajemian et al. 2015; Leontiou et al. 2021), we found that maturity also plays a role in habitat use among similar-sized fish. Based on our models, we generated four key findings as discussed below.

We found that both FL and age increased with increasing depth for both immature and mature female Red Snapper. Although we (Leontiou et al. 2021) previously found that the effect of depth on FL or age did not differ between mature and immature females, those data were based on fish of all sizes and ages. Our current study showed that although the increase in age is the same between maturity states, the rate of increase in FL with depth was greater in the immature fish. As was expected from previous work (Stanley and Wilson 2003; Wilson et al. 2006; Gallaway et al. 2009), size does make a difference with depth usage. The lack of difference in age with depth by maturity class is not surprising given the wide range of FLs within any given age and the relatively low probabilities of predicting age from FL for ages 2–5 (SEDAR 2018), which encompasses the subset of fish we used in our analyses. However, our analyses showed that at both platforms and artificial reefs, immature fish must grow at a greater rate than mature fish in order to reach a size at which they might be present at deeper depths. This suggests that immature fish are putting more energy into somatic growth—as opposed to reproductive output—to inhabit deeper depths at both structure types. This could be due to greater safety on structures, where predation is less of a threat (Workman et al. 2002).

The comparison between artificial reefs and platforms indicated no difference in FLs of immature and mature fish, but there was a difference for age. Immature fish on artificial reefs were older than those on platforms, while mature fish were the same age on both structure types, indicating differentiation in the way they use habitat outside of the framework of age. Previous research (Karnauskas et al. 2017) found older Red Snapper on artificial reefs than on platforms, but that study did not differentiate the maturity status of the fish. Our models suggest that this age difference is driven by immature Red Snapper. Other studies (Workman et al. 2002; Patterson et al. 2005; Gallaway et al. 2009; Ajemian et al. 2015) have suggested that Red Snapper move from low-complexity structure as juveniles to more complex/taller structures until they reach

maturity and then move off structure for open habitat. Our results indicate that mature and immature fish are both using artificial structures and that age may be less of a factor in that regard than originally thought. Importantly, the oldest fish in our data set were 5.3 years— younger than the age at which the literature suggests Red Snapper begin to move off structure (8 years; Gallaway et al. 2009).

When we compared rigs-to-reefs to both platforms and artificial reefs, there was a difference in FL and age for immature and mature fish. For mature fish, both FL and age were greater at rigs-to-reefs than at platforms and artificial reefs. For immature fish, there was no difference in FL or age between these structure types, which could be attributed to the small sample size of immature females at the rigs-to-reefs. The small sample size of immature fish at rigs-to-reefs, which was likely due to fewer immature fish using this structure rather than to sampling bias, decreases confidence in our predictions, but even with the larger variance we can differentiate between mature and immature individuals for FL and age with structures. The difference relies on the much smaller variance related to mature fish but still accurately reflects that there is a difference in age and FL between structures based on maturity class. Previous reports of Red Snapper captured on rigs-to-reefs suggested that larger fish inhabit these structures and that most of these fish are mature (Alexander 2015; Downey et al. 2018).

Despite their overlap in size and age, mature and immature fish showed distinct differences in the structures they inhabited. Mature fish did not differentiate between artificial reefs and platforms, but both FL and age were predicted to be larger at rigs-to-reefs compared to artificial reefs and platforms based on our models. In contrast, the oldest immature fish were predicted to occur on artificial reefs compared to platforms, despite unbiased sampling in this study. Since high catch rates on artificial reefs have been documented for Red Snapper up to age 5 (Karnauskas et al. 2017), the occurrence of older immature fish on artificial reefs leaves them vulnerable to overharvest due to the high fishing pressure on these structures. Although fishers may be targeting mature fish, these older immature fish are also being caught. Harvest of legal-sized but immature Red Snapper on the numerous artificial reefs in the northern GOM could negatively affect population size and the recovery of the species.

Previous studies have suggested that habitat use is predicted on size and age and have thus explained why differently sized Red Snapper use different habitat types (Workman et al. 2002; Patterson et al. 2005; Gallaway et al. 2009; Ajemian et al. 2015). Although immature fish are typically smaller than mature individuals, we have shown here that there may be some habitat segregation based on maturity rather than size or age, particularly

when immature and mature Red Snapper have a large, overlapping size range and/or age range, as was shown here and previously (SEDAR 2018). Glenn et al. (2017) also found habitat segregation based on maturity, with more immature female Red Snapper on shallow artificial reefs compared to a higher percentage of reproductively active fish on deeper natural reefs. Although speculation on differential utilization of artificial habitats by reproductive fish is beyond the scope of this work, our results provide an indication that this is a fruitful area for additional research.

Our results suggest potential management implications regarding occurrence of maturity on differing artificial structures due to the large overlaps in size and age between mature and immature Red Snapper. Our models indicate that larger fish captured at artificial reefs (within the size range [290–500 mm FL] and age range [1–4 years] that we analyzed) may be immature, especially in the deeper depths, and should not be kept by anglers regardless of fish size. Therefore, future studies on the placement and creation of artificial reef structures with the aim of aiding in the recovery of Red Snapper in the GOM should consider maturity as a factor in decision making. Future studies evaluating the contribution of artificial structures to fish production as related to maturity status would provide even more information as to how these structures can aid in the continued recovery of the GOM Red Snapper population.

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## SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.