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Sex-Specific Growth and Reproductive Dynamics of Red Drum in the Northern Gulf of Mexico

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Abstract

The Red Drum *Sciaenops ocellatus* stock is heavily targeted in the Gulf of Mexico (GOM) by recreational fishers and supports a small commercial fishery in Mississippi. Despite their popularity, little recent work has been done to describe their life history. In this work, we describe sex-specific growth and reproductive dynamics of Red Drum collected from the northern GOM from September 2016 through October 2017. We evaluated seven candidate growth models and found that the three-parameter von Bertalanffy growth function (VBGF) was the best candidate length-at-age model. No significant difference in growth between sexes was observed with the three-parameter VBGF, despite the female-specific curve having a larger mean asymptotic length than the male-specific curve. All seven candidate growth models predicted similar mean length-at-age estimates, and four of them exhibited significant differences in sex-specific mean length at age, with females reaching a larger length at age than males after age 5. There was no significant difference between the sex-specific weight-at-length relationships. Red Drum are batch spawners that spawn in northern GOM coastal waters during August and September. We estimated 3.7 d between spawns and 10.5 spawning events per female in 2017. Nearly 20% of fish collected during the spawning season were sexually mature but reproductively inactive, indicating the possibility of skipped spawning. The age at 50% maturity was around 3 years (length at 50% maturity = 670 mm TL) in both sexes, but fish were not spawning capable until age 4.5 (703 mm TL) in males and age 5.8 (840 mm TL) in females. Furthermore, elevated gonadosomatic indices were not observed until around age 5–6. The updated life history information presented in this work helps to address current data limitations and provides critical information for future assessments of Red Drum stocks in the northern GOM.

The Red Drum *Sciaenops ocellatus* is a large, long-lived, recreationally and commercially desirable species (Beckman et al. 1988) that ranges throughout the Gulf of Mexico (GOM) from northern Mexico to the Florida Keys and along the East Coast of the United States to Massachusetts (Matlock 1980; Murphy and Taylor 1990;

Porch et al. 2002). The GOM Red Drum stock is primarily targeted in inshore waters, although there is a history of stock exploitation in the nearshore and coastal zone. The popularity of Red Drum in the northern GOM surged in the mid-1980s, when increased demand and easily targeted spawning aggregations led to a harvest of over 6 million kg in 1985 (Powers et al. 2012). This magnitude of harvest was not sustainable and led to a moratorium on the commercial harvest of Red Drum in U.S. federal waters in 1986 (NMFS 1986). Commercial harvest of Red Drum is permissible in coastal areas, where the stock is managed by individual states rather than the federal government, although Mississippi is currently the only state to allow commercial harvest (27,215.5-kg quota in 2017; www.dmr.ms.gov). Over the past decade, Gulf-wide mean annual harvest in the United States was over 3 million kg, and as high as over 15.3 million kg; in Mississippi, the mean annual recreational harvest ranged from 383,640 kg to 1.4 million kg (NMFS 2018). In the most recent stock assessments, the GOM Red Drum stock was classified as overfished (Porch 2000; SEDAR 2016).

Despite the interest in the fishery, the GOM Red Drum stock is considered a data-limited stock (SEDAR 2016). Information on the demographic characteristics, age and growth, and reproductive dynamics of Mississippi's Red Drum stock is inferred from studies performed in coastal waters of Texas, Louisiana, Alabama, and Florida, even though Red Drum populations appear to exhibit limited genetic transfer among regional subpopulations (Gold et al. 2001; Rooker et al. 2010). Much of the biological information on the Red Drum stock in the GOM comes from studies conducted in the 1980s and 1990s, of which only one published study was specific to the Mississippi coastal region (Overstreet 1983).

Information describing age at length is essential for quantitative age-structured stock assessment, which allows determination of a population's dynamics and response to fishing pressure (Beckman et al. 1989; Denney et al. 2002). There is broad variation in reported age–growth models for Red Drum because of disagreement on the presence of sexually dimorphic growth and because there remains some question about which models best describe individual growth dynamics. Beckman et al. (1989) found a significantly better fit ($P < 0.001$) when growth was modeled for each sex separately than when sexes were aggregated in the analysis, whereas other studies aggregated the sexes (Rohr 1980; Wakefield and Colura 1983; Doerzbacher et al. 1988; Murphy and Taylor 1990; Matlock 1992; Porch 2000). From a model specification perspective, the von Bertalanffy growth function (VBGF) is commonly used to describe the length-at-age relationship (Beckman et al. 1989; Murphy and Taylor 1990; Ross et al. 1995). However, the VBGF may not be the most appropriate for Red Drum because of their seasonal growth dynamics and ontogenetic changes in

growth rate (Porch et al. 2002). Although the use of multiple models addresses the issue of model misspecification (Katsanevakis 2006), the approach will only be as effective as the models used in the analysis. Spatial variability is evident in previous growth parameter estimates, even on an intra-state level (Wakefield and Colura 1983; Matlock 1992). Regional sex-specific age–growth relationships modeled through multiple candidate models should therefore improve the estimates of mean length at age for Red Drum in Mississippi and Gulf-wide.

Knowledge of the spawning characteristics of Red Drum is also essential to developing effective management. Reproductive traits, such as the duration and start of the spawning season and maturation, influence stock productivity (Murawski et al. 2001; Lowerre-Barbieri et al. 2011), and stock assessments are sensitive to changes in the maturity schedule (Brown-Peterson et al. 2017). Previous studies have addressed the reproductive characteristics of Red Drum in the northern GOM (Overstreet 1983; Fitzhugh et al. 1988; Murphy and Taylor 1990; Wilson and Nieland 1994), but those studies were performed over two and three decades ago, and the history of stock exploitation and current recreational fishing pressure on young individuals make the stock susceptible to alterations in reproductive characteristics (Trippel et al. 1997; Murawski et al. 2001; Wright and Trippel 2009). Confidence in the current descriptions of the stock's reproductive dynamics is also hindered by variability in previous estimates of the onset of maturity and spawning season. These discrepancies may be due to geographic differences (Pearson 1929; Overstreet 1983), differences in definitions and methods of determining maturity, and differences in classifying reproductive phases (West 1990; Wilson and Nieland 1994).

Due to the variety in descriptions of Red Drum growth and reproductive characteristics and due to the regional nature of these characteristics (Matlock 1992; Wilson and Nieland 1994), current and regional descriptions are necessary for the management of Mississippi's portion of the Red Drum stock. In this work, we quantify the length-at-age relationship using multiple candidate models, determine the best-supported model, and quantify the weight-at-length relationship. We then determine whether these relationships are significantly different between male and female Red Drum. We also estimate the reproductive characteristics of Red Drum, including (1) sex-specific age and length at maturity, (2) the spawning season, and (3) the spawning interval.

METHODS

Red Drum were collected in the northern GOM off the coasts of Mississippi, eastern Louisiana, and western Alabama from September 2016 to October 2017 by using fishery-dependent methods (primarily samples collected from

fishing tournaments and charter companies that used trolling and small-tackle methods) and fishery-independent methods (cast-net, gill-net, longline, and purse-seine surveys) over the entire study period. The total weight (W; g), TL (mm), SL (mm), and FL (mm) of each specimen were recorded. A subsample (n = 71) was measured both whole and as filleted carcasses. Because all three length measurements (SL, FL, and TL) are found in the literature, for comparison we describe the linear relationship between each, as well as the relationship between each length measurement from the filleted fish and that of the whole fish. Sagittal otoliths and whole gonads were collected from each fish and weighed (nearest 0.01 g). Sex and reproductive phase were initially determined macroscopically in accordance with the methods of Brown-Peterson et al. (2011).

