

ARTICLE

Age, Growth, and Reproduction of Vermilion Snapper in the North-Central Gulf of Mexico

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Abstract

Vermilion Snapper *Rhomboplites aurorubens* is a commonly harvested species of reef fish in the northern Gulf of Mexico (GOM) and supports large commercial and recreational fisheries. Vermilion Snapper (139–535 mm TL) were collected from May 2015 through October 2016 from artificial and natural reefs in the north-central GOM. Ages ranged from 0.8 to 13 years, and there was no significant difference in growth between males and females. Nonlinear curve fitting was used to estimate growth parameters and Akaike information criterion (AIC) was used to determine relative model fit. The two-parameter von Bertalanffy growth function provided the best model fit and lowest Δ AIC score. Histological examination indicated that Vermilion Snapper are batch spawners with asynchronous oocyte development. Additionally, 17% of female Vermilion Snapper in the actively spawning subphase had 24-h postovulatory follicles (POF) suggesting daily spawning is occurring. No immature fish of either sex were collected during this study. Both histologically determined phases and gonadosomatic index patterns defined a spawning season occurring from April through September. The spawning interval for Vermilion Snapper, 1.3 and 2.1 d, was estimated using the hydrated oocyte and POF methods, respectively. Batch fecundity estimates from 5,497 to 284,468 eggs per batch were determined using fish macroscopically classified as actively spawning ($n = 25$), and total annual fecundity was estimated to range from 450,754 to 32,549,776 eggs per spawning season. Mean relative batch fecundity was 70.7 eggs/g of gonad-free body weight. Estimates from this study can be directly incorporated into population assessments and provide a region-specific overview of the life history for the Vermilion Snapper from the north-central GOM.

Reef fish fisheries in the northern Gulf of Mexico (GOM) consist of a multi species complex that includes Red Snapper *Lutjanus campechanus*, Vermilion Snapper *Rhomboplites aurorubens*, Gag *Mycoptera microlepis*, and other groupers, porgies, triggerfishes, and amberjacks

(Weninger and Waters 2003), which inhabit artificial or natural structure between 10 and 300 m deep. Reef fishes are often long lived, though differences in maximum sizes exist even on the family level. For example, the Vermilion Snapper and Yellowtail Snapper *Ocyurus chrysurus* only

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grow to around 3 kg, whereas other snappers, such as the Red Snapper and Mutton Snapper *L. cyanopterus*, can grow upwards of 10 kg or more (Burton 2002; Horst 2004). While many of these fishes exhibit different life history strategies, all are harvested commercially and recreationally.

Declines in reef fish stocks (e.g., Red Snapper, Grey Triggerfish *Balistes capricus*, Greater Amberjack *Seriola dumerili*) have led to regulatory actions (Polunin and Roberts 1996; Coleman et al. 2004; Doeringhaus et al. 2014). For example, bag and minimum length limits for Red Snapper, the most well-studied GOM reef fish (Gallaway et al. 2009; Saari et al. 2014; Simonsen et al. 2015; Glenn et al. 2017; Karnauskas et al. 2017), have undergone numerous changes starting in the 1990s (SEDAR 31 2013). However, despite regulatory changes, many stocks such as Red Snapper, Gag, and Gray Triggerfish have been classified as “overfished” in the last 10 years (SEDAR 9 2006a, 2006b). Thus, one of the outstanding research needs to increase the accuracy and precision of stock assessment output (fishery and stock status) is life history data of a species throughout its range. For example, most stock assessment models for reef fish are age structured (<http://sedarweb.org/>) and require accurate length-at-age estimates. These estimates determine spawning stock biomass, which also requires an estimated age at maturity.

Vermilion Snapper (family Lutjanidae) are found in temperate and subtropical climates from North Carolina, throughout the GOM and the Caribbean Sea, and south to Brazil (Jordan and Evermann 1896; Breder 1929). Despite its cosmopolitan distribution and abundance of biological and life history information in much of its range, there is little available information on this species for the north-central GOM (Mobile, Alabama, through New Orleans, Louisiana). Vermilion Snapper is typically associated with offshore rock outcroppings and hard-bottom reef habitats in the Atlantic Ocean (Grimes et al. 1982) and in the GOM (Collins et al. 2003). The north-central GOM differs from the eastern GOM due to the low abundance of hard-bottom reef habitats (Rezak and Bright 1985) and the presence of oil platforms, which serve as habitat for many reef fishes (Gallaway et al. 2009). Differences in habitat prevalence and type may lead to differences in the life history characteristics of the Vermilion Snapper, as it has in Red Snapper across the GOM (Woods et al. 2003; Fischer et al. 2004; Jaxion-Harm and Szedlmayer 2015; Simonsen et al. 2015; Glenn et al. 2017). These differences have not been accounted for in recent stock assessments.

Initial estimates of age and growth of Vermilion Snapper were based on data from the U.S. South Atlantic (Grimes 1978; Grimes and Huntsman 1980; Zhao et al. 1997; Potts et al. 1998). More recent data are available

from the GOM based on fish captured off Panama City, Florida, and southern Florida as well as from the Flower Gardens National Marine Sanctuary off the coast of Texas and Louisiana (Nelson 1988; Hood and Johnson 1999; Collins et al. 2003; Allman et al. 2005; Allman 2007). Only one study to date has described growth of Vermilion Snapper from the north-central GOM (Johnson et al. 2010). Age-3 to age-5 Vermilion Snapper are generally captured in both the commercial and recreational fishery, although the oldest individual recorded was estimated to be 26 years old (see VanderKooy 2009). Descriptions of the reproductive biology of Vermilion Snapper are also based on data from the eastern GOM (Collins et al. 2003) and the U.S. South Atlantic (Grimes et al. 1982; Cuellar et al. 1996; Bubley and Wyanski 2017). In both areas, the spawning season is from April to September. However, spawning intervals in the eastern GOM range from 1.6 to 2.6 d (Collins et al. 2003; Fitzhugh et al. 2015), while the spawning interval is estimated at 3 to 5 d in the U.S. South Atlantic (Cuellar et al. 1996; Bubley and Wyanski 2017) leading to smaller annual fecundity estimates. Length at maturity has been recently estimated to be around 138 mm FL in the eastern GOM (Fitzhugh et al. 2015).

Vermilion Snapper support both a recreational and commercial fishery, which increases the complexity of management for this species since needs of both sectors must be considered. For example, from 2000 to 2011 the recreational catch of Vermilion Snapper for the GOM averaged 140 metric tons annually; however, from 2012 to 2014, the recreational catch increased, averaging 360 metric tons (NMFS 2014a). This increase is likely in response to the shortened recreational season for Red Snapper (11 total days in 2014), causing the recreational sector to target other reef species like Vermilion Snapper. Commercial harvest since 2000 accounted for US\$7,000,000 in revenue and has averaged around 1,100 metric tons annually (NMFS 2014b). However, the interannual variation in total commercial catch increased after 2007 likely due to the implementation of individual fishing quotas (IFQs) in the Red Snapper fishery, which lowered quotas for individual fishers, forcing many to harvest different species. The 2015 stock assessment for GOM Vermilion Snapper (SEDAR 45 2016) showed that the stock appears to be in a healthy state and that currently no overfishing is occurring. Though the stock seems to be harvested sustainably at present, the need for information about the stock throughout its range was a recommendation in SEDAR 45 (2016).

Thus, the objectives of this study were to explore life history characteristics of Vermilion Snapper from the north-central GOM. Specifically, we (1) quantified the weight-length relationships and age and growth characteristics using a suite of nonlinear models, (2) characterized

the reproductive biology by estimating the spawning seasonality, age and length at maturity, spawning interval and frequency, and fecundity vital metrics, and (3) compared the life history characteristics estimated in this study to those from the eastern GOM and the U.S. South Atlantic regions for Vermilion Snapper.

METHODS

Fish collection.—Vermilion Snapper in the north-central GOM were collected using hook and line (fishery dependent, hook sizes 4/0–11/0) and vertical long-line (fishery independent, hook sizes 8/0 and 11/0); small individuals were collected in trawls conducted by the Southeast Area Monitoring and Assessment Program (SEAMAP). Collections were made between May and October 2015 and January and October 2016 from Pensacola, Florida, to the Mississippi River discharge (Figure 1). Samples were collected from artificial reefs (rigs-to-reef sites [i.e., rigs cut-off and left as artificial reefs and wrecks]), active petroleum platforms, and natural-reef habitats ranging from 35 to 200 m in area, as well as the Alabama Artificial Reef Zone. Fish obtained from SEAMAP trawls were collected about 50 km (30 mi) offshore near two reef sites. Fish were immediately placed on ice and processed within 24 h in the laboratory where SL (mm), FL (mm), TL (mm), sex, and weight (TW, kg) were recorded. From these measurements,

linear regressions, based on untransformed data, of SL to FL, SL to TL, and FL to TL were developed.

