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ABSTRACT

Red Snapper (*Lutjanus campechanus)* is a popular reef-associated fish species in the northern Gulf of Mexico (GOM) that supports both commercial and recreational fisheries. In this region, there is a large overlap in fork length (FL, 90%) and age (93%) range between mature and immature females. Therefore, here we investigate how age and FL of mature and immature female Red Snapper vary by artificial reef type and depth. Red Snapper (n = 695) were sampled using vertical long lines from March or April through November of 2016–2018 off the coast of Mississippi at different artificial structure types (platforms, artificial reefs, rigs-to-reefs) and depths (shallow, < 20 m; mid, 20–49 m; deep, 50–100 m). To investigate habitat use of mature and immature fish respectively, we developed linear mixed-effects models. For both immature and mature fish, FL and age increased significantly with depth. Immature fish captured at artificial reefs were older than those captured at platforms, and mature fish were older and had longer FL at rigs-to-reefs than platforms and artificial reefs. The effect of depth on FL or age did not differ between mature and immature fish while the effect of structure types did. Structure types were important to predict FL for mature fish, but not for immature fish. In addition, the differences in age between rigs-to-reefs and both platforms and artificial reefs were significantly larger in mature fish than in immature fish. Larger and older mature females are found at deeper depths where fishing pressure is lower, while smaller and younger, immature fish are most often found in shallower, reef-based areas where pressure is highest. These spatial differences in maturity can help inform management regulations for the species.

1. Introduction

Red Snapper (*Lutjanus campechanus*) is a reef-associated species found throughout the Gulf of Mexico (GOM) and along the eastern coast of North, Central and northern South America (NOAA, 2019). It is a federally and state managed species that supports sizeable commercial and recreational fisheries in the GOM (Goodyear, 1995). Red Snapper have been caught in the GOM since the 1840s (Hood et al., 2007), but decades of overharvesting have led to significant decreases in catch and the implementation of quotas. Management of the species began in 1984 (Goodyear, 1995), and has led to a recent increase in stocks, with commercial and domestic landings for the GOM in 2020 equal to the set annual catch limit of 15.1 million pounds (NOAA, 2020). The most recent stock assessment found that Red Snapper is currently not overfished and not undergoing overfishing in the GOM (SEDAR, 2018)

Red Snapper rely on hard substrate, usually inhabiting natural banks, ridges and reefs (Ajemian et al., 2015; Patterson et al., 2001), but the majority of the GOM is comprised of mud bottom with few areas of natural hard bottom (Shipp and Bortone, 2009). Red Snapper density assessments found that numbers were highest in shelf habitats that provide centimeters to meters of structural complexity (Patterson et al., 2005). The construction of platforms for oil and gas exploration in the GOM has provided structurally complex habitat in areas that otherwise would have none (Downey et al., 2018). Furthermore, the creation of reefs that result from platform decommissioning (i.e., rigs-to-reefs) provides additional deep water habitat for Red Snapper (Ajemian et al., 2015; Shipp and Bortone, 2009; Syc and Szedlmayer, 2012). Stanley and Wilson (1996) found that fish densities were up to 25 times higher within 16 m of a platform than over natural bottom. The construction of a large-scale artificial reef system on the continental slope of Alabama turned that region from an area of low productivity to one of high productivity for GOM Red

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Snapper (Shipp and Bortone, 2009). Mississippi waters contain 82 artificial reefs, 8 rigs-to-reefs and 172 standing oil platforms within 32 km of shore (T. Williams, Mississippi Department of Marine Resources, pers. comm.) that can provide habitat for Red Snapper.

Of all the various life history traits, the timing of sexual maturity is believed to have the most influence on fitness (Stearns, 1992). The age at which a fish reaches maturity determines generation time, and as an extension, the inherent rate of population growth. Sexual maturity data are often used as a biological reference point to determine catch limits that allow female fish to spawn one or more times before being harvested (Caddy and Agnew, 2004). Typically, long-lived fish species tend to reach sexual maturity at an older age than short-lived species. Although Red Snapper have been reported to live to 50 years, one hundred percent of female Red Snapper in the GOM have been reported to reach maturity by four years of age (Brulé et al., 2010; Gallaway et al., 2009; Glenn et al., 2017; Kulaw et al., 2017).

Red Snapper habitat preference appears to depend on fish size and changes with ontogeny (Ajemian et al., 2015; Gallaway et al., 2009), with snapper moving to increasingly complex habitat as they grow (Patterson et al., 2005). Juvenile Red Snapper show a preference for low-relief habitats, such as patches of rubble, squid eggs and single pieces of debris like bottles and cans (Szedlmayer and Conti, 1999; Szedlmayer and Howe, 1997; Workman et al., 2002). They tend to occupy sand and mud areas, where the rubble offers protection from predators, but still enables them to find prey (Wells et al., 2008). As they grow to a size that renders predation less of a threat, Red Snapper begin to favor larger, and more complex structure (Workman et al., 2002). Once they enter the directed fishery, around age two (200–375 mm TL), they begin to recruit to structures meters in height, such as oil and gas platforms, artificial reefs, and wrecks (Patterson et al., 2001; Wells, 2007). Between the ages of two and seven, a large number of Red Snapper can be found on platforms and artificial reefs. Despite the fact that these structures make up just a small portion of high-relief habitat, they tend to provide sanctuary to a high percentage of Red Snapper in this age range (Gallaway et al., 2009; Gitschlag et al., 2003; Karnauskas et al., 2017; Patterson et al., 2001). Once Red Snapper reach around eight years of age, they are frequently found over open habitat as they have reached a size that reduces predation by other fishes (Gallaway et al., 2009).

In addition to their preference for structure, Red Snapper also display preferences for different depths depending on their age and size. Surveys have found that Red Snapper of all ages are most abundant in the GOM at 50–90 m depth (Karnauskas et al., 2017), although smaller fish are usually found in waters less than 50 m (Gallaway et al., 2009). Recent analyses show that both size and age of female Red Snapper increase with increasing depth (Leontiou et al., in review), and that size and depth are important predictors for classifying maturity (Brown-Peterson et al., 2021). Previous studies in the GOM have found stratification in Red Snapper communities on platforms, with smaller, younger fish closer to the surface and larger, older fish in deeper water (Gallaway et al., 2009; Stanley and Wilson, 2000; Wilson et al., 2006).