Otolith processing and age determination followed the procedures presented by VanderKooy (2009). The left sagittal otolith (or the right otolith when the left was unavailable) was used by two independent readers to estimate the age of each specimen. If the age estimates from the two readers did not agree, then a third independent reader also aged the otolith. If all three resulting estimates still differed, the fish's other otolith was read in the same manner. If the age estimates were still not in agreement, the age was rejected. The translucent outer edge margin of the otolith between the otolith's edge and the most recent fully formed opaque zone was measured using i-Solution Lite software and was compared to the width of the most recently formed translucent zone measured in the same manner. This proportion was assigned a categorical margin code based on the percent translucent area: 1 = 0% translucent edge (i.e., an opaque margin); 2 = >0% to 33%; 3 = 33–66%; and 4 = 66–99%. Following Ditty (1986) and Beckman et al. (1988, 1989), we assumed a birthdate of October 1, and we assumed that February 1 was the date of deposition for the annulus' opaque zone. However, because the first complete opaque zone is not deposited until the fish's second winter (Beckman et al. 1988, 1989; Murphy and Taylor 1990), the first opaque zone indicates an age of about 1.5 years, with each subsequent opaque zone indicating an additional year of age. We added the number of days between October 1 and the catch date to the annulus-derived age estimate. Fish with no discernable annuli were assigned ages based on capture date and margin code: individuals with a margin code of 3 or 4 were assigned an annulus-derived age of 1 year plus the number of days at large (number of days between October 1 and the date of capture divided by 365), and those collected with a margin code of 1 or 2 were assigned partial-year ages equal to the number of days at large. As a potential cost-savings method to estimate fish age without sectioning the otolith, we also modeled age as a function of otolith weight by using a power function.

To examine sex and reproductive phase microscopically, a cross section (<1 cm^3) from the center of the left gonad (when available, or the right gonad when the left was missing) was fixed in 10% neutral buffered formalin within 24 h of collection, dehydrated, embedded, sectioned at 4 μm, and stained following a regressive method of hematoxylin staining and eosin counterstaining (Luna 1968). We examined stained slides microscopically to determine sex, classify each individual as mature or not mature, and assign a reproductive phase following the terminology described by Brown-Peterson et al. (2011). Wilson and Nieland (1994) and Fitzhugh et al. (1988) found oocyte development in Red Drum to be homogeneous throughout the gonad; to corroborate their findings, we examined tissue from anterior, middle, and posterior sections of both the left and right lobes of the gonad from one spawning-capable female. When identifying reproductive phases, every histology slide was read by two independent readers with no prior knowledge about the sample. If the two readers disagreed on the phase, the slide was examined a second time by both readers together; if an agreement was still not reached, the sample was removed from analysis. Although the presence of cortical alveolar oocytes in females and primary spermatocytes in males signifies physiological maturity (Brown-Peterson et al. 2011), individuals with these early gamete developmental stages are in the early developing subphase and are considered reproductively inactive (Brown-Peterson et al. 2017). We considered Red Drum to be sexually mature when they entered the developing phase, with primary vitellogenic oocytes present in females (following the definition of Wilson and Nieland 1994) and secondary spermatocytes present in males. We classified fish in the immature and virgin early developing phases as not mature. Fish that were identified to be in the early developing (and had obviously spawned during the previous year), developing, spawning-capable, actively spawning, regressing, or regenerating phases were classified as mature.

We described the Red Drum age–growth relationship using seven length-at-age functions and a power function for the weight-at-length relationship. The length-at-age candidate models included a three-parameter VBGF, a two-parameter VBGF, a "double" VBGF, a "linear" VBGF, the Gompertz growth model, a three-parameter logistic model, and the Porch et al. (2002) seasonal and damped model. The double VBGF and Porch et al. (2002) models were fitted to the data using Bayesian methods for nonlinear regression in the program JAGS (Plummer 2003) by using the R package "rjags" (Plummer et al. 2016). All other candidate length-at-age models were fitted with a nonlinear least-squares regression (R Development Core Team 2016). We evaluated relative model fit by using Akaike's information criterion (AIC), a measure of

a model's goodness of fit relative to other candidate models (Katsanevakis 2006). The best representative model was indicated by the lowest AIC value. We constructed both sex-specific and sex-aggregated relationships for each of the candidate models.

The three-parameter VBGF (von Bertalanffy 1938) is a nonlinear regression and is defined by

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)}\right],$$

where L_t is the TL (mm) at age t (years); L_∞ is the mean hypothetical maximum TL; k is a growth rate coefficient (year^{-1}); and t_0 is the theoretical age (years) at a length of zero. The two-parameter VBGF is defined in the same manner, but the parameter t_0 is set equal to zero.

The double VBGF (Vaughan and Helser 1990) is a segmented nonlinear regression model that is defined as

$$L_t = \begin{cases} L_\infty[1 - e^{-k_1(t-t_1)}], & t < t_p \\ L_\infty[1 - e^{-k_2(t-t_2)}], & t \geq t_p \end{cases}$$

$$t_p = (k_2 t_2 - k_1 t_1)/(k_2 - k_1),$$

where L_t is the TL (mm) at age t (years); L_∞ is the mean hypothetical maximum TL; k_1 and k_2 are instantaneous growth rate coefficients (year^{-1}); and t_1 and t_2 are the hypothetical ages at which TL is equal to zero. This model allows the growth rate to change at a pivotal age, t_p.

Another variant of the VBGF is the linear VBGF (Hoese et al. 1991; Vaughan 1996). This function describes the maximum length asymptote as a linear function of age with an intercept of b_0 and a slope of b_1:

$$L_t = (b_0 + b_1 t)\left[1 - e^{-k(t-t_0)}\right],$$

with growth rate coefficient k (year^{-1}) and age t (years). The parameter t_0 is the theoretical age (years) at a length of zero.

Gompertz (1825) developed a differential equation to describe survival, which has been solved and parameterized to model growth (Ebert 1999; Grosjean 2001). It is a sigmoidal curve with an exponential decrease in growth rate with size:

$$L_t = L_\infty e^{-e^{-k(t-t_0)}},$$

where L_t is the TL (mm) at age t (years); L_∞ is the mean maximum TL (mm); k is a relative growth rate parameter (year^{-1}); and t_0 is a location parameter that represents the age at inflection and controls the horizontal position of the curve.

The three-parameter logistic length-at-age model (Ricker 1975) is defined as

$$L_t = \frac{L_\infty}{(1 + ae^{-bt})},$$

where L_t is the TL (mm) at age t (years); L_∞ is the mean maximum TL (mm); and the parameters a (unitless) and b (year^{-1}) determine the shape of the curve.

The Porch et al. (2002) seasonal and damped model incorporates a growth rate that declines with age and varies with the seasons. This model is defined as

$$L_t = L_\infty \left[1 - e^{\beta_1 + \beta_2 - k_0(t-t_0)}\right]$$

$$\beta_1 = \frac{k_1}{\lambda_1}\left(e^{-\lambda_1 t} - e^{-\lambda_1 t_0}\right)$$

$$\beta_2 = \frac{k_2}{4\pi^2 + (\lambda_2)^2}\left(e^{-\lambda_2 t}\begin{Bmatrix} 2\pi\cos[2\pi(t_c - t)]- \\ \lambda_2\sin[2\pi(t_c - t)] \end{Bmatrix}\right. \\ \left. - e^{-\lambda_2 t_0}\begin{Bmatrix} 2\pi\cos[2\pi(t_c - t_0)]- \\ \lambda_2\sin[2\pi(t_c - t_0)] \end{Bmatrix}\right),$$

where L_t is the TL (mm) at age t (years); L_∞ is the mean hypothetical maximum TL (mm); k_0, k_1, and k_2 are instantaneous growth rate coefficients (year^{-1}); λ_1 and λ_2 are damping coefficients; t_0 is the theoretical age (years) at a length of zero; and t_c is a shifting parameter for the sine wave, valued between 0 and 1. The sex-specific weight-at-length relationships were described with the power function:

$$W = aL^b,$$

where W is weight (g); a is a coefficient; L is TL (mm); and b is an exponent that represents the change in length relative to weight.