Age and growth.—Sectioned otoliths were used for age estimation following standard procedures (VanderKooy 2009). Annuli were defined as dark bands, and the area of the otolith between the last annuli and the edge (margin code) was measured. Two independent readers first estimated ages and margin codes for each individual without prior knowledge of fish size or date of capture, and if any disagreement occurred the otolith was then read jointly. If the two readers did not agree, the otolith in question was removed from further analysis. All ages were converted to biological age prior to fitting growth models, and the percentage of disagreement along with final average percent error (APE) was calculated. Percent of fish ages for length classes in 20-mm-TL bins were used to construct an age-length key. Annual annuli formation has been validated by marginal increment analysis (MIA; Campana 2001) in multiple studies (Zhao et al. 1997; Hood and Johnson 1999) and thus was not estimated in this study.

Using a multimodel approach, length at age was described using the two-parameter Von Bertalanffy growth function (VBGF), three-parameter VBGF (von Bertalanffy 1938), and the logistic growth function (Ricker 1975). The two-parameter VBGF is $L_t = L_\infty(1 - e^{-kt})$, where L_t represents the TL (mm) at age (t) in years, L_∞ is the hypothetical mean maximum TL, and k is the growth

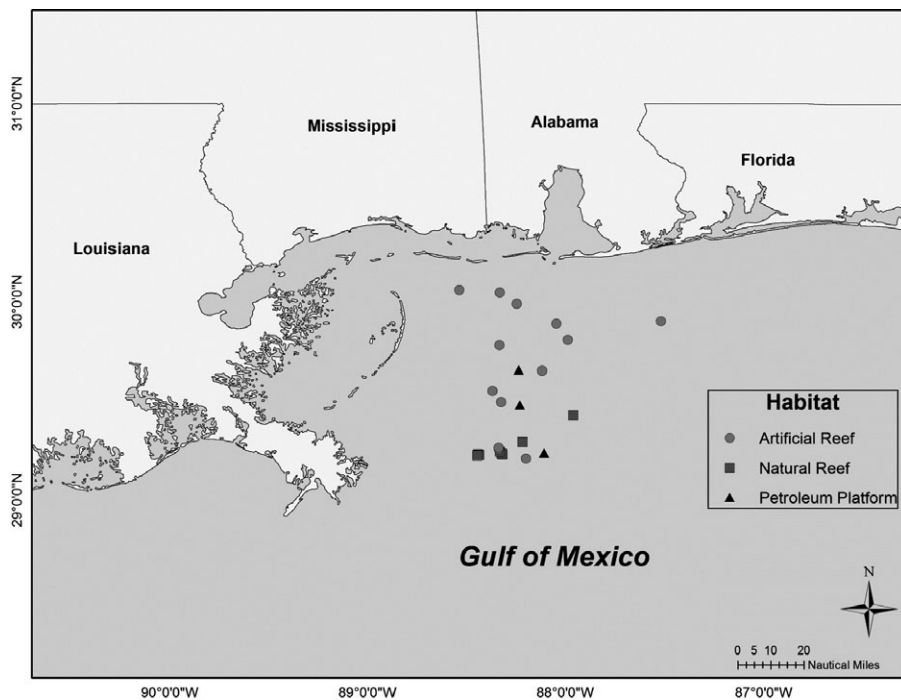


FIGURE 1. Sampling area in the north-central Gulf of Mexico. Each point marks a reef location where Vermilion Snapper were collected by habitat type.

coefficient. The three-parameter VBGF equation is $L_t = L_\infty [1 - e^{-k(t-t_0)}]$; this function includes a third parameter, t_0 , which is the theoretical age of a fish at length zero. The logistic growth equation (Ricker 1975) is $L_t = L_\infty / (1 + e^{-k(t-t_i)})$, where the growth parameters k and t_i are incorporated to limit growth to a maximum size.

Growth between sexes was determined not to be different if the mean parameter estimates fell between the 95% CIs of the mean for the opposite sex. Model support across all three equations was compared using the Akaike information criterion (ΔAIC ; Burnham and Anderson 2004); the model with the lowest ΔAIC value was considered the best-supported model. Additionally, an analysis of the residual sum of squares (ARSS) was also used for the most-supported model to compare growth curves to determine whether there was a difference in growth between sexes (Chen et al. 1992; Haddon 2011). Finally, all models were fit to individual and combined sexes and TL so that comparisons could be made to past studies of the species.

Weight at length was described using the power function: $TW = aTL^b$, where a is a scaling coefficient and b is an exponent describing the change in TL relative to weight. Similar to length-at-age models, differences in weight at length between sexes was determined by comparing the mean parameter estimate to the 95% CI of the mean estimate for the opposite sex as well as by using the ARSS approach.

Reproduction.—All gonads were removed and weighed (gonad weight [GW], to 0.01 g) in the laboratory within 24 h of capture. Gonads were assigned a macroscopic phase and sex based on physical appearance and size following Brown-Peterson et al. (2011). A subsample (~5 g) of the ovary from fish macroscopically identified as actively spawning was removed, weighed (to 0.01 g), and put into Gilson's fluid (Bagenal and Braum 1971) for 3 months for later fecundity determination. Three additional samples from Vermilion Snapper captured at rigs-to-reef sites within the sampling area using vertical long lines on June 9, 2017, were also included in the fecundity analysis to increase sample size.

A portion of gonadal tissue from the center of the right gonad of each fish was fixed in 10% neutral buffered formalin for a minimum of 7 d for histological processing. Tissues were dehydrated, cleared, embedded in paraffin, sectioned at 4 μm , and stained with hematoxylin and eosin following standard histological techniques. Microscopic classification of gonadal tissue followed histological descriptions and terminology from Brown-Peterson et al. (2011) and included the developing, spawning capable, regressing, and regenerating phases as well as the early developing, actively spawning (females), and germinal epithelium (GE; males) subphases. Different stages of

vitellogenic oocytes (Vtg1, Vtg2, Vtg3) were differentiated based on the amount of vitellogenin and lipids present in the cytoplasm. Fish were considered sexually mature if cortical alveolar (CA) oocytes or primary spermatocytes (SC1) were present in ovaries or testes, respectively, as they entered the gonadotropin-dependent portion of the reproductive cycle during the spawning season (Brown-Peterson et al. 2011).

Spawning seasonality was determined using the gonadosomatic index (GSI), calculated as $\text{GSI} = \frac{\text{GW}}{\text{TW} - \text{GW}} \times 100$, and monthly mean GSI values were determined for males and females. Prior to statistical analysis, GSI values were tested for normality and homogeneity of variance using Shapiro-Wilk's and Levene's tests, respectively. If the assumptions were not met, a Welch's ANOVA along with a Games-Howell post hoc test were used ($\alpha < 0.05$). A linear regression of gonad-free body weight (GFBW) and GSI was calculated for each sex separately to test whether GFBW was independent of GSI.

Spawning seasonality was verified using histological observations. Quantification of spermatogenetic stages was conducted using ImageJ software (Schneider et al. 2012) to further describe relative spawning preparedness of males. For each individual, three areas were haphazardly selected from the histological slide of the tissue, and photos were taken at 40 \times using a Nikon compound microscope with DCIM imaging software. An ImageJ software 80-point grid was overlaid on the photo, and for each grid point spermatogenic stages were counted for each photo. The spermatogenetic maturity index (SMI; Tomkiewicz et al. 2011) was used to quantify seasonal testes development but was modified to take into account residual spermatozoa in the regressing and regenerating phases. The frequency of each testis tissue type—somatic cells (Ts), spermatogonia (SG), spermatocytes (SC), spermatids (SC), spermatozoa (SZ), and residual spermatozoa (RSz)—was calculated for the sum of the three areas from each individual. The SMI was then calculated using the equation, $\text{SMI} = 0.0F_{\text{Ts}} + 0.4F_{\text{SG}} + 0.6F_{\text{SC}} + 0.08F_{\text{SC}} + 1.0F_{\text{SZ}} + 0.2F_{\text{RSz}}$, where F is the frequency of each indicated cell type. The index describes testis development on a scale from 0 to 1, with higher SMI values indicating more SZ in the testes regardless of GSI value.

Batch fecundity (BF) was estimated for fish confirmed histologically to be in the actively spawning subphase and included ovaries undergoing oocyte maturation (OM). To determine which oocytes to count for BF calculations, the oocyte size-frequency distribution of all oocytes >80 μm was determined for a spawning capable female and an actively spawning female. The largest size bin of oocytes (>450 μm ; Figure S1 available in the Supplement in the online version of this article), corresponding to hydrated oocytes or those undergoing OM, were used for BF estimates. The volumetric method (Bagenal and Braum 1971)

was used to calculate BF; oocytes were suspended in a known volume of water, and all oocytes $>450\ \mu\text{m}$ were counted from six subsamples with replacement. Relative Batch Fecundity (RBF) was estimated by using the equation, $\text{RBF} = \frac{\text{BF}}{\text{OFBW}}$, where OFBW is the ovary-free body weight (g). Linear regressions of both raw and \log_{10} -transformed estimates were used to determine the relationship between BF and age and BF and TL.