The objective of this study is to determine how immature and mature female Red Snapper use artificial habitat in the GOM off Mississippi, as information on Red Snapper from this region of the Gulf has historically been lacking. To do this we evaluated the size and age of both immature and mature female fish captured from three different depth strata (shallow, mid, deep) and on three different artificial structure types (platforms, artificial reefs, rigs-to-reefs) using linear mixed-effects models. Understanding habitat use based on maturity is important for effective management of Red Snapper, and to ensure that females have an opportunity to reproduce prior to capture and removal from the population

2. Methods

2.1. Study area and sample collection

Red snapper were collected in the north-central (GOM) from April to November 2016, April to October 2017, and March to October 2018. Samples were collected from varying artificial structure types including active petroleum platforms, artificial reefs, and rigs-to-reefs (decommissioned petroleum platforms cut-off and toppled) at three depth strata (shallow, $<$ 20 m; mid, 20–49 m; deep, 50–100 m; Fig. 1). Petroleum platforms have been deployed in the north-central GOM from 1947 to the present time, with the mean age of platforms estimated to be 16–18 years old (Pulsipher et al., 2001). Rigs-to-reefs were first created off Mississippi after 1999, despite the presence of a relatively large number of platforms in the offshore waters prior to that time (Dauterive, 2000). Artificial reefs consisted of a variety of substrates including rubble, concrete culverts, concrete pyramids, fish balls, and submerged vessels. These ranged in height from 0.7 to 11.3 m above the bottom and were deployed between 1978 and 2015, although the majority were deployed between 2003 and 2010 (Mississippi Department of Marine Resoures, 2016). Only 9.7% of the 227 artificial reefs in Mississippi waters were deployed prior to 2000, and these were all either submerged vessels or rubble (Mississippi Department of Marine Resoures, 2016). Petroleum platforms were sampled at all depth strata, artificial reefs were sampled in the shallow and mid strata, and rigs-to-reefs occurred in the deep strata only and ranged in height from 7.4 to 50.0 m above the bottom. Each month, 17 randomly stratified sites were sampled that included three stations in one reef permit zone from both the shallow and mid depth strata, and one station at each of two rigs-to-reefs sites in deep water. Additional monthly sampling included a station at three separate platforms per depth zone. Site location (latitude and longitude) and depth were recorded for each station, and many sites were sampled more than once over the three-year sampling period. Sampling was done using vertical lines with 30 baited hooks (Atlantic Mackerel, *Scomber scomber*) per station. Three lines containing one of three hook sizes (8/0, 11/0, and 15/0) were simultaneously deployed for 5 min at each station. Fish were immediately placed on ice, and processed within 24 h of capture.

In the laboratory, standard length (SL, mm), FL (mm), total length (TL, mm), weight (0.01 kg) and sex were recorded for all Red Snapper. At this time, otoliths were also taken to determine age. The entire gonad was removed, weighed to 0.01 g, assigned a macroscopic sex, and a subsample (1 cm^3) was fixed in 10% neutral buffered formalin for a minimum of seven days for histological analysis. Ovarian tissue was then rinsed overnight in running tap water, dehydrated, cleared, embedded in paraffin, sectioned at 4μm and stained with hematoxylin and eosin following standard histological techniques.

2.2. Sample analysis

Microscopic determination of ovarian developmental phase was completed histologically following Brown-Peterson et al. (2011). Fish were considered sexually mature if cortical alveolar or vitellogenic oocytes were the leading oocyte stage, or if there were indications of previous spawning in non-reproductively active females (i.e., atretic oocytes, postovulatory follicles, enlarged blood vessels, muscle bundles).

Sectioned otoliths were used to determine age following VanderKooy (2009). Opaque bands were counted as annuli, and the area between the last annuli and otolith edge – the margin – was measured. Three independent readers determined age and margin codes for each individual fish, and later did a joint reading

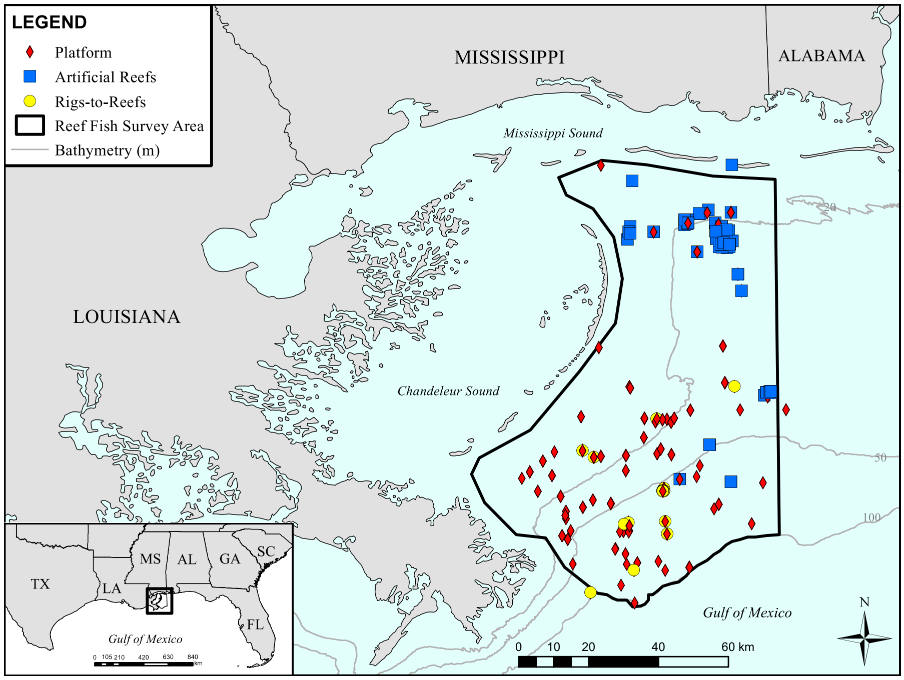

Fig. 1. Sampling area in the north central Gulf of Mexico where Red Snapper were collected from 2016–2018. Depth strata are indicated by contour lines, and structure types indicated by symbols. Each month 17 randomly stratified sites (structures) were sampled but the same sites were sampled more than once over the duration of the study.

to remedy any discrepancies. All ages were then converted to biological age, which was determined based on annulus count, date of collection, mean birthdate, and mean timing of annuli formation. Red Snapper birthdate is defined as June, the middle month of their spawning season (VanderKooy, 2009).