We used an analysis of residual sum of squares (F-ratio) to test for a significant difference ($\alpha < 0.05$) between male- and female-specific models for the length-at-age and weight-at-length relationships (Chen et al. 1992). Parameter-specific differences were also evaluated, and differences in L_∞, k, and t_0 were deemed nonsignificant if the 95% confidence intervals (CIs) overlapped the means. Growth parameter estimates obtained in this study were compared to others reported for the GOM in the same manner.

We estimated mean length at 50% maturity using a two-parameter logistic model:

$$M_{TL} = \frac{100\%}{1 + e^{-r(TL - L_{50})}},$$

where r is the instantaneous rate of change (mm^{-1}); and L_{50} is the TL (mm) at 50% maturity. Age at 50% maturity was calculated using a similar model:

$$M_{\text{Age}} = \frac{100\%}{1 + e^{-r(\text{Age}-A_{50})}},$$

where r is the instantaneous rate of change (year^{-1}); and A_{50} is the age (years) at 50% maturity. The 95% CIs for the mean length and age at 50% maturity were also estimated and reported.

We determined spawning season timing and duration by using a sex-specific gonadosomatic index (GSI) for mature fish, and we verified these by histological examination of gonads. The GSI is one measure of temporal gonadal development and is calculated as

$$\text{GSI} = \left(\frac{\text{GW}}{\text{GFBW}}\right) \times 100,$$

where GW is gonad weight (g); and GFBW is gonad-free body weight (g). Immature fish were not included in the GSI calculations. We used linear regression to determine whether there was a relationship between GSI and GFBW, with no significant relationship indicating that GSI is a valid indicator of spawning preparedness (Jons and Miranda 1997). Normality and homogeneity of variance of GSI values were tested with the Shapiro–Wilk test and Bartlett's test, respectively. Mean monthly GSI values were calculated with SEs and compared using a nonparametric Kruskal–Wallis test and a post hoc Dunn's test for pairwise comparisons to determine the months in which mean GSI values were significantly different ($\alpha = 0.05$). The distribution of reproductive phases by month was also used to estimate the spawning season, with the presence of fish in the spawning-capable and actively spawning phases indicating the spawning season.

We used spawning-capable and actively spawning females to estimate spawning interval, as Red Drum are batch spawners (Fitzhugh et al. 1988; Wilson and Nieland 1994). Spawning interval is the average number of days between successive individual female spawns. This was determined using histology by taking the inverse of the proportion of spawning-capable females that were spawning imminent or had spawned in the last 24 h (Hunter and Macewicz 1985; Wilson and Nieland 1994):

$$\text{spawning interval} = \frac{\text{SC}}{S},$$

where SC is the number of spawning-capable females; and S is the number of females with 24-h postovulatory follicles (POFs) and/or oocytes in the oocyte maturation (OM)

phase. To obtain the spawning frequency, the spawning interval was multiplied by the number of days between the first and last observations of the spawning-capable phase in females.

RESULTS

In total, 791 individual Red Drum were collected (550 and 241 by fishery-dependent and fishery-independent methods, respectively), including a total of 334 males (242 and 92, respectively), 361 females (259 and 102, respectively), and 96 unsexed individuals (49 and 47, respectively); fish ranged in size from 105 to 1,115 mm TL (Figure 1). Otolith-derived age estimates were obtained from 451 individuals (418 and 33 collected by fishery-dependent and fishery-independent methods, respectively; Figure 1), and age estimates ranged from 0.56 to 31.4 years. The linear relationships between TL and SL ($r^2 = 0.984$) explained slightly less of the variance than that between TL and FL ($r^2 = 0.995$), but both relationships had significant slopes ($P < 0.001$; Table S.1 available separately online in the Supplement). The regression of filleted-fish TL versus whole-fish TL had the strongest relationship among all of the filleted length regressions ($r^2 = 0.999$; Table S.1); therefore, we used it to convert all TL measurements obtained from filleted carcasses ($n = 320$).

Otolith-derived age estimates had strong agreement between two readers (93.9%; coefficient of variation = 3.57; average percent error = 2.52%), and all otoliths had age agreement by at least two of the three readers after analysis by the third reader; thus, no ages were removed due to disagreement. There was a strong nonlinear relationship in otolith-derived age estimates with respect to otolith weight, which was described by the following power function parameters: $a = 3.74$ (95% CI = 3.54–3.95) and $b = 1.45$ (95% CI = 1.40–1.51). The SD of the unexplained variance in the model was relatively small (root mean square error = 1.67). We evaluated the patterns of residuals in the nonlinear regression qualitatively. We did not find patterning (runs of positive and negative residuals).

The seven candidate models that were used to describe length at age all had similar mean length-at-age predictions for the sex-aggregated data (Figure 2). The three-parameter VBGF had the most parsimonious fit, while the other six models had little to no support (Table 1). The estimated mean L_∞ values were significantly different between sexes for all of the length-at-age models, with the exception of the Porch et al. (2002) model (Table 2), but there was no significant difference in the sex-specific relationships for the two-parameter VBGF ($F = 0.88$, $P = 0.45$), three-parameter VBGF ($F = 0.68$, $P = 0.56$), or double VBGF ($F = 2.61$, $P = 0.051$) model. There was a significant difference between male- and female-specific
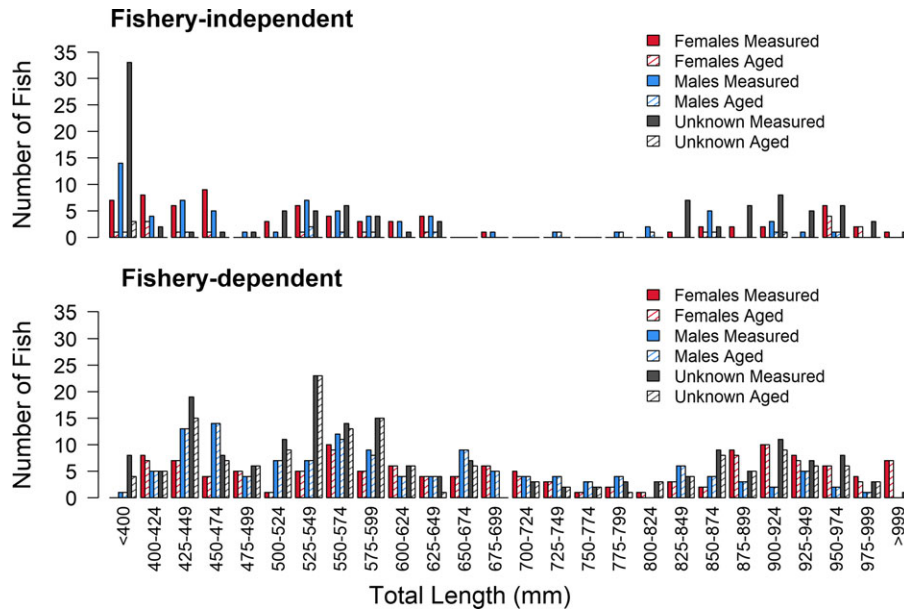
FIGURE 1. Frequencies of Red Drum males (blue bars), females (red bars), and undetermined-sex individuals (gray bars) that were collected using fishery-independent (top panel) and fishery-dependent (bottom panel) methods. Solid bars represent fish that were collected and measured only, whereas hatched bars represent those for which lengths and otolith-derived age estimates were obtained.