Spawning interval (SI) was estimated two ways in spawning capable fish, including those in the actively spawning subphase, by using (1) the presence of oocytes undergoing OM (hydrated oocyte method [HO]) and (2) the presence of 24-h postovulatory follicles (POF; postovulatory follicle method: Hunter and Macewicz 1985). Oocytes of the congener Red Snapper enter OM ~ 12 h prior to spawning (Jackson et al. 2006), and Vermilion Snapper oocytes undergoing OM have a similar time course. Estimates of SI were made bimonthly, and all data were combined to yield an annual spawning interval. All statistical analyses were completed in R 3.1.1 (R Core Team 2016), Microsoft Excel, and/or SPSS version 23 (IBM SPSS Statistics), and differences were considered significant if $P < 0.05$.

RESULTS

Fish Collection

A total of 445 Vermilion Snapper were collected: 306 from recreational hook and line, 47 from headboat hook and line, 16 from SEAMAP trawls, and 76 from vertical long-line sampling (Figure 2). All fish collected from independent surveys conducted by other states

only included length, weight, gonad weight, and tissue samples; thus, they were not included in the age and growth portion of the analysis. Female Vermilion Snapper were collected during all sampling months, and males were collected during all sampling months with the exception of January 2016. Fish were collected from a variety of habitats; however, most fish came from artificial reefs (65%), followed by natural reefs (17.8%), and petroleum platforms (17.2%). Lengths ranged from 139 to 554 mm TL (Figure 2), and a total of 226 females and 219 males were collected, yielding a sex ratio of 1.03:1 in favor of females but not significantly different from 1:1.

Age and Growth

A total of 370 Vermilion Snapper were collected for age estimation, and ages ranged from 0.8 up to 13 years old. Age-3 fish were most commonly collected, although Vermilion Snapper showed a wide overlap in length at age (Figure 3; Table S1). Reader agreement was 73% for the first separate reading; however, during the second joint reading, agreement increased to 98% (APE = 0.61). Linear regressions were used to compare relationships between TL, FL, and SL. All four equations derived from the linear regressions showed high correlation ($r^2 > 0.98$) and are: (1) $\text{TL} = 1.264 \times \text{SL} - 0.620$, (2) $\text{TL} = 1.128 \times \text{FL} - 2.112$, (3) $\text{FL} = 1.126 \times \text{SL} - 0.820$, and (4) $\text{FL} = 0.884 \times \text{TL} - 2.845$; all $n = 445$.

Growth models were first separated by sex and fit to TL at age. For female-specific growth, the logistic growth function provided the best fit, though ΔAIC scores were all similar ($\Delta\text{AIC} < 1.1$); whereas, for males, the two-parameter VBGF provided the best fit overall (Table S2).

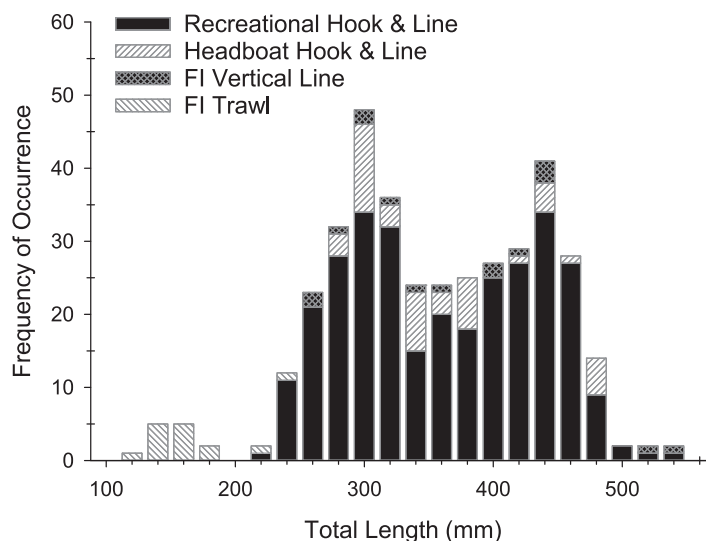


FIGURE 2. Length frequency distribution of Vermilion Snapper sampled by gear type (FI = fishery independent).

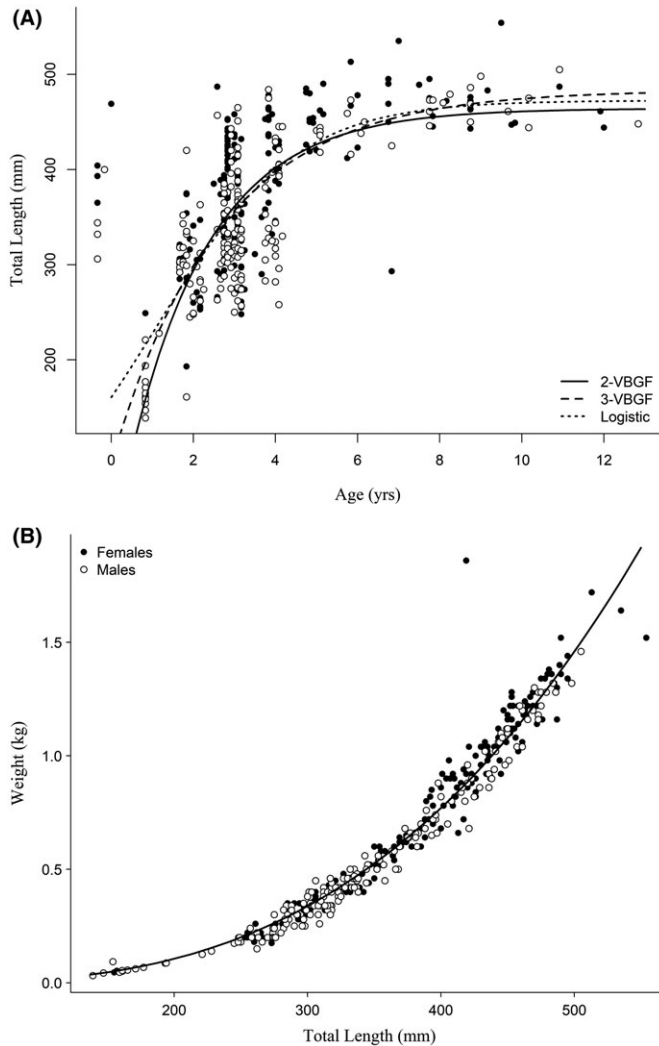


FIGURE 3. (A) Plot of multiple models describing the length-at-age relationship of male and female Vermilion Snapper from the north-central Gulf of Mexico ($n = 370$). Models include the two-parameter Von Bertalanffy growth function (2-VBGF), three-parameter Von Bertalanffy growth function (3-VBGF), and the logistic growth function (Logistic). (B) Plot of the weight-at-length relationship of male ($n = 182$) and female ($n = 178$) Vermilion Snapper from the north-central Gulf of Mexico. The power function was used to fit the data.

Comparison of the 95% CIs showed no significant differences for growth between sexes, with the exception of the logistic growth function, where the mean L_{∞} values did not lie within the CI of the mean for the opposite sex (Table S2). Furthermore, an ARSS of the two-parameter VBGF showed that growth was not significantly different between sexes ($F_{2, 358} = 1.06$, $P = 0.45$); thus, combined sex data were used to analyze growth models. All growth models showed similar mean TL-at-age estimates of Vermilion Snapper (Figure 3A). For combined sexes, the two-parameter VBGF fit to TL provided the lowest ΔAIC score and was the most supported model (Table 1).

The weight-at-TL relationship was fit using the power function for both sexes and did not show significant differences between sexes (Table S3). An additional ARSS was completed to compare between males and females and found no significant differences; thus we used combined sexes to fit an overall model ($F_{2, 369} = 0.23$, $P = 0.26$; Table S3). For combined sexes, a was estimated to be 2.74×10^{-8} (95% CI: 1.70×10^{-8} to 4.36×10^{-8}), and b was estimated at 2.86 (95% CI: 2.79 to 2.94; Figure 3B).

Reproduction

A total of 444 Vermilion Snapper were collected to estimate spawning seasonality using GSI, and 386 of those fish were used for histological examination. No immature fish for either sex were collected during this study. The smallest female captured was 155 mm TL (age 1) and was actively spawning, and the smallest male captured was 139 mm TL (age 1) and was spawning capable. This suggests Vermilion Snapper recruit into the reproductive stock at a young age. The highest percentage of actively spawning females (26.5%) were captured on natural reefs despite natural reefs containing the lowest percentage of spawning capable females (6.2%). The percentage of actively spawning (14.5%, 16.4%) and spawning capable (11.1%, 11.5%) females were similar for artificial reefs and petroleum platforms, respectively.

Histological descriptions.—The ovary of Vermilion Snapper has a typical cystovarian structure. Asynchronous oocyte development and the presence of POF in ovaries of spawning capable females indicate Vermilion Snapper are batch spawners (Figure 4A). Histological assignment of the actively spawning subphase included oocytes in any stage of OM (i.e., lipid coalescence, germinal vesicle migration, yolk coalescence, and hydration). The presence of 24-h POF in ovaries of actively spawning fish suggests daily spawning in those individuals (Figure 4B).