2.3. Statistical analyses

A series of competing linear mixed effects models were constructed to derive how FL or age for both mature and immature fish varied by depth and structure (Tables S1, S2). Fixed effects for analysis of immature or mature females were depth and structure. The independence of the response variables required by traditional regression models was violated due to the fact that multiple fish were caught at the same sites and the same sites could be visited multiple times. The incorporation of random effects not only helps to explain additional variance and interclass correlation, but also saves degrees of freedom that would otherwise be used for every level of each random variable (Wu et al., 2017). We selected the best model based on Akaike Information Criterion (AIC), an estimator of the expected Kullback discrepancy between the true model and a fitted candidate model (Burnham and Anderson, 2004). The difference of AIC can be used as a guideline for model selection, with the best model indicated by the lowest AIC. If the difference between the AIC value of two models was less than two, then the models were considered to have similar prediction capabilities.

The first step in model selection was to determine whether random effects improved model predictions, and if so, the optimum random effects to use. Models with all the fixed effects (full fixed effects model) without random effects vs. the models with different combinations of random effects (month or site location or both) were compared to select the best random effect(s) based on lowest AIC using restricted maximum likelihood. Then the models with unique fixed effects structures nested within the full fixed effects model, all having the same optimum random effect(s) derived from the previous step, were compared. The best model and optimum fixed effect(s) were identified based on the lowest AIC using maximum likelihood. The models were then refit using restricted maximum likelihood to estimate the parameters (Zuur et al., 2009). The models were implemented using lmerTest package in R (https://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf).

Based on the final models of FL or age for immature and mature females respectively, we further compared whether the impact of depth or structure on FL/age differed between mature and immature females. We calculated 95% confidence intervals of the coefficient for depth and contrasts of different structures in each model, and then determined whether the intervals of depth or structure type overlapped between mature and immature fish models. Overlapping intervals indicated lack of difference in these relations between mature and immature females.

3. Results

3.1. Sample collection

Six hundred ninety-five female Red Snapper were collected during the survey. Of these, 121 were immature and 574 were mature. Immature fish ranged in size from 168 to 525 mm FL and mature from 232 to 795 mm FL, and there was a 90% overlap in FL between the two maturity groups (Fig. 2, top). Age ranged from 0.8 to 5.3 years for immature fish and 0.9 to 22.3 years for mature, and there was a 93% overlap in age between immature and mature fish (Fig. 2, bottom). Immature and mature fish were collected during all months of the sampling season (March–November), at all three depths, and on all three structure types. The majority of fish, regardless of maturity, were found on platforms (60%) and at mid-depth (56%).

3.2. Immature fish

The majority of immature Red Snapper were found at mid-depths (61%), and the fewest at deep depths (4%). They were also

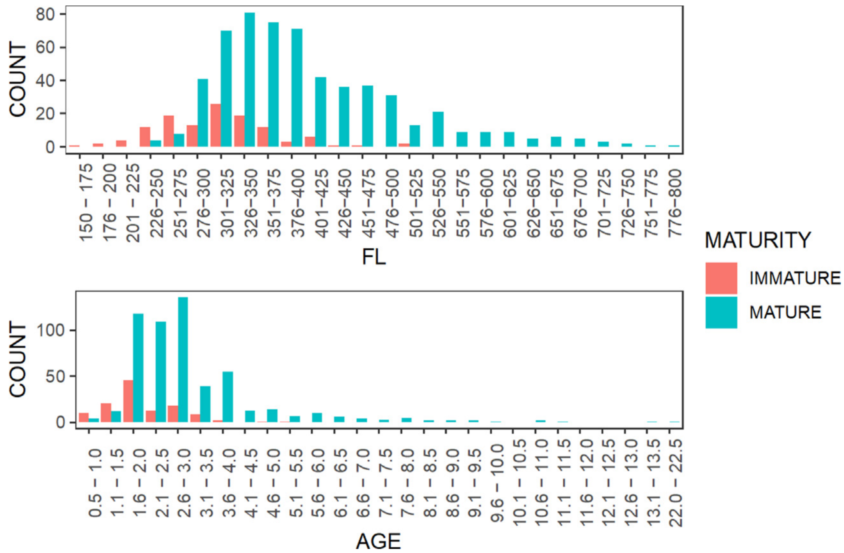

Fig. 2. Distribution of fork length (FL, top) and age (bottom) for immature and mature female Red Snapper collected from 2016–2018 in the north-central Gulf of Mexico.

Table 1
Competing linear mixed effect models for immature female Red Snapper in the north-central Gulf of Mexico describing the effect of depth and structure on size (FL) and age.

Response variable	Fixed effects included in the model	Estimate	Standard error of estimate	*P*-value	Ratio of variance of random effect to residual
Model 1					16.4% (location)
FL	Depth	0.617	0.1528	2.56×10^{-4}	
Model 2					
Age	Depth	0.0063	0.0018	7.98×10^{-4}	
	Artificial reefs	0.4401	0.1448	2.93×10^{-3}	
	Rigs-to-reef	−0.4865	0.5611	0.388	

caught in the greatest amounts on platforms (58%) and the least on rigs-to-reefs (2%).