growth for the three-parameter logistic ($F = 4.25$, $P = 0.006$), Gompertz ($F = 4.28$, $P = 0.005$), linear VBGF ($F = 3.24$, $P = 0.022$), and Porch et al. (2002; $F = 2.82$, $P = 0.005$) models, with similar predicted growth until about age 5, after which females reached a larger length at age than males (Figure 3).
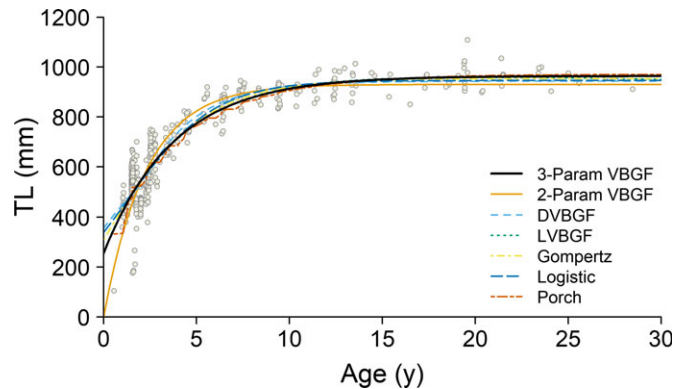

FIGURE 2. Seven candidate models were used to describe the sex-aggregated mean length-at-age relationship for Red Drum collected in the northern Gulf of Mexico ($n = 451$; gray points) from August 2016 through October 2017 (y = years). The candidate models included four variations of a von Bertalanffy growth function (VBGF): three-parameter (3-Param VBGF), two-parameter (2-Param VBGF), double (DVBGF), and linear (LVBGF). The other three models evaluated were the Gompertz function, the three-parameter logistic function, and the seasonal and damped model described by Porch et al. (2002).

Nearly equal numbers of males and females ($n = 92$ and 96, respectively) were used in the weight-at-length regressions. There was no significant difference between the male- and female-specific mean weight-at-length relationships ($F = 1.19$, $P = 0.31$). Fish were therefore pooled into a combined-sex regression, along with fish of unknown sex, where $a = 1.45 \times 10^{-5}$ (95% CI = 9.24×10^{-6} to 2.25×10^{-5}) and $b = 2.94$ (95% CI = 2.87–3.01).

Reproductive tissue was collected for histological analysis from a total of 694 of the samples ($n = 409$ with otolith-derived age estimates), and 23 samples (15 male and 8 female) were removed from the analysis due to irreconcilable disagreement on phase identification between readers. Body weight (W) was estimated from TL for individuals missing weight information ($n = 113$) by using the sex-aggregated weight-at-length relationship: $W = (1.45 \times 10^{-5}) \times \mathrm{TL}^{2.94}$. We used a linear regression to show that one gonad was roughly half the weight of both gonads together (slope = 1.9; intercept = 3.5; $r^2 = 0.96$, $P < 0.0001$); thus, the gonad weight for samples with only one non-damaged gonad ($n = 100$) was estimated to be two times the weight of the non-damaged gonad.

All histological reproductive phases and subphases were detected for female and male Red Drum. Some spawning-capable females had all stages of oocytes present, along with POFs, indicating that Red Drum are batch spawners with asynchronous oocyte development. However, no females in the actively spawning subphase had POFs, indicating that Red Drum are not daily spawners. Percent

TABLE 1. Mean parameter estimates (with associated 95% confidence intervals [CIs]) for the seven candidate length-at-age models used to describe sex-aggregated growth of Red Drum (n = 451) captured in the northern Gulf of Mexico from September 2016 through October 2017 (VBGF = von Bertalanffy growth function). Parameter symbols are defined in Methods. Relative model support is represented by the difference in Akaike's information criterion (ΔAIC), with a lower value indicating better support and zero indicating the best candidate model. The AIC weight (ω_i) represents the relative weight of support for each model. Asterisks indicate models for which Bayesian estimation was used; thus, the 95% credible interval is reported rather than the 95% CI.

Model	Parameter	Unit	Mean parameter estimate	95% CI	ΔAIC	ω_i
Three-parameter VBGF	L_∞	mm	964.1	943.9–985.5	0	1
	k	year^{-1}	0.26	0.23–0.30		
	t_0	years	−1.17	−1.52 to −0.87		
Two-parameter VBGF	L_∞	mm	920.3	903.6–937.2	45.54	0
	k	year^{-1}	0.46	0.44–0.48		
Porch et al. 2002*	L_∞	mm	971.8	952.7–993.6	1,201.15	0
	k_0	year^{-1}	0.23	0.05–0.26		
	t_0	years	−1.26	−1.65 to −0.78		
	k_1	year^{-1}	0.02	0.0008–0.20		
	λ_1		0.31	0.004–0.97		
	k_2	year^{-1}	0.73	0.58–0.92		
	λ_2		0.02	0.001–0.15		
	t_c		0.04	0.003–1.0		0
Double VBGF*	L_∞	mm	944.2	925.4–964.5	1,247.05	
	k_1	year^{-1}	0.17	0.16–0.21		
	t_1	years	−2.73	−2.99 to −2.00		
	k_2	year^{-1}	0.37	0.31–0.46		
	t_2	years	−0.15	−0.62 to 0.33		
Three-parameter logistic	L_∞	mm	946.7	929.0–965.0	1,262.30	0
	a		1.79	1.63–1.97		
	b		0.43	0.38–0.49		
Gompertz	L_∞	mm	954.2	935.5–973.6	1,263.72	0
	k	year^{-1}	0.34	0.30–0.39		
	t_0		0.33	0.15–0.49		
Linear VBGF	b_0	mm	987.8	909.9–1,094.9	1,269.97	0
	b_1	year^{-1}	−1.20	−6.07–2.75		
	k	year^{-1}	0.25	0.19–0.31		
	t_0	years	−1.24	−1.70 to −0.86		

agreement of phase classification between macroscopic inspection and histology was 76.0% for males and 57.1% for females. Percent agreement in males was greatest (86.4%) for the immature phase and lowest (29.6%) for the developing phase. Percent agreement in females was greatest (70.2%) for the spawning-capable phase and lowest (33.3%) for the regressing phase (Table S.2). The anterior, middle, and posterior portions of both the left and right ovaries from one spawning-capable fish were all classified the same, providing further evidence that oocyte development in Red Drum is homogeneous throughout the gonad.

The probability of maturity was modeled with respect to both length and age using the two-parameter logistic function (Figure 4). When modeled with respect to length, the mean L_{50} parameter was estimated to be 673 mm TL (95% CI = 653.7–694.5 mm) for males and 672 mm TL (95% CI = 659.4–687.2 mm) for females. The mean r-parameter was estimated to be 0.0144 mm^{-1} (95% CI = 0.0116–0.0185 mm^{-1}) for the male-specific model and 0.0218 mm^{-1} (95% CI = 0.0170–0.0286 mm^{-1}) for the female-specific model. The age-at-maturity models had mean A_{50} parameters of 3.4 years (95% CI = 2.98–4.02 years) and 3.1 years (95% CI = 2.83–3.34 years), with a mean r-parameter of 1.03 year^{-1} (95% CI = 0.659–1.664 year^{-1}) and 1.9070 year^{-1} (95% CI = 1.344–2.968 year^{-1}) for the male- and female-specific models, respectively.

There was a significant linear relationship between GSI and GFBW in sexually mature Red Drum, but the relationship explained little of the variance in the female-specific (r^2 = 0.10, P < 0.001) and male-specific

TABLE 2. Mean parameter estimates (with 95% confidence interval [CI] in parentheses) for sex-specific length at age of Red Drum captured in the northern Gulf of Mexico from September 2016 through October 2017. Parameter symbols are defined in Methods. Models include the best candidate model from this study (three-parameter von Bertalanffy growth function [VBGF]) and the models that indicated significantly ($\alpha = 0.05$) different length-at-age relationships between males and females. Relative model support is represented by the difference in Akaike's information criterion (ΔAIC), with a lower value indicating better support and zero indicating the best candidate model. The AIC weight (ω_i) represents the relative weight of support for each model. The asterisk indicates a model for which Bayesian nonlinear regression was used; thus, the 95% credible interval is reported rather than the 95% CI.