The testis of Vermilion Snapper has not been previously described histologically. The testes have an unrestricted spermatogonial type of structure, in which spermatogonia is most common at the distal end of the testis during active spermatogenesis. Spermatocysts containing all stages of spermatogenesis are present in the developing phase, but no SZ are present in the lumen of the lobule or in the sperm ducts (Figure 5A). Spermatozoa are abundant in both the lumen of the lobule and the sperm ducts during the spawning capable phase, and active spermatogenesis is seen throughout the testis in the form of a continuous GE at the beginning of the spawning season (Figure 5B). Spermatogenesis decreases as the spawning season progresses, resulting in a discontinuous GE in some lobules of spawning capable males (Figure 5C). Spermatogonial proliferation is evident in the periphery of the testis towards the end of the spawning season, and males in the regressing phase show

TABLE 1. Growth model parameter estimates for Vermilion Snapper in the north-central Gulf of Mexico from three growth functions for combined sexes. Mean parameters are displayed along with the 95% CIs and Δ AIC values. 95% CI = 95% confidence interval, VBGF = Von Bertalanffy growth function, L_{∞} = hypothetical mean maximum TL (mm), k = growth coefficient (y^{-1}), t_0 = theoretical length at age 0, t_i = age at maximum growth rate.

Model	Parameter	Parameter estimate	95% CI	Δ AIC
Two-parameter VBGF	L_{∞}	464.08	446.48 to 482.94	0
	k	0.50	0.45 to 0.59	
Logistic growth function	L_{∞}	472.46	454.27 to 492.87	2.76
	k	0.59	0.48 to 0.71	
	t_i	1.12	0.87 to 1.34	
Three-parameter VBGF	L_{∞}	483.28	461.80 to 509.20	9.22
	k	0.38	0.30 to 0.46	
	t_0	-0.55	-1.04 to -0.20	

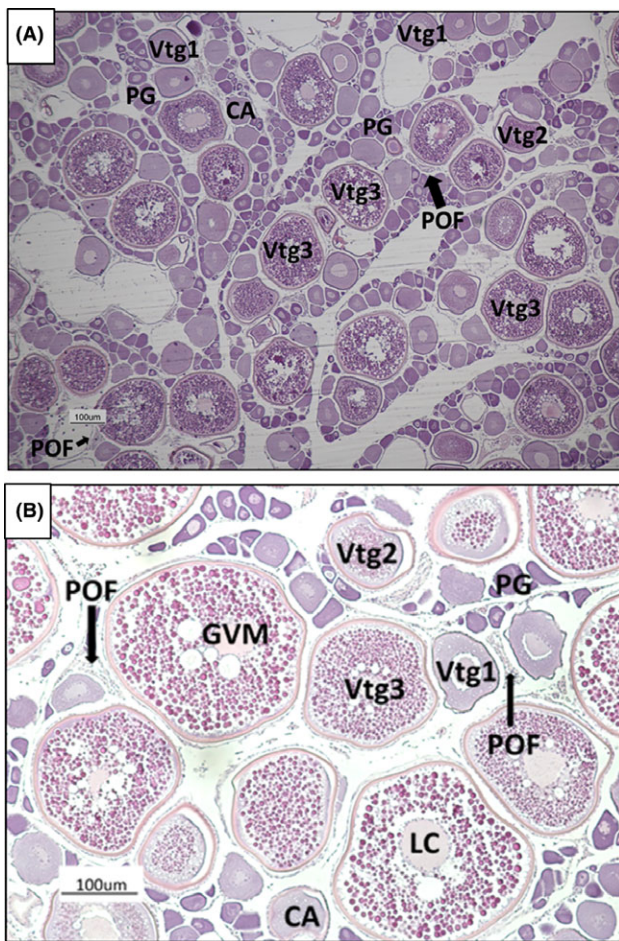


FIGURE 4. Photomicrographs of ovarian tissue from Vermilion Snapper collected from the north-central Gulf of Mexico. (A) Spawning-capable phase, showing asynchronous oocyte development and postovulatory follicles, indicating batch spawning (385 mm TL, captured in August). (B) Actively spawning subphase with 24-h postovulatory follicles, indicating daily spawning (433 mm TL, captured in May). CA = cortical alveolar, GVM = germinal vesicle migration, LC = lipid coalescence, PG = primary growth, POF = postovulatory follicle, Vtg1 = primary vitellogenic, Vtg2 = secondary vitellogenic, Vtg3 = tertiary vitellogenic. [Color figure can be viewed at afs.journals.org.]

spermatogonial proliferation, few to no spermatocysts, and residual SZ in the lumen of the lobules (Figure 5D). No males in the regenerating phase were captured during this study.

Spawning Seasonality.—Comparisons of GSI and GFBW indicated there was a significant ($F_{1, 225} = 43.988$, $P < 0.001$) relationship for females, and GFBW accounted for 16% of the variation in GSI ($r^2 = 0.16$). There was also a significant ($F_{1, 218} = 117.964$, $P < 0.001$) relationship in males with 34% of the variation in GSI accounted for by GFBW ($r^2 = 0.35$). Despite the relationship, when comparing GSI values and histological evidence, we concluded that elevated GSI values did coincide with the spawning season and that GSI was sufficient to describe reproductive preparedness. Elevated GSI values in both male and female Vermilion Snapper indicated a spawning season from April through September (Figure 6A). The peak mean GSI value occurred in May for females (2.7%) and in August for males (2.0%). Mean female GSI values were significantly different across months (Welch's ANOVA: $F_{9, 210} = 6.113$, $P < 0.001$), and a post hoc Games–Howell test indicated that GSI values in April, May, July, August, and September were significantly higher than values observed in January, February, March, and October. Male GSI values were also significantly different across months (Welch's ANOVA: $F_{8, 208} = 3.723$, $P < 0.001$), but due to large variation, the Games–Howell post hoc test did not show clear monthly differences. Both male and female GSI values showed a decrease in July during the spawning season, which was attributed to all individuals captured <350 mm TL being in the regenerating and regressing reproductive phases.

Male SMI values provided additional evidence of spawning seasonality. The SMI increased gradually up to April and then sustained values of around 0.79 until October when the SMI decreased to 0.45 (Figure 6B). Male SMI was significantly different among months (ANOVA: $F_{8, 59} = 6.546$, $P < 0.001$), and the SMI in October was

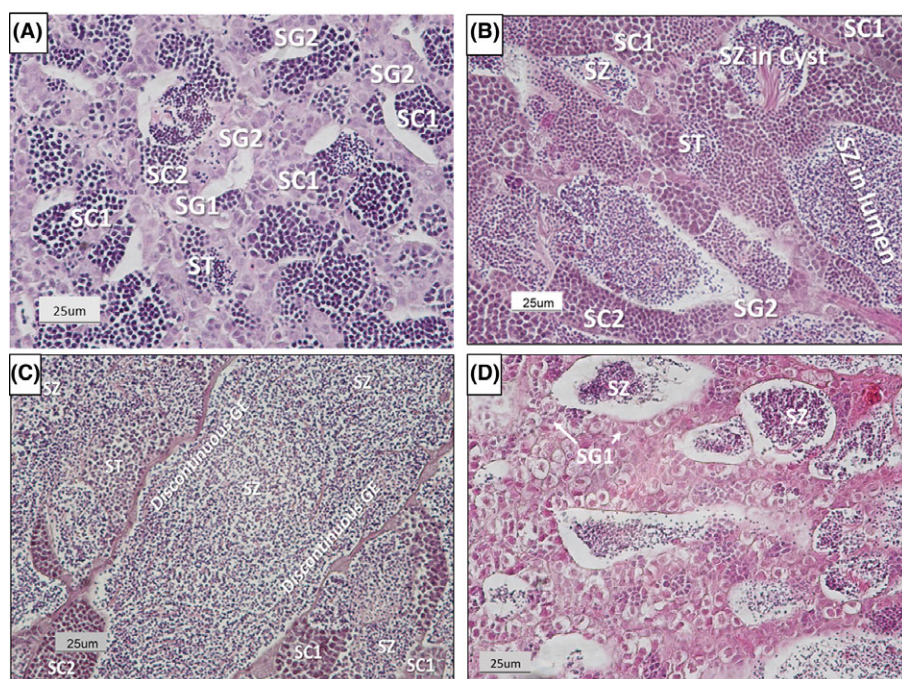


FIGURE 5. Photomicrographs of testes from Vermilion Snapper collected from the north-central Gulf of Mexico showing various reproductive phases. (A) Developing phase, showing all stages of spermatogenesis but no spermatozoa in the lumen (337 mm TL, captured in February). (B) Early germinal epithelium (GE) subphase of the spawning capable phase, showing a continuous GE (371 mm TL, captured in May). (C) Late GE subphase of the spawning capable phase, showing a discontinuous GE (348 mm TL, captured in August). (D) Regressing phase, with residual spermatozoa in the lumen, few spermatocysts, and spermatogonial proliferation (330 mm TL, captured in October). SC1 = primary spermatocytes, SC2 = secondary spermatocytes, SG1 = primary spermatogonia, SG2 = secondary spermatogonia, ST = spermatids, SZ = spermatozoa in both the lumen and spermatocyst. [Color figure can be viewed at afs.journals.org.]

significantly lower than for all months within the spawning season (April through September). This index shows the increasing presence of SZ in the testis relative to other spermatogenic stages at the beginning of the reproductive season, as well as the predominance of SZ throughout the spawning season. Both GSI and SMI showed a rapid decrease in October (Figure 6A, B), a time when spermatogenesis ceases and only residual SZ is present in the testes (Figure 5D).