Different linear and linear mixed-effects models were compared using AIC to determine how FL and age related to depth and structure type for immature fish (Table S1). The best model for FL has depth as the fixed effect, and site location as the random effect. The variance for the random intercept (between-site variance) was 16.4% of the residual variance (within-site variance) (Table 1). The inclusion of random effects in the model accounts for additional variance that is not explained by the fixed effects; here, 16.4% (1+16.4%) = 14% of total variance not explained by depth (also called interclass correlation) that corrects the p-values of the model. The best model showed that for immature fish, FL increased with depth ($p = 0.0002$) but structure type was not important in explaining variation (Table 1, Fig. 3 A, B, C). For age, the best model is linear and includes both depth and structure as the predictor variables without a random effect. As with length, age increased with depth ($p = 0.0008$, Fig. 3D, E, F). This model also found that immature fish captured at artificial reefs were older than those captured at platforms (Tukey's pairwise comparison, $p = 0.0082$), but not at rigs-to-reefs (Tukey's pairwise comparison, $p = 0.21$; Fig. 3D, E, F) assuming depths are the same. When comparing platforms to rigs-to-reefs, there was no significant difference in ages (Tukey's pairwise comparison, $p = 0.66$).

3.3. Mature fish

Most mature fish were also found at mid-depths (54%), with a relatively similar percentage at mid (24%) and deeper depths (22%). As with immature, the majority of mature Red Snapper were found on platforms (60%) and the fewest on rigs-to-reefs (6%).

Models were assessed for determining differences in FL and age across depth strata and structure type (Table S2). The best model for FL had depth and structure type as fixed effects, and location and month as random effects (Table 2). As with immature fish, FL increased with increasing depth ($p = 1.33 \times 10^{-11}$, Fig. 3G, H, I). Further pairwise comparisons determined that for mature fish, FL is larger at rigs-to-reefs than both platforms (Tukey's pairwise comparison, $p = 0.0015$) and artificial reefs (Tukey's pairwise comparison, $p = 0.0100$). There was no difference between FL when comparing platforms and artificial reefs (Tukey's pairwise comparison, $p = 0.992$; Fig. 3G, H, I).

For age, the best model used depth and structure as fixed effects and location as the random effect (Table 2). In mature fish, age increased with increasing depth ($p = 3.98 \times 10^{-13}$, Fig. 3J, K, L). Tukey's post-hoc pairwise comparisons showed that fish on rigs-to-reefs were older than those on platforms ($p < 0.001$) and artificial reefs ($p = 0.0026$), but there was no difference in age between platforms and artificial reefs ($p = 0.3090$) assuming depth is the same.

3.4. Immature vs. mature fish

As FL and age related to depth and/or structure types for both mature and immature fish, we took a further step to compare whether the relations with depths or structures differed between maturity groups. The results show that the effect of depth on FL or age did not differ between mature and immature fish due