Model	Parameter	Unit	Females			Males		
			Values	ΔAIC	ω_i	Values	ΔAIC	ω_i
Three-parameter VBGF	L_∞	mm	990.4 (957.0–1,027.6)	0	1	934.5 (888.4–989.2)	0	1
	k	year^{-1}	0.26 (0.20–0.32)			0.26 (0.20–0.34)		
	t_0	years	-1.22 (-1.92 to -0.68)			-1.39 (-2.22 to -0.81)		
Porch et al. 2002*	L_∞	mm	991.42 (968.6–1,018.1)	649.45	0	949.1 (918.0–1,079.1)	481.83	0
	k_0	year^{-1}	0.23 (0.04–0.27)			0.21 (0.009–0.26)		
	t_0	years	-1.30 (-1.67 to -0.69)			-1.13 (-1.78 to -0.79)		
	k_1	year^{-1}	0.03 (0.001–0.22)			0.04 (0.002–0.22)		
	λ_1		0.31 (0.004–0.97)			0.37 (0.008–0.98)		
	k_2	year^{-1}	0.84 (0.61–0.99)			0.86 (0.57–0.99)		
	λ_2		0.07 (0.003–0.25)			0.06 (0.002–0.27)		
	t_c		0.98 (0.007–1.00)			0.99 (0.08–1.0)		
Three-parameter logistic	L_∞	mm	970.4 (948.1–993.9)	688.75	0	918.9 (891.7–948.0)	477.25	0
	a		1.62 (1.46–1.81)			1.51 (1.33–1.73)		
	b		0.39 (0.34–0.45)			0.41 (0.34–0.48)		
Gompertz	L_∞	mm	977.7 (954.2–1,002.8)	690.35	0	926.6 (896.55–956.73)	478.54	0
	k	year^{-1}	0.32 (0.27–0.37)			0.32 (0.26–0.38)		
	t_0	years	0.15 (-0.11 to 0.37)			-0.03 (-0.34 to 0.28)		
Linear VBGF	b_0	mm	1,034.7 (929.0–1,206.5)	695.37	0	947.4 (839.98–1,126.75)	482.90	0
	b_1	year^{-1}	-2.26 (-9.34 to 2.82)			-0.54 (-8.31 to 5.03)		
	k	year^{-1}	0.22 (0.15–0.30)			0.24 (0.16–0.34)		
	t_0	years	-1.57 (-2.28 to -1.02)			-1.61 (-2.44 to -0.99)		

($r^2 = 0.18$, $P < 0.001$) relationships; thus, GSI can be used as an indication of spawning seasonality. Mean GSI values were distinctly greater in August and September than during the rest of the year for both males and females (Figure 5), suggesting that Red Drum have a 2-month spawning season in the northern GOM. There was a significant correlation between monthly male and female mean GSIs (Spearman's rank correlation coefficient $r = 0.92$, $P < 0.0005$). The GSI values violated the assumption of normality, so a Kruskal–Wallis test was used to evaluate monthly differences nonparametrically. We found strong significant differences in the mean ranks of GSI for at least one of the months in both females ($\chi^2 = 64.17$, $P < 0.001$) and males ($\chi^2 = 66.65$, $P < 0.001$). The post hoc Dunn's test with a Bonferroni adjustment for pairwise comparisons indicated that the sums of female and male GSI ranks in August and September were significantly different from those in July and October ($P < 0.01$) but were not significantly different from each other ($P = 1.00$). The sums of ranks for

July and October were not significantly different ($P > 0.05$) than the sums from any other months.

Young Red Drum appear to contribute minimally to the spawning population based on GSI values. Throughout the year, we collected many Red Drum younger than age 5 that were histologically identified as mature, but both male and female GSI values during the spawning season were less than 1, with little variance (Figure 6). In contrast, older fish had mean ($\pm$SE) GSI values of 2.83 ± 0.35 for males and 2.72 ± 0.23 for females during August and September.

We also described the spawning season using the monthly distribution of reproductive phases. Histological examination revealed that August and September were the peak months for spawning in both females and males (Table 3). Spawning-capable males and females were collected in August and September, with a few spawning-capable males ($n = 5$) collected in October, and actively spawning (subphase of spawning capable) females were collected in September ($n = 3$). The mid-germinal epithelium
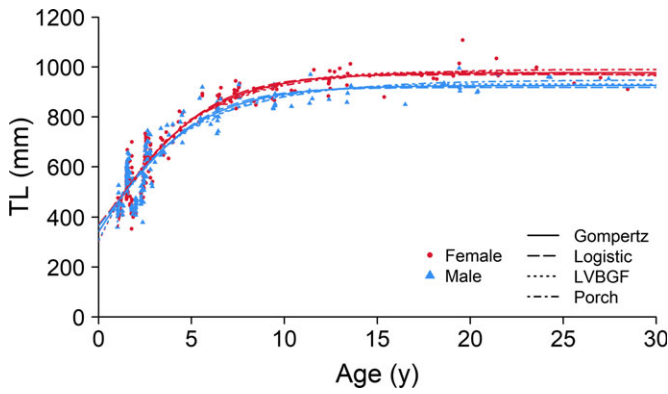
FIGURE 3. Four models describing the sex-specific mean length at age of Red Drum collected in the northern Gulf of Mexico ($n = 391$; 188 males and 203 females) from August 2016 through October 2017 had significantly different ($\alpha = 0.05$) relationships between male- and female-specific growth (y = years). Observed male (blue triangles) and female (red circles) values are displayed along with male-specific (blue lines) and female-specific (red lines) mean relationships. The four models included the Gompertz function, the three-parameter logistic function, the linear von Bertalanffy growth function (LVBGF), and the seasonal and damped model described by Porch et al. (2002).
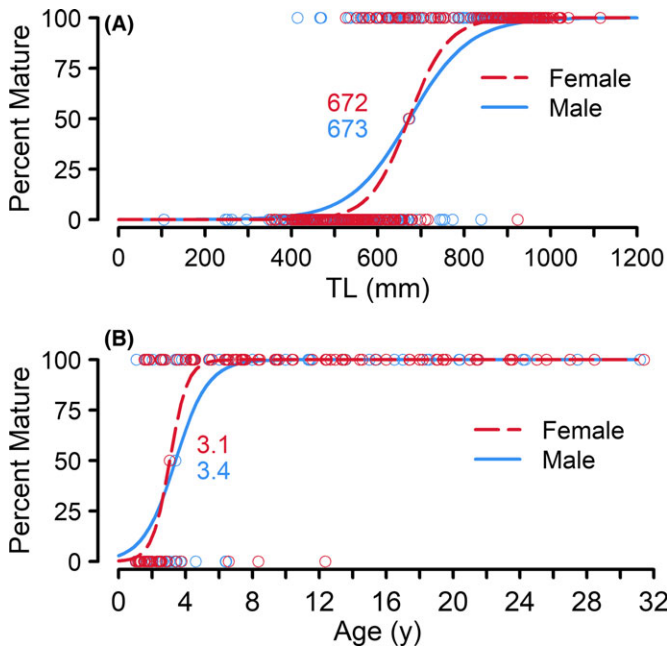

FIGURE 5. Mean ($\pm$SE) monthly gonadosomatic indices (GSIs) of sexually mature Red Drum females (red dashed line) and males (blue solid line; total $n = 249$) captured in the northern Gulf of Mexico from September 2016 through October 2017. Numbers above data points indicate female (red) and male (blue) sample sizes.