Histological analysis verified the spawning season indicated by GSI and SMI values. All female Vermilion Snapper captured in January, March, and October were in the regenerating phase (Table 2). Ovarian recrudescence was first observed in February with the appearance of the early developing phase (Table 2). Actively spawning and spawning capable females were found from April through September, supporting the GSI trend of a spawning season from April through September. The high percentage of regenerating females in July mirrors the observed dip in mean GSI during that month (Figure 6A); all females <350 mm TL captured in July were regenerating, suggesting they had ceased spawning for the year. The first actively spawning individual was captured on April 4 and the last was captured on

September 26, resulting in an estimated 172-d spawning season.

Males captured in February were undergoing gonadal recrudescence, and by March spawning capable fish were observed (Table 3). Spawning capable males were found in high percentages from April through September in all subphases, consistent with elevated GSI and SMI values during these months. Males in the early GE subphase were more common at the beginning of the reproductive season, and the increased occurrence of the late GE subphase near the end of the spawning season was observed. Regressing males were first observed in September, and all males captured in October were in the regressing phase, corresponding to the decrease in GSI and SMI values (Table 3; Figure 6).

Spawning frequency.—Vermilion Snapper spawn frequently from April through September. The HO and POF methods provided the same estimates of SI for June–July and August–September (2.2 and 1.8 d, respectively, between spawning events; Table 4). However, during the beginning of the spawning season (April–May), the HO method provided the shortest SI estimate (1.4 d between spawning events), while the POF method provided the longest estimate (3.0 d between spawning events). Combining data from all months resulted in an overall SI of

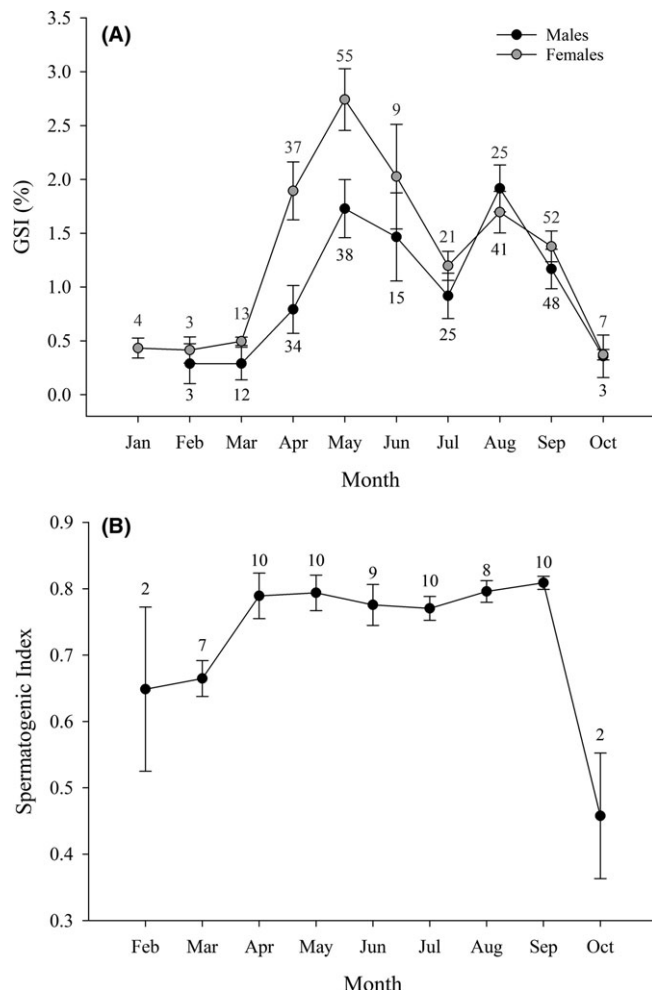


FIGURE 6. Spawning seasonality of Vermilion Snapper in the north-central Gulf of Mexico. (A) Monthly gonadosomatic index (mean GSI \pm SE) for males and females. (B) Monthly spermatogenic index (mean SMI \pm SE) score for males. Numbers indicate samples sizes for each month.

TABLE 2. Percent occurrence of each reproductive phase by month for female Vermilion Snapper in the north-central Gulf of Mexico. RGN = regenerating, EDEV = early developing, DEV = developing, SC = spawning capable, AS = actively spawning, RGR = regressing, n = number of samples.

Phase	<i>n</i>	RGN	EDEV	DEV	SC	AS	RGR
January	4	100.0	0	0	0	0	0
February	3	66.7	33.3	0	0	0	0
March	10	100.0	0	0	0	0	0
April	34	44.1	8.8	2.9	14.7	29.4	0
May	55	20.0	5.5	0	18.2	54.5	1.8
June	9	22.2	0	0	22.2	44.4	11.1
July	15	40.0	6.7	0	40.0	13.3	0
August	24	12.5	0	0	29.2	50.0	4.2
September	30	16.7	0	0	33.3	46.7	3.3
October	7	100.0	0	0	0	0	0

1.6 and 2.5 d between spawning events for the HO and POF methods, respectively (Table 4). Histological evidence showed that some females are capable of daily spawning (Figure 4B), supporting the calculated SI of < 2 d. When incorporated into a 172-d spawning season, these SI estimates suggest a potential spawning frequency of 110 and 69 spawn events per season using the HO and POF methods, respectively.

Fecundity.—Batch fecundity was estimated from 25 fish that ranged from 394 to 513 mm TL and ages 3 to 12 years during the months of April through August. Estimates ranged from 5,497 to 284,468 eggs per batch (mean \pm SD = 77,612 \pm 58,589 eggs). While BF did not show a significant linear relationship when compared with fish size ($F_{1, 24} = 2.345$, $P = 0.14$) for both raw and log₁₀-transformed data, a general trend of increasing BF with increasing fish size is evident. A significant linear relationship was found between BF and age, however ($F_{1, 24} = 6.248$, $P = 0.02$). We modeled an exponential relationship between BF and both age and TL, which showed a better fit to the data: $BF = 19.583 \cdot e^{0.1742 \times \text{age}}$ ($n = 25$) and $BF = 23.395 \cdot e^{0.0177 \times \text{TL}}$ ($n = 25$) (Figure S2). Relative batch fecundity yielded estimates from 8.1 eggs/g of GFBW up to 276.9 eggs/g of GFBW, with a mean \pm SD RBF of 70.7 \pm 57.9 eggs/g of GFBW. A linear regression of RBF and fish size showed no significant relationship ($r^2 = 0.02$, $P = 0.548$). Annual fecundity was estimated by multiplying BF and the spawning frequency, and it ranged from 604,670 eggs per spawning season up to 31,291,480 eggs per spawning season for the POF and HO methods, respectively.

DISCUSSION

This study investigated the life history characteristics for the Vermilion Snapper and provides pertinent parameter estimates for this species from the north-central GOM, a region where reef structure and substrate are distinctly different from the eastern GOM (Rezack and Bright 1985). Female Vermilion Snapper with hydrated oocytes were found on most high-relief artificial structures, but despite the importance of artificial structures to Vermilion Snapper spawning, a higher percentage of actively spawning females were found over natural reefs than artificial structures, similar to findings by Glenn et al. (2017) for north-central GOM Red Snapper. Vermilion Snapper mature at an early age (less than age 1) and the oldest individual captured in this study was age 13. Vermilion Snapper have a 6-month spawning season, and females can spawn as many as 100 times in a single season. We also described length at age for both sexes and found no differences between male and female growth. These estimates add to our knowledge of the biology of Vermilion Snapper in the northern GOM.

TABLE 3. Mean percent occurrence of each reproductive phase by month for male Vermilion Snapper in the north-central Gulf of Mexico. Note: EGE, LGE and MGE are subphases of spawning capable males, and percentages represent spawning capable males only. EDEV = early developing, DEV = developing, SC = spawning capable, EGE = early germinal epithelium, LGE = late germinal epithelium, MGE = midgerminal epithelium, RGS = regressing, RGN = regenerating, n = number of samples.

Phase	n	EDEV	DEV	SC	SC			RGS	RGN
					EGE	LGE	MGE		
February	3	33.3	66.7	0	0	0	0	0	0
March	12	0	33.3	66.7	83.3	0	16.7	0	0
April	33	0	0	100	61.8	5.9	32.4	0	0
May	38	0	0	100	40.5	2.7	56.8	0	0
June	15	0	0	100	28.6	28.6	42.9	0	0
July	25	0	0	100	54.5	22.7	22.7	0	0
August	40	0	2.9	97.1	39.4	9.1	51.5	0	0
September	48	0	0	91.3	38.1	19	42.9	8.7	0
October	3	0	0	0	0	0	0	100	0

TABLE 4. Bimonthly spawning interval estimates (days between spawns) for Vermilion Snapper in the north-central Gulf of Mexico using both the hydrated oocyte (HO) and postovulatory follicle (POF) methods following Hunter and Macewicz (1985). Only fish in the spawning capable reproductive phase, including the actively spawning subphase, were used for these calculations. n = number of samples.