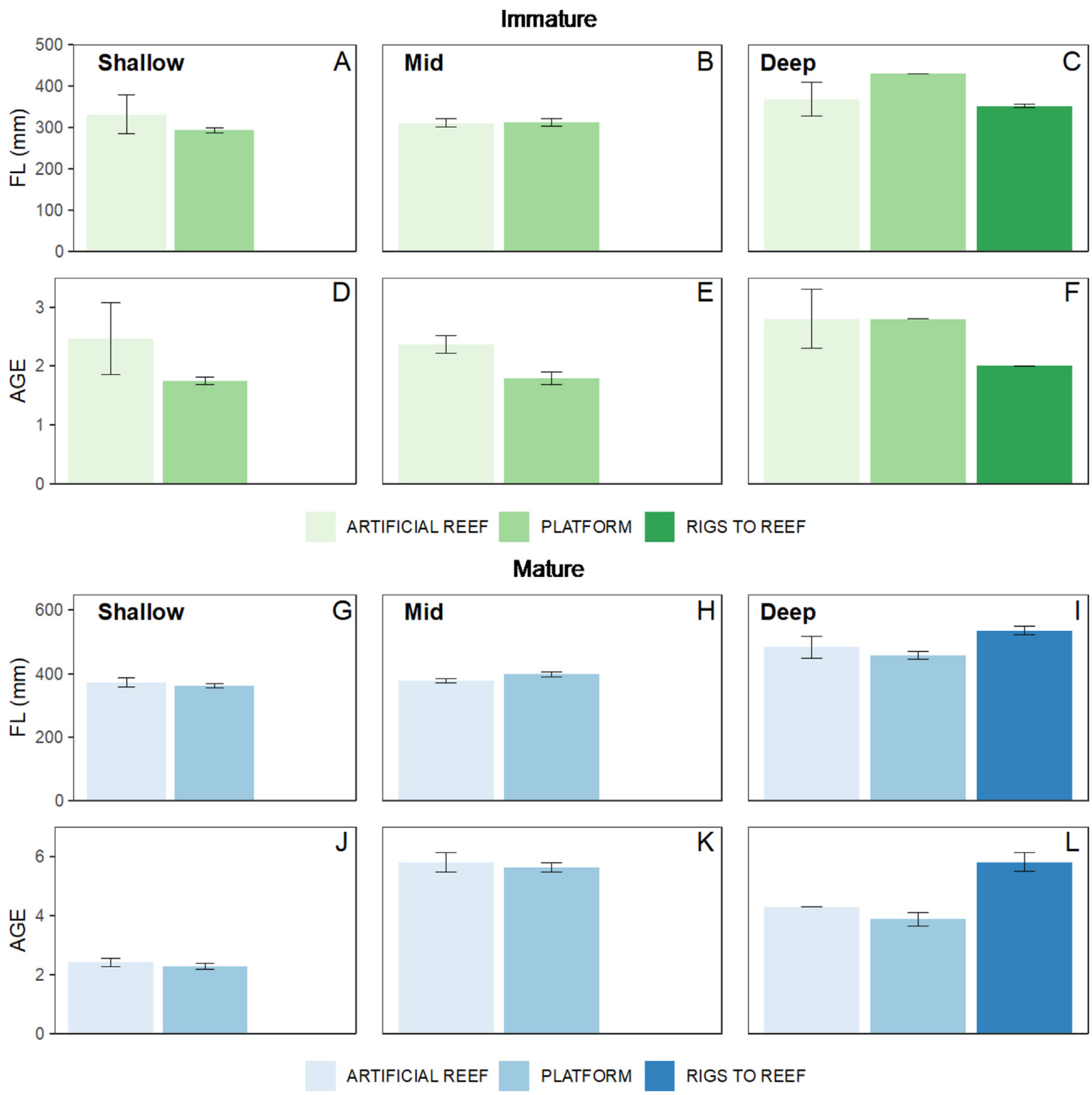

Fig. 3. Mean (± SE) fork length (FL) and age for immature (top, green) and mature (bottom, blue) female Red Snapper by structure type and depth in the north-central Gulf of Mexico. A, D, G, and J: shallow (<20 m). B, E, H, and K: Mid depth (20–49 m). C, F, I, and L: Deep (50–100 m).. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Competing linear mixed effect models for mature female Red Snapper in the north-central Gulf of Mexico describing the effect of depth and structure on size (FL) and age.

Response variable	Fixed effects included in the model	Estimate	Standard error of estimate	*P*-value	Ratio of variance of random effects to residual
Model 1					12.6% (location); 3.0% (month)
FL	Depth	0.5822	0.07537	1.33×10^{-11}	
	Artificial reefs	2.0001	15.9847	0.901	
	Rigs-to-reef	94.3169	24.8883	4.37×10^{-4} 0.000437	
Model 2					6.13% (location)
Age	Depth	0.01005	0.001236	3.98×10^{-13}	
	Artificial reefs	0.3747	0.2412	0.131	
	Rigs-to-reef	2.100	0.3863	1.92×10^{-6}	

to the overlapping 95% confidence intervals of the coefficients for depths (Table 3). However, structure types showed different effects on length or age between immature fish and mature fish. First, structure types were important to predict FL for mature fish, but not for immature fish as the FL model for immature fish did not include structure types (Table 1). In addition, the differences of the age between rigs-to-reefs and platforms, and between rigs-to-reefs and artificial reefs, were significantly larger in mature

Table 3
Comparison of the relations between fork length/age and depth/structure types in immature vs. mature female Red Snapper in the north-central Gulf of Mexico. Numbers in bold indicate non-overlapping 95% confidence intervals.

Response variable	Coefficient for	Maturity	Estimate	Lower 2.5 percentile	Upper 2.5 percentile
Fork length	Depth	Immature	0.617	0.308	0.926
		Mature	0.582	0.433	0.732
Age	Depth	Immature	0.00631	0.00268	0.00994
		Mature	0.0100	0.00760	0.0125
	Artificial reef – platform	Immature	0.440	0.0963	0.784
		Mature	0.375	−0.258	1.010
	Rigs-to-reefs – platform	Immature	−0.487	**−1.819**	**0.846**
		Mature	2.100	**1.130**	**3.070**
	Rigs-to-reefs – artificial reef	Immature	−0.927	**−2.228**	**0.375**
		Mature	1.725	**0.584**	**2.870**

fish than in immature fish based on the non-overlapping 95% confidence intervals (highlighted, Table 3). Since few immature fish were captured at rigs-to-reefs sites (n = 2), these results may be biased by sample size.

4. Discussion

Determining how immature and mature Red Snapper use differing depths and structures makes it possible to examine whether reproductively capable fish (i.e., sexually mature) use habitat differently than reproductively incapable fish (i.e., sexually immature), which in turn can help to better guide future management decisions for Red Snapper stocks in the GOM. This is particularly important as there is a large overlap in both age and FL between immature and mature fish – in contrast to what is generally thought to be true, that mature fish are larger and older than immature fish – and differences in maturity status may help explain habitat use beyond simply looking at fish size or age. Furthermore, data from this study are the first to document Red Snapper habitat use during a time of increasing abundance, since the GOM population was reclassified as recovering in 2018 (SEDAR, 2018); previous studies were done prior to 2012 when the Red Snapper stock was considered overfished (SEDAR, 2013).

While our findings support those of previous studies in other parts of the GOM (Gallaway et al., 2009; Karnauskas et al., 2017; Patterson et al., 2005), which show larger, older fish more prevalent at deeper depths, our modeling approach allowed a more granular analysis and greater clarification of spatial and depth distributions of immature and mature females in the GOM. For example, we found that depth, but not structure type, significantly explained differences in the length of immature females. For age, both depth and structure type explained the distribution of immature fish, with the oldest immature fish found on artificial reefs. While Karnauskas et al. (2017) also found older Red Snapper on artificial reefs than on platforms, their study did not differentiate between maturity, and focused on comparing natural reefs to either artificial reefs or platforms rather than comparing artificial structures to each other. However, recent Bayesian analyses of our data also found that immature females were older at artificial reefs than platforms (Leontiou et al., in review); the results presented here confirm this age difference among structures. Our results in the GOM are in contrast to those from the southeastern Atlantic, where size and age of young (predominately immature) fish did not vary by depth (Lowerre-Barbieri et al., 2015).

For mature Red Snapper, both depth and structure type explained differences in length and age. This concurs with Bayesian analysis that showed both FL and age of mature fish were greater at rigs-to-reefs than at platforms or artificial reefs (Leontiou et al., in review). Previous reports of larger and older mature Red Snapper being most common in waters > 60 m and on rigs-to-reefs sites (Ajemian et al., 2015) are supported by our modeling results. Although our models were not designed to show during which months larger, older females use various depths and types of artificial structures, the majority of our samples were taken during the May through August Red Snapper spawning season (Brown-Peterson et al. 2019) when fish were reproductively active. Spawning capable females have previously been reported from artificial structures at various depths (Alexander 2015, Glenn et al., 2017; Downey et al., 2018).