FIGURE 4. Percentage of Red Drum that were mature by (A) TL (mm; $n = 694$) and (B) age (years [y]; $n = 409$), modeled with a two-parameter logistic function, for females (red dashed line) and males (blue solid line) sampled from the northern Gulf of Mexico. The mean TL (mm) and age (years) at 50% maturity (L_{50} and A_{50}) parameter estimates are labeled at the inflection point. Individuals were assigned a binary maturity classification of 0% or 100%.

FIGURE 6. Box plot of age-specific gonadosomatic index (GSI) values for sexually mature Red Drum (A) females ($n = 79$) and (B) males ($n = 62$) captured in the northern Gulf of Mexico during the spawning season (August and September; y = years). Dark bands represent the median, box edges represent the 25% and 75% quartiles, and open circles represent outliers in the data.

subphase of spawning-capable males was most common in both August and September, and the early germinal epithelium subphase was less common as the spawning
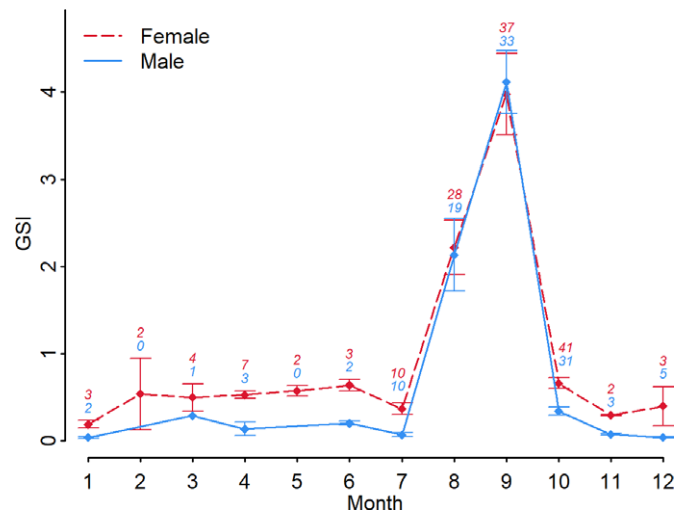
season progressed. The late germinal epithelium (LGE) subphase first appeared in September, and all of the spawning-capable males collected in October were in the LGE subphase. Females in the developing phase and early developing subphase were found during early August. For males, the developing phase was first seen in July, prior to the start of the spawning season, and was also commonly seen in August. The developing phase was also identified

TABLE 3. Monthly frequencies of reproductive phases for female and male Red Drum collected in the northern Gulf of Mexico from September 2016 through October 2017. The phases as defined by Brown-Peterson et al. (2011) are immature (IMM), developing (DEV), early developing (EDEV; a subphase of developing), spawning capable (SC), regressing (RGR), and regenerating (RGN). The spawning-capable phase is further separated into an actively spawning (AS) subphase for females and early germinal epithelium (EGE), mid-germinal epithelium (MGE), and late germinal epithelium (LGE) subphases for males.

| | | | | SC females | | SC males | | | | | |
Month	IMM	EDEV	DEV	SC	AS	EGE	MGE	LGE	RGR	RGN	n
Females											
Jan	87.5	0	0	0	0				0	12.5	32
Feb	71.4	0	0	0	0				0	28.6	7
Mar	66.7	0	0	0	0				0	33.3	12
Apr	0	0	0	0	0				0	100	7
May	50.0	0	0	0	0				0	50.0	4
Jun	50.0	0	0	0	0				0	50.0	6
Jul	78.7	0	0	0	0				0	21.3	47
Aug	24.4	4.9	4.9	46.3	0				0	19.5	41
Sep	21.2	0	0	57.7	5.8				0	15.4	52
Oct	62.5	0	0	0	0				2.5	35.0	120
Nov	81.8	0	0	0	0				0	18.2	11
Dec	71.4	0	0	0	0				0	28.6	14
Males											
Jan	84.6	3.8	0			0	0	0	0	11.5	26
Feb	100	0	0			0	0	0	0	0	6
Mar	75.0	8.3	0			0	0	0	0	16.7	12
Apr	37.5	12.5	0			0	0	0	0	50.0	8
May	100	0	0			0	0	0	0	0	2
Jun	0	0	0			0	0	0	0	100	2
Jul	69.8	11.3	3.8			0	0	0	0	15.0	53
Aug	38.5	5.1	12.8			17.9	23.1	0	0	2.6	39
Sep	19.2	2.1	0			10.6	46.8	17.0	4.3	0	47
Oct	60.7	2.2	4.5			0	0	5.6	14.6	12.4	89
Nov	53.3	20	0			0	0	0	6.7	20.0	15
Dec	52.6	5.3	0			0	0	0	0	42.1	19

in male samples collected during October, and the early developing subphase was present during most months. The regressing phase was identified in females collected during October and in males collected during late September, October, and early November. Only one regenerating male was collected during the peak spawning months of August and September, but 16 regenerating females were collected in the peak spawning months. Immature Red Drum were collected throughout the year and made up a large percentage of the samples, but no immature males were collected in June and no immature females were collected in April.

We used the presence of POFs and OM-stage oocytes in histology sections to estimate the spawning interval. Sampling in 2016 started late in September, and only four spawning-capable females were collected, all from the same day. Consequently, the spawning interval for 2016 was not estimated. Spawning interval was calculated for

2017, with 13 of the 48 spawning-capable females collected in August and September containing POFs or OM-stage oocytes. The resulting mean spawning interval was estimated to be every 3.7 d. Collections of the 48 spawning-capable females spanned a 39-d period, indicating about 10.5 spawning events per female during the 2017 spawning season.

DISCUSSION

This study provides the first sex-specific growth curves using a multi-model approach for the Mississippi Red Drum stock and describes the maturity and spawning dynamics. We found that the three-parameter VBGF was the best candidate length-at-age model, with no significant sex-specific difference, but females had a larger mean L_∞. Four other candidate models showed significant differences between sexes, but these did not model Red Drum

age–growth optimally. We described Red Drum as batch spawners, with 3.7 d between successive spawns during the August–September spawning season. The A_{50} was around 3 years in both sexes, but spawning capability and elevated GSI values were not evident until approximately age 5 or 6.

The conclusion that the three-parameter VBGF had the best fit of the seven candidate length-at-age models is in contrast to previous studies. Porch et al. (2002) reported that the three-parameter VBGF was the least supported of the six candidate models they evaluated, including four of the same models evaluated in this study. The difference could be attributable to the relatively narrow temporal and geographic scope of our work or to differences in sample demographics. Additional data with more temporal and geographic variance would likely support a more highly parameterized model. Goodyear (1989) and Condrey et al. (1988) indicated that rapid growth in young Red Drum subsides quickly and that the standard VBGF does not adequately describe the ontogenetic growth, necessitating the use of the double VBGF. However, our findings support Hightower's (2013) conclusion that the three-parameter VBGF is the best-supported model for Red Drum in the northern GOM. Model support in our study was evaluated based on AIC, which has a tendency to select more parameterized models in comparison with other frequently used methods of objective model selection, such as the Bayesian information criterion (Dziak et al. 2012). Despite this tendency, we found that one of the least parameterized models (the three-parameter VBGF) was the best candidate model and that there was little support for the other six models. Despite the overwhelming support found for the three-parameter VBGF in this study, all seven growth models had very similar mean predicted lengths at age. We suggest the continued use of the three-parameter VBGF for describing Red Drum growth dynamics because it is widely used and has biologically relevant parameters that are applied in estimating other life history characteristics and establishing fishery reference points (Pauly 1980; Chen et al. 1992; Clark 1999; Williams and Shertzer 2003).