Months	n	HO method	POF method
April–May	55	1.4	3.0
June–July	14	2.2	2.2
August–September	43	1.8	1.8
Overall	112	1.6	2.5

Previous studies on Vermilion Snapper have yielded an observed left-truncation of ages with the majority of fish occurring from ages 3 to 5. Fish collected during this study showed a similar age distribution; only a small proportion of fish collected were less than 2 years old or greater than 10 years old. Despite the numerous studies that have observed this truncation, it is difficult to surmise the reason behind its occurrence. For example, it could be an accurate representation of the population, the effect of harvest on the age distribution, or simply the sampling bias resulting from targeting these fish with hook-and-line gear. The approach of this study was to limit selectivity bias of Vermilion Snapper by using multiple gears to collect a representation of fish from multiple size and age-classes.

To ensure growth was accurately described in this study, we used a multimodel approach by fitting data to a suite of common growth models and comparing them with Δ AIC. Multimodel approaches can more accurately describe growth than can single models (Dippold et al. 2016; Corey et al. 2017). The models used here were chosen based on their prevalence in fisheries and multimodel literature. The two-parameter VBGF provided the lowest Δ AIC score, which is

surprising due to criticism of this model being “inflexible” by those who have used it to describe growth (Roff 1980). We also found that for both sexes the three-parameter VBGF, which is the most prevalent growth model used in fisheries literature and stock assessments, had the highest Δ AIC score and provided the worst fit to the data. These results may be due to a very small value for t_0 (i.e., close to 0), which would result in a “penalization” of the three-parameter VBGF in the AIC calculations.

We found no significant differences in the growth of male and female Vermilion Snapper as has been reported previously for the U.S. South Atlantic (Grimes 1978). This is contrary to the findings of Johnson et al. (2010), who found that females grew at a faster rate and reached older ages than males in the northeastern GOM. In the eastern GOM, Allman (2007) noted significant differences in growth between sexes with females growing larger and faster, while Hood and Johnson (1999) found no significant differences. These inconsistent results may be due to the small-scale variation in growth exhibited and documented in Vermilion Snapper (Allman 2007).

Despite our findings showing a lack of support for the three-parameter VBGF, Vermilion Snapper growth has been described using this model throughout their range (Nelson 1988; Zhao et al. 1997; Potts et al. 1998; Hood and Johnson 1999; Allman et al. 2005; Allman 2007; Johnson et al. 2010; Table 5). Furthermore, Vermilion Snapper growth is described in multiple studies as highly variable with fish of multiple ages comprising the same size-class, similar to what we saw in this study. While many of the previous studies did not report 95% CIs, their parameter estimates fell close to those found in this study (Table 5). When comparing our data to the only previous study in the north-central GOM (Johnson et al. 2010), the calculated L_∞ and k estimates in this study were significantly lower when compared with 95% CIs (Table 5). This

TABLE 5. Length-at-age parameter estimates for Vermilion Snapper. All comparisons are for the three-parameter Von Bertalanffy growth function; 95% CIs are displayed in parentheses if available. GOM = Gulf of Mexico, SA = U.S. South Atlantic, L_{∞} = hypothetical mean maximum TL (mm), k = growth coefficient (y^{-1}), t_0 = theoretical length at age 0, n = number of fish.

Citation	Location	Sex	n	L (mm)	k	t_0
Nelson (1988)	Western GOM	Combined	881	500	0.22	-0.30
		Male	242	862 (± 35.3)	0.05 (± 0.04)	-5.67 (± 1.56)
Johnson et al. (2010)	North-central GOM	Female	317	655 (± 4.7)	0.13 (± 0.03)	-2.78 (± 0.56)
		Combined	621	707 (± 6.4)	0.09 (± 0.01)	-3.97 (± 0.59)
Zhao et al. (1997)	SA	Combined	192	562	0.202	-0.117
Grimes (1978)	SA	Combined	815	626.6	0.198	-0.128
Schirripa (1992)	SA	Combined	886	535	0.203	-0.940
Potts et al. (1998)	North Carolina to Florida Keys	Combined	1,465	650.24	0.144	-0.238
Allman et al. (2007)	GOM	Combined	1,135	271	1.17	0.31
Hood and Johnson (1999)	Eastern GOM	Combined	858	297.18	0.25	-3.9
		Male	187	489.29 (± 34.95)	0.31 (± 0.09)	-0.80 (± 0.72)
This study	North-central GOM	Female	183	479.67 (± 24.13)	0.45 (± 0.13)	-0.38 (± 0.82)
		Combined	370	483.28 (± 21.48)	0.38 (± 0.08)	-0.55 (± 0.49)

may be due to Johnson et al. (2010) lacking fish that were <200 mm TL, which would likely shift the curve when using the three-parameter VBGF. Additionally, when comparing our results to Hood and Johnson (1999), we find that our L_{∞} estimates are much higher (>200 mm) than what was reported in their study. While these two studies show the largest amounts of difference from our estimates, there is considerable variation in Vermilion Snapper growth on a small scale (Allman 2007) and seemingly on a large scale as well.

Determining the age and size at sexual maturity is a critical component of the population dynamics of a species (Stearns 1992; Trippel 1995). Increased fishing pressure can affect age and length at maturity (Beverton and Holt 1957), often resulting in fish achieving sexual maturity at a smaller size due to compensatory responses after population declines (Colby and Nepsky 1981; Trippel 1995). In the U.S. South Atlantic, a temporal shift in TL and age at maturity of Vermilion Snapper was observed over a 9-year period and was hypothesized to be linked to fishing pressure (Zhao et al. 1997). Since Vermilion Snapper have not been well studied throughout their historical exploitation in the GOM, a change in age and TL at maturity could have gone undetected. The most recent stock assessment for Vermilion Snapper in the GOM, based predominantly on fish in the eastern GOM, estimated female 50% length at maturity to be around 138 mm FL (154 mm TL; Fitzhugh et al. 2015; Table 6). While we could not estimate length or age at maturity in the current study due to lack of immature fish, females as small as 155 mm TL (121 mm FL) in our collections were capable of spawning, comparable with data from the eastern GOM. This suggests a similar size and age at maturity throughout the

northern GOM as well as the U.S. South Atlantic (151 mm TL; Zhao et al. 1997).

While there was a significant relationship between GSI and body size, we believe that GSI still accurately describes the spawning season, as confirmed with histological analysis. Male and female GSI values for Vermilion Snapper peaked in May and again in August, with a decline in GSI in the months of June and July in the north-central GOM. This supports histological evidence of a spawning season from April to September in the region, similar to previous reports for the U.S. South Atlantic (Grimes and Huntsman 1980; Cuellar et al. 1996; Bubley and Wyanski 2017) and the eastern GOM (Collins et al. 2003; Fitzhugh et al. 2015; Table 6). Some variation in peak spawning seems to exist in the GOM, as Hood and Johnson (1999) found elevated values from May to September while Collins et al. (2003) reported a peak in June. The June–July decline in GSI documented in this study is likely due to multiple reasons such as gear bias, regional temperature differences, energetics, or forage availability. However, the most likely cause was that all females <350 mm TL captured during July (40% of total July sample) were in the regenerating phase, suggesting these fish had already ceased spawning for the season. Smaller fish have shorter spawning seasons than larger individuals (Lowerre-Barbieri et al. 2011, 2015; Fitzhugh et al. 2012). Interestingly, some individual male GSI values were equal to and sometimes higher than individual female GSI values when both were in the spawning capable phase, results that are not common in many teleost fishes. One explanation may be that males are undergoing sperm competition, a biological mechanism that is common to fishes that spawn in large groups or in

TABLE 6. Comparison of reproductive estimates for Vermilion Snapper. SA = U.S. South Atlantic, GOM = Gulf of Mexico, RBF = relative batch fecundity; blank spaces indicate no data were available. Values for batch fecundity and RBF are expressed as mean \pm SD. An asterisk (*) indicates no immature fish were captured. Numbers in parentheses under each value represent the sample size for each determination.

Citation	Location	Length at maturity	Age at maturity (years)	Spawning interval (d)	Spawning frequency (number of spawns per season)	Annual fecundity (number of eggs)	Batch fecundity (number of eggs)	RBF (number of eggs/g)	Spawning season
Grimes and Huntsman (1980) ($n = 852$)	SA	186–324 mm TL	3 to 4			8,168 to 1.79 million ($n = 41$)			April to September
Nelson (1988) ($n = 881$)	Western GOM	209 mm FL	2				61,000 to 392,000 ($n = 21$)	710.8 to 865.7 ($n = 21$)	April to August
Cuellar et al. (1996) ($n = 1,004$)	SA	<165 mm FL*	<2*	5 ($n = 282$)	35 ($n = 282$)	140,175 to 3.15 million	4,000 to 90,000 ($n = 85$)		April to September
Zhao et al. (1997) ($n = 5,026$)	SA	151 mm TL	<1						
Bubley and Wyanski (2017) ($n = 24,210$)	SA		0.85	3 to 4	41 to 49		22,641 to 160,775 ($n = 45$)		April to September
Fitzhugh et al. (2015) ($n = 31,112$)	Eastern GOM	138 mm FL ($n = 1,770$)		1.79	82		6,106 to 407,570 (76,465 \pm 79,093) ($n = 147$)	224 \pm 112 ($n = 147$)	April to October
Collins et al. (2003) ($n = 572$)	Eastern GOM	<153 mm TL*		1.6 ($n = 419$)	87 ($n = 419$)	0.7 to 35 million ($n = 59$)	7,385 to 407,570 ($n = 123$)		April to September
Hood and Johnson (1999) ($n = 858$)	Eastern GOM	<200 mm TL	1				5,535 to 86,811 ($n = 27$)		May to September
This study ($n = 445$)	North-central GOM	<155 mm TL*	<0.8*	1.6 to 2.5 ($n = 112$)	69 to 110	544,203 to 28.2 million	5,497 to 284,468 (77,612 \pm 58,589) ($n = 25$)	70.7 \pm 57.9 ($n = 25$)	April to September

aggregations, as seen for lutjanids and serranids (Grimes 1987; Petersen and Warner 1998; Heppell 2007). Thus, a larger testis allows males to increase the total number of possible fertilizations in a given spawning event (Petersen and Warner 1998).