Our analyses contribute to understanding habitat use for immature vs. mature female Red Snapper and highlight differences between maturity types. Although age and FL increased significantly with depth for both mature and immature fish, we found that structure type is important to predict FL for mature fish but not for immature fish. Interestingly, random forest analysis indicated that the best predictors of maturity status for female Red Snapper are FL, depth, structure height, and month, and that structure type was not an important predictor (Brown-Peterson et al., 2021). Furthermore, previous analyses have shown no difference in FL or age of immature fish among the three structure types, while both FL and age are larger at rigs-to-reefs compared to both platforms and artificial reefs in mature fish (Leontiou et al., in review). We show here that the differences in age between rigs-to-reefs and both platforms and artificial reefs were significantly larger in mature fish than in immature fish. Taken together, the results from these studies suggest that while structure type may not be a good predictor of maturity status, structure type is likely important in predicting both age and FL of mature female Red Snapper.

The majority of immature fish in this study were found in shallow and mid depths (96%) and on artificial reefs (40%), with the oldest immature fish also found on artificial reefs. Most recreational fishing in north-central GOM waters is concentrated on artificial reefs at shallow and mid depths (Ajemian et al., 2015), T. Moncrief, Mississippi Department of Marine Resources, pers. comm.). Although only 11% of the 121 immature fish captured during this study were above the MS state size limit (> 406 mm TL [381 mm FL], (Mississippi Department of Marine Resoures, 2019), these largest immature fish were likely found on artificial reefs with the highest fishing pressure. This size limit was implemented to ensure that when immature fish are captured, they will be released so they may have the opportunity to mature and reproduce. However, catch and release fishing of immature fish leads to unnecessary stress, which in turn could result in death (Campbell et al., 2010). Indeed, Curtis et al. (2015) found that 28% of Red Snapper captured after release suffered barotrauma and immediate or delayed mortality, although smaller fish were less affected than larger fish. However, even if the fish does survive, the stress of capture can still lead to reduced growth and fecundity later in life (Campbell et al., 2010; Davis, 2007). Innovative management ideas, such as closure of some artificial reefs to fishing pressure during portions of the year, could help ensure greater survival of immature Red Snapper, and result in the increase and sustainability of the stock. Since there is an active recreational fishery for Red Snapper throughout the GOM, particularly on artificial habitats in waters less than 40 m, a reduction in the catch or catch and release of immature fish could increase their chances of survival and ultimately reproduction. This in turn could continue to increase the recovery of Red Snapper production and stocks in the north-central GOM.

Unlike the immature Red Snapper in this study, 83% of the mature fish found in areas of high fishing pressure were larger than the legal catch limit for the state. This could suggest they would be removed from the population and unable to reproduce. However, we found that the largest and oldest mature females – which have a longer spawning season and higher fecundity than smaller females (Lowerre-Barbieri et al. 2015) – are predicted to be more commonly found in deep water on rigs-to-reefs structures, where there is less recreational fishing pressure. As such, these fish will be able contribute more to the recovering population, not only due to their higher fecundity and spawning frequency, but also because of lower fishing pressure. However, since only 6% of mature fish were found on rigs-to-reefs structures, the total reproductive contribution to the stock may be limited.

Both immature and mature Red Snapper were found at all structures and depths, although immature fish were uncommon in deep water and at rigs-to-reefs. Our models suggest that both depth and structure have an important effect on the distribution of mature, spawning Red Snapper, and that the greatest reproductive potential may occur at rigs-to-reefs, despite previous indications that reproductive potential between platforms and rigs-to-reefs is equivalent in the northwestern GOM (Downey et al., 2018). As more platforms are decommissioned in the GOM, the potential for additional rigs-to-reefs habitat may be an important consideration for the distribution of larger, older Red Snapper and, by extension, foster increased reproductive output of the GOM's Red Snapper population. In contrast, only depth is an important predictor of the size of immature fish, but our models show that the largest immature Red Snapper tend to be in deeper depths, where they are likely comingling with mature females. Furthermore, those larger immature females in deep water grow faster than mature fish (Leontiou et al., in review) and thus may obtain the minimum catch limit size at a younger age.

Red Snapper's dependence on reef structure begins soon after they grow out of their planktonic life stage (Bailey, 1995; Szedlmayer and Conti, 1999; Szedlmayer and Howe, 1997), and as they grow they move to larger, more complex structures (Bailey, 1995) and deeper depths. The results from this study support our previous understanding of the movement of Red Snapper through habitat types based on ontogeny, and further highlights the synergy and importance of both depth and artificial structure when predicting Red Snapper distributions. A recent meta-analysis found that habitat complexity and intra-specific abundance had the largest effects on Red Snapper abundance, both overall and for juveniles (Erisman et al., 2020). In particular, Erisman et al. (2020) found that density-dependent mechanisms, such as habitat quality and availability, shape the regional abundance of Red Snapper, although this study did not distinguish between mature and immature adult fish. Environmental factors could also influence Red Snapper distribution. For instance, Bolser et al. (2020) found that temperature, salinity, dissolved oxygen and depth are significant predictors of Red Snapper distribution among platforms although size/maturity of the fish were not included in the analyses. Future studies that focus on evaluating the contribution of artificial structures to fish production as related to maturity status would provide even more information as to how these structures aid in the recovery of the Red Snapper population in the GOM, particularly given the large overlap in age and size between mature and immature females. Additionally, the interaction of abiotic factors with depth and structure, and how they influence Red Snapper distribution and life history, is a fruitful topic for future studies.

CRediT authorship contribution statement

A.J. Leontiou: Data curation, Writing - original draft, Editing, Figure creation. **Wei Wu:** Model development and data analysis, Writing - original draft, Editing, Table and supplemental content creation. **Nancy J. Brown-Peterson:** Conceptualization, Methodology, Investigation, Writing - original draft, Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2021.101715.

References

Ajemian, M.J., Wetz, J.J., Shipley-Lozano, B., Dale Shively, J., Stunz, G.W., 2015. An analysis of artificial reef fish community structure along the northwestern Gulf of Mexico shelf: potential impacts of rigs-to-reefs programs. PLoS One 10, 1–22. http://dx.doi.org/10.1371/journal.pone.0126354.