In comparison with other studies, our parameter estimates for the three-parameter VBGF were similar to recent mean values reported from studies that also sampled the inshore and offshore components of the northern GOM stock (Table 4). There was no significant difference in estimated L_∞ values between this study and others from the northern GOM, Alabama, or Louisiana when comparing sex-aggregated, male-specific, and female-specific three-parameter VBGFs, with the exception of the sex-aggregated value reported by Powers et al. (2012), which was larger, and the female-specific value reported by Hightower (2013), which was smaller. The k and t_0 estimates were significantly smaller than those reported from Louisiana and significantly larger than those reported

from the northern GOM and Alabama by Powers et al. (2012). However, the k and t_0 estimates did not significantly differ from the Alabama estimates generated by Hightower (2013) for all three growth curves, except the k-value for the sex-aggregated relationship, which was slightly smaller in this study than in the Hightower (2013) study (Table 4).

Many factors can affect fish growth rates, including environmental conditions, such as salinity and temperature (Bœuf and Payan 2001); food availability (Björnsson et al. 2001; Lorenzen 2016); population dynamics, such as survival rate, density, and size-selective mortality (Sinclair et al. 2002; Aikio et al. 2013); and parasitism (Barber et al. 2000). The observed differences in the mean parameter estimates for the three-parameter VBGF from this study and those from previous studies may be due to (1) a change in the population density since the installation of the federal harvest moratorium or (2) geographic variation in environmental conditions. Differences in population density and environmental conditions have led to spatially variable length-at-age parameter estimates in another sciaenid, the Spotted Seatrout *Cynoscion nebulosus* (Murphy and Taylor 1994). Growth models may also be affected by the gear used to collect samples and by the location of sampling. Hightower (2013) found significant differences in parameter estimates for Red Drum based on the three-parameter VBGF fitted using fishery-independent versus fishery-dependent data. The length selectivity of the gear types from these two sectors is different and can bias the resulting parameter estimates (Wilson et al. 2015). Length-selectivity bias is also evident in some previous studies describing Red Drum growth (Beckman et al. 1989; Powers et al. 2012). These studies lacked small individuals, thus resulting in uncharacteristically small k and t_0 estimates. Although we used both fishery-independent and fishery-dependent data, most of our samples came from recreational fishers within a small geographic range and mainly reflect the size-classes targeted by this sector.

Despite the lack of a significant difference in the overall sex-specific length-at-age relationships, the estimated mean L_∞ value for the male-specific three-parameter VBGF was not within the range of the female-specific 95% CI for L_∞, and vice versa. This highlights a potential issue with only comparing parameter estimates without consideration of the covariance structure of the parameters. All four length-at-age models that explained significantly more variance with sex-specific relationships had similar trajectories. The sex-specific growth curves were indistinguishable until around age 5, after which there was a clear separation, with the female-specific mean predicted length reaching a larger L_∞ than the male-specific model. This indicates that young male and female Red Drum grow similarly, but after they reach maturity, the females may reach a larger size. The length-at-age models that did not

TABLE 4. Mean length-at-age parameter estimates for two- and three-parameter von Bertalanffy growth functions from previous studies in the Gulf of Mexico (GOM) for male (M), female (F), and combined-sex (C) Red Drum (L_∞ = asymptotic length, mm; k = von Bertalanffy growth coefficient, year^{-1}; t_0 = theoretical age [years] at a length of zero). The sample size (n) is reported when known.

Study	Location	Sex	n	Maximum age (years)	Size range (mm TL)	L_∞	k	t_0
Present study	Northern GOM	C	451	31.4	105–1,115	964	0.26	−1.17
		F	203	31.2	354–1,115	990	0.26	−1.22
		M	189	31.4	360–996	935	0.26	−1.39
Miles 1950	Texas	C				900	0.42	−0.08
Wakefield and Colura 1983	Lower Laguna Madre, Texas	C	30		312–890	717	0.52	−0.01
	Matagorda Bay, Texas	C	339			835	0.35	−0.02
	Galveston Bay, Texas	C	23			804	0.41	−0.01
Doerzbacher et al. 1988	Texas	C	2,010		256–864	918	0.42	
Matlock 1992	Upper Laguna Madre, Texas	C				879	0.46	
	Galveston Bay, Texas	C				900	0.42	
	Corpus Christi Bay, Texas	C				940	0.5	
	Lower Laguna Madre, Texas	C				957	0.27	
	San Antonio Bay, Texas	C				978	0.41	
	Aransas Bay, Texas	C				1,177	0.27	
Murphy and Taylor 1990	Florida	C	551	24	225–980[a]	934[a]	0.46	0.03
Rohr 1980	Louisiana	C	62		96–1,012	950	0.37	−0.33
Hightower 2013	Alabama	C	572	40	179–1,040	946	0.32	−1.2
		F	249			953	0.32	−1.4
		M	178			928	0.31	−1.2
Powers et al. 2012	Alabama	F				965	0.109	−10.0
		M				923	0.110	−10.0
	Northern GOM	C	403	38	660–1,156	993	0.109	−10.0
		F	166			1,012	0.109	−10.0
		M	221			969	0.110	−10.0
Porch et al. 2002	Northern GOM	C				958	0.323	−0.65
Beckman et al. 1989	Northwestern GOM	F	1,544	36	~560–1,150[a]	1,013[a]	0.088	−11.3
		M		37	~600–950[a]	909[a]	0.137	−7.74

[a] mm FL; ~ indicates size was estimated from figures.

TABLE 5. Reproductive characteristics of male (M) and female (F) Red Drum in the Gulf of Mexico (GOM). The sample size (n) is reported when known. Mean length at 50% maturity (L_{50}) and age at 50% maturity (A_{50}) parameter estimates are given with 95% confidence intervals in parentheses. Asterisks indicate values that were converted using the TL–FL regression from Table S.1.

Study	Length	Location	Sex	n	Size range (mm)	L_{50} (mm)	L_{100} (mm)	A_{50} (years)	Spawning season
Present study	TL	Northern GOM	M	318	105–996	673 (654–695)	839	3.4 (3.0–4.0)	Aug and Sep
			F	353	353–1,115	672 (659–687)	924	3.1 (2.8–3.3)	
	FL		M		128–930*	639 (622–659)*	788*		
			F		351–1,037*	638 (626–651)*	865*		
Wilson and Nieland 1994	FL	Northern GOM	M	1,337	399–1,115	665	850	4	Mid-Aug to early Sep
			F	1,262	399–1,115	695	850	4	
Overstreet 1983	FL	Mississippi	M	323		792			Late Sep and Oct
			F	159		792			
Murphy and Taylor 1990	FL	Florida	M	265	250–999	529	700	1–2	Sep to Oct
			F	260	200–1,049	825	850	3–5	

show significant sex-specific variation also estimated the L_∞ parameter to be larger in females than in males. The nonsignificant F-ratio test in our study may have been influenced by the large number of younger individuals relative to older fish. Hightower (2013) and Beckman et al. (1989) had a relatively large representation of fish older than age 10 from offshore waters and found significant sexual dimorphism, with females reaching a larger size than males. This highlights the need for a well-represented range of age-classes, which requires sampling the offshore component of the stock.

This study used a relatively large sample of Red Drum from the northern GOM to assess reproductive characteristics via histological techniques, which is the least subjective method (West 1990; Wilson and Nieland 1994). Previous studies using histology in Red Drum have classified oocyte development as group-synchronous (Overstreet 1983; Fitzhugh et al. 1988; Wilson and Nieland 1994), but we report asynchronous oocyte development. However, the descriptions of oocyte development from those previous studies appear to indicate asynchronous development, despite the classification as group-synchronous. We collected fish from every month, and we were able to identify the presence of all reproductive phases. Despite the number of individuals sampled, there was an unexpected lack of early developing or actively spawning subphases among females. Red Drum may only occupy these subphases for a very limited time, which would explain the low frequencies. This study was limited to sampling state waters (<16.668 km [<9 nautical miles] from shore), and Red Drum are thought to spawn in offshore and coastal waters at night (Lowerre-Barbieri et al. 2008, 2016b; Powers et al. 2012). The addition of night sampling and sample collection from federal waters (>16.668 km [>9 nautical miles] offshore) would likely increase the frequency of

encountering individuals in the actively spawning subphase. The small percent agreement between macroscopic and microscopic reproductive phase classifications reveals the low precision of the macroscopic method. Past studies on a variety of species have reported even lower total percent agreement between macroscopic inspection and histology (West 1990; García-Díaz et al. 1997; Corey et al. 2017; Fogg et al. 2017). Based on our findings, we recommend the use of microscopic techniques to properly classify reproductive phases in Red Drum, regardless of sex.