The spawning interval for Vermilion Snapper estimated in this study was similar to that for fish in the eastern GOM, which ranged between 1.6 and 1.78 d between spawns (Collins et al. 2003; Fitzhugh et al. 2015; Table 6). Additionally, the spawning frequency in the north-central GOM is within the range of spawns per season estimated for the eastern GOM (Collins et al. 2003; Fitzhugh et al. 2015; Table 6). These estimates vary greatly from Vermilion Snapper in the U.S. South Atlantic, where Cuellar et al. (1996) and Bubley and Wyanski (2017) found a spawning interval of 3–5 d between spawns and a spawning frequency of 35 to 58 spawns per season, although duration of the spawning season was similar (Table 6). Since the duration of the spawning season is the same between the U.S. South Atlantic and the GOM, the increase in spawning frequency is a direct result of the much shorter SI for GOM fish. Spawning-interval calculations using only fish with hydrated oocytes may vary based on the time of day the fish are captured. Vermilion Snapper spawn around dusk (Collins et al. 2003; Fitzhugh et al. 2015), and SI estimates of fish captured earlier in the day can be lower if fish with hydrated oocytes are used (Collins et al. 2003). However, since we included fish in all stages of OM in our SI calculations, we are confident that time of capture did not influence our estimates. Finally, fish undergoing OM could be more active and therefore more susceptible to the gear than nonspawning fish, which would support the high numbers of fish with hydrated oocytes caught in May in this study. This behavior is well noted in aggregate spawning fishes since most fish are located in a small area or around a single reef structure (van Overzee and Rijnsdorp 2015).

With a relatively narrow range of fish sizes examined in this study for fecundity (394–513 mm TL), coupled with considerable variation in estimates, it is not surprising that no relationship existed between BF and fish size. However, the larger range of ages (3–12 years) resulted in a significant relationship between BF and age, despite the wide overlap of TL within ages. Wide ranges in BF have been previously documented in GOM Vermilion Snapper (Collins et al. 2003; Fitzhugh et al. 2015), and our BF estimates fall within the previously reported range (Table 6). Large variation in BF estimates are typical of batch-spawning species, since large amounts of energy are required to produce a single batch of eggs, and thus the size of the batch can have large variability throughout the spawning season (Hunter et al. 1985). In contrast, RBF in the north-central GOM was lower than the previous estimate by Fitzhugh et al. (2015) for the eastern

GOM ($\text{RBF} \pm \text{SD} = 70.7 \pm 57.9$ eggs/g of GFBW versus 224 ± 112 eggs/g of GFBW, respectively). This may be a result of the relatively small sample size in the present study. However, our annual fecundity estimates are similar to those from the eastern GOM (Collins et al. 2003) but much higher than estimates from the U.S. South Atlantic (Grimes and Huntsman 1980; Cuellar et al. 1996; Table 6). This regional difference in annual fecundity was caused by the higher spawning frequency of Vermilion Snapper in the GOM relative to the U.S. South Atlantic.

Current management regulations for the Vermilion Snapper are a minimum length limit of 25.4 cm TL (10 in) for both the commercial and recreational fisheries. Based on the growth documented in this study, individuals are vulnerable to the fishery between the ages of 2 and 4 years old. Since Vermilion Snapper likely mature at <1 year, based on findings from previous literature on length at maturity (Fitzhugh et al. 2015), they are harvested after they have reproduced for 1 to 3 years. The ability of Vermilion Snapper to spawn for several seasons prior to recruitment into the fishery may account for the healthy state of the fishery and lack of overfishing (SEDAR 45 2016) and suggests current length restrictions should be maintained.

In conclusion, there are variable growth and reproduction data for Vermilion Snapper in the GOM, although our data are the first to quantitatively document various aspects of reproduction in the north-central GOM. We have provided a detailed histological description for both males and females and documented daily spawning of females. Additionally, we have reported the first evidence of Vermilion Snapper spawning on artificial structures; these structures are more prevalent in the north-central GOM than in the eastern GOM. Region-specific growth and reproduction estimates will increase the clarity of population level characteristics as well as provide a more robust understanding of the life history of this commercial and recreationally important species. Though this study did not address the management of this species directly, the growth and reproductive characteristics reported here will allow for more representative and therefore more accurate estimates of life history characteristics throughout the GOM, which are vital to sustainably managing a species with a large distribution such as the Vermilion Snapper.

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REFERENCES

- Allman, R. J. 2007. Small-scale spatial variation in the population structure of Vermilion Snapper (*Rhomboplites aurorubens*) from the north-east Gulf of Mexico. *Fisheries Research* 88:88–99.
- Allman, R. J., J. A. Tunnell, and B. K. Barnett. 2005. Vermilion Snapper otolith aging: 2001–2004 data summary. National Marine Fisheries Service, Panama City Laboratory Contribution Series 05-02, Panama City, Florida.
- Bagenal, T. B., and E. Braum. 1971. Eggs and early life history. Pages 159–181 in W. E. Ricker, editor. *Methods for assessment of fish production in fresh waters*, 2nd edition. Blackwell Science, International Biological Programme handbook 3, Oxford, UK.
- Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Chapman and Hall, Fishery Investigations 11, London.
- Breder, C. M. Jr. 1929. Field book of marine fishes of the Atlantic coast from Labrador to Texas. G. P. Putnam's Sons, New York.
- Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre-Barbieri. 2011. A standardized terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 3:52–70.
- Bubley, W. J., and D. M. Wyanski. 2017. Update of Vermilion Snapper, *Rhomboplites aurorubens*, reproductive life history from the MAR-MAP/SERFS program. Southeast Data, Assessment, and Review, SEDAR55-WP03, North Charleston, South Carolina.
- Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261–304.
- Burton, M. L. 2002. Age, growth and mortality of Mutton Snapper, *Lutjanus analis*, from the east coast of Florida, with a brief discussion of management implications. *Fisheries Research* 59:31–41.
- Campana, S. E. 2001. Accuracy, precision, and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59:197–242.
- Chen, Y., D. Jackson, and H. Harvey. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1228–1235.
- Colby, P. J., and S. Nepsky. 1981. Variations among stocks of Walleye (*Stizostedion vitreum vitreum*): management implications. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1814–1831.
- Coleman, F. C., W. F. Figueira, J. S. Ueland, and L. B. Crowder. 2004. The impact of United States recreational fisheries on marine fish populations. *Science* 305:958–1960.
- Collins, L. A., W. T. Walling Jr., J. H. Brusher, M. G. Remy, J. J. Mikulas, G. M. Chandler, and D. M. La Fond. 2003. Preliminary results from a study of reproduction in the Vermilion Snapper (Lutjanidae: *Rhomboplites aurorubens*) from the eastern Gulf of Mexico, 1991–2001. *Proceedings of the Gulf and Caribbean Fisheries Institute* 54:580–591.
- Corey, M. M., R. T. Leaf, N. J. Brown-Peterson, M. S. Peterson, S. D. Clardy, and D. A. Dippold. 2017. Growth and spawning dynamics of Southern Flounder in the north-central Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 9:231–243.
- Cuellar, N., G. R. Sedberry, and D. M. Wyanski. 1996. Reproductive seasonality, maturation, fecundity, and spawning frequency of the Vermilion Snapper, *Rhomboplites aurorubens*, off the southeastern United States. *U.S. National Marine Fisheries Service Fishery Bulletin* 94:635–653.
- Dippold, D. A., R. T. Leaf, J. R. Hendon, and J. S. Franks. 2016. Estimation of the length-at-age relationship of Mississippi's Spotted Seatrout. *Transactions of the American Fisheries Society* 145:295–304.
- Doeringhaus, J., K. Hentrich, M. Troup, A. Stavrinsky, and S. Anderson. 2014. An assessment of sector separation on the Gulf of Mexico recreational Red Snapper fishery. *Marine Policy* 50:309–317.
- Fischer, A. J., M. S. Baker Jr., and C. A. Wilson. 2004. Red Snapper (*Lutjanus campechanus*) demographic structure in the northern Gulf of Mexico based on spatial patterns in growth rates and morphometrics. *U.S. National Marine Fisheries Service Fishery Bulletin* 102:593–603.
- Fitzhugh, G. R., H. M. Lyon, and B. K. Barnett. 2015. Reproductive parameters for Gulf of Mexico Vermilion Snapper, *Rhomboplites aurorubens*, 1991–2014. Southeast Data, Assessment, and Review, SEDAR45-WP-02, North Charleston, South Carolina.
- Fitzhugh, G. R., K. W. Shertzer, G. T. Kellison, and D. M. Wyanski. 2012. Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. *U.S. National Marine Fisheries Service Fishery Bulletin* 110:413–425.
- Gallaway, B. J., S. T. Szedlmayer, and W. J. Gazey. 2009. A life history review for Red Snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. *Reviews in Fisheries Science* 17:48–67.
- Glenn, H. D., J. H. Cowan, and J. E. Powers. 2017. A comparison of Red Snapper reproductive potential in the northwestern Gulf of Mexico: natural versus artificial habitats. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 9:139–148.
- Grimes, C. B. 1978. Age, growth, and length-weight relationship of Vermilion Snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina waters. *Transactions of the American Fisheries Society* 107:454–456.
- Grimes, C. B. 1987. Reproductive biology of the Lutjanidae: a review. Pages 339–294 in J. J. Polovina and S. Ralston, editors. *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder, Colorado.
- Grimes, C. B., and G. R. Huntsman. 1980. Reproductive biology of the Vermilion Snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina. *U.S. National Marine Fisheries Service Fishery Bulletin* 78:137–146.
- Grimes, C. B., C. S. Manooch, and G. R. Huntsman. 1982. Reef and rock outcropping fishes of the outer continental shelf of North Carolina and South Carolina, and ecological notes on the Red Porgy and Vermilion Snapper. *Bulletin of Marine Science* 32:277–289.
- Haddon, M. 2011. *Modeling and quantitative methods in fisheries*. CRC Press, Boca Raton, Florida.
- Heppell, S. A. 2007. Behavior, physiology, and life history comparison in four species of grouper: what do they mean for grouper management? *Proceedings of the Gulf and Caribbean Fisheries Institute* 59:171–174.
- Hood, P. B., and A. K. Johnson. 1999. Age, growth, mortality, and reproduction of Vermilion Snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico. *U.S. National Marine Fisheries Service Fishery Bulletin* 97:828–841.