Bailey, H.K., 1995. Potentail Interactive Effects of Habitat Complexity and Sub-Adults on Young-of-Year Red Snapper (*Lutjanus campechanus*) Behavior (Masters thesis). University of South Alabama.

Bolser, D.G., Egerton, J.P., Grüss, A., Loughran, T., Beyea, T., McCain, K., Erisman, B.E., 2020. Environmental and structural drivers of fish distribution among petroleum platforms across the U.S. Gulf of Mexico. Mar. Coast. Fish. 12, 142–163. http://dx.doi.org/10.1002/mcf2.10116.

Brown-Peterson, N.J., Leaf, R.T., Leontiou, A.K., 2021. Importance of depth and artificial structure as predictors of female Red Snapper reproductive parameters. Trans. Amer. Fish. Soc. 150, 115–129. http://dx.doi.org/10.1002/tafs.10277.

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. Mar. Coast. Fish. 3, 52–70. http://dx.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. Trans. Am. Fish. Soc. 139, 957–968. http://dx.doi.org/10.1577/t09-125.1.

Burnham, K.P., Anderson, R.P., 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304. http://dx.doi.org/10.1177/0049124104268644.

Caddy, J.F., Agnew, D.J., 2004. An overview of recent global experience with recovery plans for depleted marine resources and suggested guidelines for recovery planning. Rev. Fish Biol. Fish. 14, 43–112.

Campbell, M.D., Tolan, J., Strauss, R., Diamond, S.L., 2010. Relating angling-dependent fish impairment to immediate release mortality of Red Snapper (*Lutjanus campechanus*). Fish. Res. 106, 64–70. http://dx.doi.org/10.1016/j.fishres.2010.07.004.

Dauterive, L., 2000. Rigs to Reefs Policy, Progress and Perspective. Minerals Management Service OCS Report MMS-2000-073. New Orleans, LA, USA. p. 11.

Davis, M.W., 2007. Simulated fishing experiments for predicting delayed mortality rates using reflex impairment in restrained fish. ICES J. Mar. Sci. 64, 1535–1542. http://dx.doi.org/10.1093/icesjms/fsm087.

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. Trans. Am. Fish. Soc. 147, 1030–1041. http://dx.doi.org/10.1002/tafs.10104.

Erisman, B.E., Bolser, D.G., Ilich, A., Frasier, K.E., Glaspie, C.N., Moreno, P.T., Dell'Apa, A., du Mutsert, K., Yassin, M.S., Nepal, S., Tang, T., Sacco, A.E., 2020. A meta-analytical review of the effects of environmental and ecological drivers on the abundance of Red Snapper (*Lutjanus campecheanus*) in the U.S. Gulf of Mexico. Rev. Fish Biol. Fish. 30, 437–462. http://dx.doi.org/10.1007/s11160-020-09608-w.

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. Rev. Fish. Sci. 17, 48–67. http://dx.doi.org/10.1080/10641260802160717.

Gitschlag, G.R., Schirripa, M.J., Powers, J.E., 2003. Impacts of Red Snapper mortality associated with the explosive removal of oil and gas structures on stock assessments of Red Snapper in the Gulf of Mexico. Am. Fish. Soc. Symp. 36, 83–94.

Glenn, H.D., Cowan, J.H., Powers, J.E., 2017. A comparison of Red Snapper reproductive potential in the northwestern Gulf of Mexico: natural versus artificial habitats. Mar. Coast. Fish. 9, 139–148. http://dx.doi.org/10.1080/19425120.2017.1282896.

Goodyear, C.P., 1995. Red Snapper in U.S. waters of the Gulf of Mexico 1992 assessment update. Miami FL.

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

Karnauskas, M., Walter, J.F., Campbell, M.D., Pollack, A.G., Drymon, M.J., Powers, S., 2017. Red Snapper distribution on natural habitats and artificial structures in the northern gulf of Mexico. Mar. Coast. Fish. 9, 50–67. http://dx.doi.org/10.1080/19425120.2016.1255684.

Kulaw, D.H., Cowan, J.H., 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, 1–39. http://dx.doi.org/10.1371/journal.pone.0172360.

Leontiou, A.L., Wu, W., Brown-Peterson, N.J., 2021. The role of maturity in artificial habitat selection by female Red Snapper. Mar. Coast. Fish. (submitted for publication).

Lowerre-Barbieri, S.L., Crabtree, L., Switzer, T., Burnsed, S.W., Guenther, C., et al., 2015. Assessing reproductive resilience: An example with South Atlantic red snapper *Lutjanus campechanus*. Mar. Ecol. Prog. Ser. 526, 125–141. http://dx.doi.org/10.3354/meps11212.

Mississippi Department of Marine Resoures, 2016. Artificial Reef Habitat Mapping Program. Fish Havens Feature Report, p. 229, [WWW Document] URL https://dmr.ms.gov/wp-content/uploads/2019/11/offshore-reefs-feature-report.pdf.

Mississippi Department of Marine Resoures, 2019. Recreational catch limits [WWW Document]. URL https://dmr.ms.gov/recreational-catch-limits/.

National Oceanic and Atmospheric Administration, 2019. Red snapper [WWW Document]. URL https://www.fisheries.noaa.gov/species/red-snapper.

NOAA, 2020. FB20-018: Gulf of Mexico Fishery Bulletin. https://www.fisheries.noaa.gov/bulletin/noaa-announces-2020-gulf-mexico-red-snapper-hire-season accessed 26 Feb 2021.

Patterson, W.F., Watterson, J.C., Shipp, R.L., Cowan, J.H., 2001. Movement of tagged Red Snapper in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 130, 533–545. http://dx.doi.org/10.1577/1548-8659(2001)130<0533:motrsi>2.0.co;2.

Patterson, W., Wilson, C., Bentley, S., Cowan, J.H., Henwood, T., Dufrene, T., 2005. Delineating juvenile Red Snapper habitat on the northern Gulf of Mexico continental shelf. Am. Fish. Soc. Symp. 41, 277–288.