- Horst, J. 2004. Red Snapper age and growth. Louisiana State University Agricultural Center, Louisiana Sea Grant College Program, Baton Rouge.
- Hunter, J. R., N. C. Lo, and R. J. Leong. 1985. Batch fecundity in multiple spawning fishes. NOAA Technical Report NMFS 36:67–77.
- Hunter, J. R., and B. J. Macewicz. 1985. Measurement of spawning frequency in multiple spawning fishes. NOAA Technical Report NMFS 36:79–94.
- Jackson, M. W., D. L. Nieland, and J. H. Cowan Jr. 2006. Diel spawning periodicity of Red Snapper, *Lutjanus campechanus*, in the northern Gulf of Mexico. *Journal of Fish Biology* 68:695–706.
- Jaxion-Harm, J., and S. T. Szedlmayer. 2015. Depth and artificial reef type effects on size and distribution of Red Snapper in the northern Gulf of Mexico. *North American Journal of Fisheries Management* 35:86–96.
- Johnson, M. W., S. P. Powers, C. L. Hightower, and M. Kenworthy. 2010. Age, growth, mortality, and diet composition of Vermilion Snapper from the north-central Gulf of Mexico. *Transactions of the American Fisheries Society* 139:1136–1149.
- Jordan, D. S., and B. W. Evermann. 1896. A check-list of the fishes and fishlike vertebrates of North and Middle America. Pages 207–284 in *Report of the Commissioner for 1928, appendix 5*. U.S. Commission of Fish and Fisheries, Washington, D.C.
- Karnauskas, M., J. F. Walter III, M. D. Campbell, A. G. Pollack, J. M. Drymon, and S. Powers. 2017. Red Snapper distribution on natural habitats and artificial structures in the northern Gulf of Mexico. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 9:50–67.
- Lowerre-Barbieri, S., L. Crabtree, T. Switzer, S. W. Burnsed, and C. Guenther. 2015. Assessing reproductive resilience: an example with South Atlantic Red Snapper *Lutjanus campechanus*. *Marine Ecology Progress Series* 526:125–141.
- Lowerre-Barbieri, S. K., K. Ganas, F. Saborido-Rey, H. Murua, and J. R. Hunter. 2011. Reproductive timing in marine fishes: variability, temporal scales, and methods. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 3:71–91.
- Nelson, R. S. 1988. A study of the life history, ecology, and population dynamics of four sympatric reef predators (*Rhomboplites aurorubens*, *Lutjanus campechanus*, Lutjanidae; *Haemulon melanurum*, Haemulidae; and *Pagrus pagrus*, Sparidae) on the east and west Flower Garden banks, northwestern Gulf of Mexico. Doctoral dissertation. North Carolina State University, Raleigh.
- NMFS (National Marine Fisheries Service). 2014a. Recreational fisheries statistics. Available: <http://www.st.nmfs.noaa.gov/recreational-fisheries/data-and-documentation/queries/index>. (March 2016).
- NMFS (National Marine Fisheries Service). 2014b. Commercial landing statistics. Available: <https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index>. (March 2016).
- Petersen, C. W., and R. R. Warner. 1998. Sperm competition in fishes. Pages 435–463 in T. R. Birkhead and A. P. Moller, editors. *Sperm competition and sexual selection*. Academic Press, San Diego, California.
- Polunin, N. V. C., and C. M. Roberts. 1996. Reef fisheries. Chapman and Hall, London.
- Potts, J. C., C. S. Manooch III, and D. S. Vaughan. 1998. Age and growth of Vermilion Snapper from the southeastern United States. *Transactions of the American Fisheries Society* 127:787–795.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rezak, R., and T. J. Bright. 1985. Reefs and banks of the northwestern Gulf of Mexico: their geological, biological, and physical dynamics. Wiley, New York.
- Ricker, W. E. 1975. Computation and interpretation of biological sciences of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Roff, D. A. 1980. A motion for the retirement of the Von Bertalanffy function. *Canadian Journal of Fisheries and Aquatic Sciences* 37:127–129.
- Saari, C. R., J. H. Cowan Jr., and K. M. Boswell. 2014. Regional differences in the growth of Red Snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico. *U.S. National Marine Fisheries Service Fishery Bulletin* 112:261–273.
- Schirripa, M. 1992. Analysis of the age and growth of Vermilion Snapper with an assessment of the fishery in the Gulf of Mexico. National Marine Fisheries Service, Contribution MIA-91/92-74, Miami.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675.
- SEDAR 31 (Southeast Data, Assessment, and Review 31). 2013. Gulf of Mexico Red Snapper Stock Assessment Report. Southeast Data, Assessment, and Review, North Charleston, South Carolina.
- SEDAR 45 (Southeast Data, Assessment, and Review 45). 2016. Gulf of Mexico Vermilion Snapper, Stock Assessment Report. Southeast Data, Assessment, and Review, Charleston, South Carolina.
- SEDAR 9 (Southeast Data, Assessment, and Review 9). 2006a. Stock assessment report of SEDAR 9: Gulf of Mexico Vermilion Snapper, assessment report 3. Southeast Data, Assessment, and Review, Charleston, South Carolina.
- SEDAR 9 (Southeast Data, Assessment, and Review 9). 2006b. Stock assessment report of Gray Triggerfish, assessment report 1. Southeast Data, Assessment, and Review, Charleston, South Carolina.
- Simonsen, K. A., J. H. Cowan Jr., and K. M. Boswell. 2015. Habitat differences in the feeding ecology of Red Snapper (*Lutjanus campechanus*, Poey 1860): a comparison between artificial and natural reefs in the northern Gulf of Mexico. *Environmental Biology of Fishes* 98:811–824.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.
- Tomkiewicz, J., M. N. Kofoed, and J. S. Pedersen. 2011. Assessment of testis development during induced spermatogenesis in the European Eel *Anguilla anguilla*. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 3:106–118.
- Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. *BioScience* 45:759–771.
- van Overzee, H. M., and A. D. Rijnsdorp. 2015. Effects of fishing during the spawning period: implications for sustainable management. *Reviews in Fish Biology and Fisheries* 25:65–83.
- VanderKooy, S., editor. 2009. A practical handbook for determining the ages of Gulf of Mexico fishes, 2nd edition. Gulf States Fisheries Commission, Publication 167, Ocean Springs, Mississippi.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* 10:181–213.
- Weninger, Q., and J. R. Waters. 2003. Economic benefits of management reform in the northern Gulf of Mexico reef fish fishery. *Journal of Environmental Economics and Management* 46:207–230.
- Woods, M. K., A. J. Fischer, J. H. Cowan Jr., and D. L. Nieland. 2003. Size and age at maturity of female Red Snapper *Lutjanus campechanus* in the northern Gulf of Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 54:526–537.
- Zhao, B., J. C. McGovern, and P. J. Harris. 1997. Age, growth, and temporal change in size at age of the Vermilion Snapper from the South Atlantic Bight. *Transactions of the American Fisheries Society* 126:181–193.

SUPPORTING INFORMATION

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