Pulsipher, A.G., Iledare, O.O., Mesyanzhinov, D.V., Dupont, A., Zhu, Q.L., 2001. Forecasting the Number of Offshore Platforms on the Gulf of Mexico OCS to the Year 2023. Center for Energy Studies, Louisiana State University, Baton Rouge, La, Prepared by, OCS Study MMS 2001-013. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, La. 52 pp. https://www.lsu.edu/ces/publications/2001/forecasting.pdf.

SEDAR, 2013. SEDAR 31 – Gulf of Mexico Red Snapper Stock Assessment Report. SEDAR Stock Assess. Rep. 1103.

SEDAR, 2018. SEDAR 52 - Gulf of Mexico Red Snapper Assessment Report. SEDAR, North Charlest. SC 413.

Shipp, R.L., Bortone, S.A., 2009. A prospective of the importance of artificial habitat on the management of Red Snapper in the Gulf of Mexico. Rev. Fish. Sci. 17, 41–47. http://dx.doi.org/10.1080/10641260802104244.

Stanley, D.R., Wilson, C.A., 1996. Abundance of fishes associated with a petroleum platform as measured with dual-beam hydroacoustics. ICES J. Mar. Sci. 53, 473–475. http://dx.doi.org/10.1006/jmsc.1996.0067.

Stanley, D.R., Wilson, C.A., 2000. Seasonal and spatial variation in the biomass and size frequency distribution of fish associated with oil and gas platforms in the northern Gulf of Mexico. Am. Fish. Soc. Symp. 2003, 123–153.

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, New York.

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. Fish. Bull. 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. Fish. Bull. 97, 626–635.

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

VanderKooy, S., 2009. A Practical Handbook for Determining the Ages of Gulf of Mexico Fishes, second ed. Gulf States Marine Fisheries Commission, Ocean Springs, MS.

Wells, R.J.D., 2007. The Effects of Trawling and Habitat Use on Red Snapper and the Associated Community (Ph.D. Dissertation). Louisiana State University.

Wells, R.J.D., Cowan, J.H., Fry, B., 2008. Feeding ecology of Red Snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 361, 213–225. http://dx.doi.org/10.3354/meps07425.

Wilson, C.A., Miller, M.W., Allen, Y.C., Boswell, K.M., Nieland, D.L., 2006. Effects of Depth, Location, and Habitat Type on Relative Abundance and Species Composition of Fishes Associated with Petroleum Platforms and Sonnier Bank in the Northern Gulf of Mexico Final Report. Baton Rouge, LA.

Workman, I., Shah, A., Foster, D., Hataway, B., 2002. Habitat preferences and site fidelity of juvenile Red Snapper (*Lutjanus campechanus*). ICES J. Mar. Sci. 59, http://dx.doi.org/10.1006/jmsc.2002.1211.

Wu, W., Huang, H., Biber, P., Bethel, M., 2017. Litter decomposition of *Spartina alterniflora* and *Juncus roemerianus*: Implications of climate change in salt marshes. J. Coast. Res. 332, 372–384. http://dx.doi.org/10.2112/JCOASTRES-D-15-00199.1.

Zuur, A., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer-Verlag, New York.

Table S1. The structures and AICs of a series of models that were compared for immature female Red Snapper. The lowest AIC in each step is indicated by bold font. Step 1 represents the procedure of choosing the optimum random effect(s) based on AIC from restricted maximum likelihood (REML). Step 2 represents the procedure of choosing the optimum fixed effect(s) based on AIC from maximum likelihood (ML). If the AIC is similar, we choose the parsimonious structured model. The AICs from REML and ML are not comparable (Zuur et al., 2009). *X indicates inclusion in the model.*

Step	Response variable	Fixed effect (Depth)	Fixed effect (Structure)	Random effect (Location)	Random effect (Month)	AIC (ML)	AIC (REML)
Model for FL							
Step 1	FL	x	x				1302.16
	FL	x	x		x		1300.89
	FL	x	x	x			**1289.64**
	FL	x	x	x	x		1289.88
The optimum random effect is location.							
Step 2	FL	x	x	x		1310.26	
	FL	x		x		**1306.61**	
	FL		x	x		1322.03	
The optimum fixed effect is depth.							
Model for Age							
Step 1	Age	x	x				**288.77**
	Age	x	x		x		290.77
	Age	x	x	x			287.39
	Age	x	x	x	x		289.39
Random effect does not improve model performance, so there is no need to include random effect.							
Step 2	Age	x	x			**272.72**	
	Age	x				280.23	
	Age		x			282.40	
The optimum fixed effects are depth and structure type.							

Table S2. The structures and AICs of a series of models that were compared for mature female Red Snapper. The lowest AIC in each step is indicated by bold font. Step1 represents the procedure of choosing the optimum random effect(s) based on AIC from restricted maximum likelihood (REML). Step 2 represents the procedure of choosing the optimum fixed effect(s) based on AIC from maximum likelihood (ML). If the AIC is similar, we choose the parsimonious structured model. The AICs from REML and ML are not comparable (Zuur et al., 2009). *X indicates inclusion in the model.*

Step	Response variable	Fixed effect (Depth)	Fixed effect (Structure)	Random effect (Location)	Random effect (Month)	AIC (ML)	AIC (REML)
Model for FL							
Step 1	FL	x	x				6667.03
	FL	x	x		x		6663.03
	FL	x	x	x			6642.14
	FL	x	x	x	x		**6640.03**
The optimum random effects are location and month.							
Step 2	FL	x	x	x	x	**6657.80**	
	FL	x		x	x	6666.81	
	FL		x	x	x	6707.33	
The optimum fixed effects are depth and structure type.							
Model for Age							
Step 1	Age	x	x				2029.17
	Age	x	x		x		2031.17
	Age	x	x	x			**2018.14**
	Age	x	x	x	x		2020.14
The optimum random effect is location.							
Step 2	Age	x	x			**2002.12**	
	Age	x				2022.78	
	Age		x			2055.44	
The optimum fixed effects are depth and structure type.							