The method used to estimate the age and length at which maturity is reached can affect the parameter estimates and subsequent fishery reference points. Previous studies have used different methods—and different definitions of maturity—to estimate the onset of maturity in Red Drum, leading to variable estimates among those studies (Table 5). Wilson and Nieland (1994) estimated maturity in females by using histology and the same definition of maturity used here, but they only included individuals that were captured during the spawning season, estimated maturity with size-bins rather than a logistic function, and only used macroscopic assessment (the release of milt) for males. Wilson and Nieland (1994) reported a slightly greater A_{50} (4 years) and L_{50} than we report (Table 5). Their method of only using fish from the spawning season meant that the developing phase was excluded from the maturity estimate, and our smaller maturity estimates may be partially due to the inclusion of such individuals. Although we estimated the L_{50} to be around 670 mm TL and the A_{50} to be 3 years, the spawning-capable phase was not observed until 703 mm TL (age 4.5) in males or 840 mm TL (age 5.8) in females. This indicates that Red Drum may reach maturity while inshore before actually joining the spawning stock. This may also account for the small GSI values observed in fish

younger than age 5. Lowerre-Barbieri et al. (2016b) high-lighted the need to distinguish between physiological maturity and functional maturity after they observed Red Drum that were displaying signs of maturity (and, in some cases, males that even released milt) prior to being prepared to spawn, based on the location of catch and the low levels of milt present. It is evident that fish younger than age 5 are not critical components of the spawning stock, as efforts to describe the offshore size distribution of Red Drum have reported negligible frequencies of fish younger than 5 years and smaller than 750 mm TL (Powers et al. 2012; Lowerre-Barbieri et al. 2016a).

We found that two methods of estimating spawning season, GSI and histological reproductive phase classifications, were in agreement with each other. The estimated spawning season was slightly earlier and of reduced duration than those reported previously by some authors (Overstreet 1983; Peters and McMichael 1987; Murphy and Taylor 1990) but was very similar to spawning season reported by Wilson and Nieland (1994; Table 5). The Red Drum spawning season of 6–7 weeks is shorter than that seen in other north-central GOM sciaenids (6 months in Spotted Seatrout: Brown-Peterson and Warren 2001; 6 months in Silver Perch *Bairdiella chrysoura*: Grammer et al. 2009; 6 months in Southern Kingfish *Menticirrhus americanus*: Clardy et al. 2014; 14–15 weeks in Black Drum *Pogonias cromis*: Nieland and Wilson 1993). Wilson and Nieland (1994) used over 6 years of data and found that interannual differences in spawning season were minimal. The GSI is an indicator of spawning season, independent of fish size, when there is no relationship between GSI and GFBW. We found that although the relationship between GSI and GFBW in Red Drum was significant, it explained very little of the variance (10% for female-specific values; 18% for male-specific values), indicating that GSI is a good indicator of spawning preparedness (Corey et al. 2017). The significant relationship was likely attributable to the number of young (age < 5) individuals that were histologically identified as mature but had very low GSI values. These young, pubescent individuals were physiologically mature but did not yet show any gonadal enlargement. It was not surprising to see signs of spawning capability in males later in the season than in females, given the lower energy demands for spermatogenesis compared to oogenesis (Schärer and Robertson 1999; Lowerre-Barbieri et al. 2016a). All spawning-capable males collected in October were in the LGE subphase, indicating limited spermatogenic activity in the testes. We were surprised, however, to find developing males captured immediately after the spawning season and early developing males captured from October through April. These males were likely young, precocious individuals that missed the spawning window; thus, although they were physiologically mature, they did not contribute to spawning.

Another surprising finding was the capture of regenerating females during the spawning season. Many of these females were larger than 900 mm TL and should have been important components of the spawning stock. The presence of these large, regenerating females during the spawning season suggests the occurrence of some skipped spawning (i.e., some females do not spawn every year). This can be caused by hormone changes or as a response to poor nutritional condition (Marshall et al. 1998; Rideout et al. 2005; Rideout and Tomkiewicz 2011). Skipped spawning is widespread in fishes and is being reported at an increasing rate, with evidence of occurrence in at least 31 species (Rideout et al. 2005; Rideout and Tomkiewicz 2011). Many of these are from northern latitudes, but there has been evidence of skipped spawning in warmwater pelagic species, such as Atlantic Bluefin Tuna *Thunnus thynnus* (Secor 2007). To our knowledge, skipped spawning has not yet been reported in any sciaenids, but this may be because standard reproductive assessments can easily overlook the signs or because of the difficulty in distinguishing between immature individuals and mature, non-reproductive adults (Rideout et al. 2005). Identification of skipped spawning is further complicated in fishes with indeterminate fecundity, as the fish could potentially still recruit oocytes by the end of the season even if they are not present during the peak, particularly in warmer waters (Rideout and Tomkiewicz 2011). For that reason, Lowerre-Barbieri et al. (2009) recommended that in species with indeterminate fecundity, the recrudesce and reabsorption times of spawning indicators must be greater than the spawning season to make an accurate assumption of skipped spawning. Due to the relatively short spawning season of Red Drum, this species likely meets this criterion. The presence of large, regenerating fish during the spawning season has been used to indicate skipped spawning in other species with indeterminate fecundity and with longer spawning seasons than Red Drum, including the Wahoo *Acanthocybium solandri* (Brown-Peterson et al. 2000; Jenkins and McBride 2009), Gag *Mycteroperca microlepis* (Fitzhugh et al. 2006), Red Grouper *Epinephelus morio* (Collins et al. 2002), and Blue Marlin *Makaira nigricans* (Brown-Peterson et al. 2008). Furthermore, the Red Drum is a relatively long-lived species, and skipped spawning is positively correlated with longevity (Secor 2007). When skipped spawning occurs, the assumptions of fishery reference points that are established using spawning stock biomass (SSB) are violated because fewer females are contributing to the reproductive effort. Thus, a failure to account for skipped spawning can lead to overestimates of egg production and stock sustainability (Secor 2008; Lowerre-Barbieri et al. 2009). Based on our findings from a relatively small proportion of large, mature female Red Drum and the potential impact of overlooking skipped spawning, the additional sampling of

large, mature females in Mississippi waters and elsewhere is recommended to further investigate this theory.

Although we only identified a few females as actively spawning, we were still able to estimate the spawning interval due to the presence of 24-h POFs. Our estimate of 3.7 d coincides with Wilson and Nieland's (1994) year-specific estimates ranging from 2 to 4 d for the period 1986–1991 and is the same as their year-aggregated estimate. Our estimated spawning season duration of 39 d results from 1 year of data and thus is a conservative estimate. If the spawning-capable females from 2016 were included, this estimate would increase to 47 d, and the resulting average number of spawning events per female in each season would increase from 10.5 to 12.7. The spawning interval is essential for estimating annual fecundity, and to our knowledge, Wilson and Nieland (1994) provided the only other spawning interval estimate for Red Drum in the GOM. Thus, our spawning interval estimates will be useful when combined with future batch fecundity estimates for Red Drum.

This study provides updated and much-needed information on the growth and reproductive dynamics of Red Drum in the northern GOM, particularly for the Mississippi portion of the stock. We used otolith-derived age estimates and a multi-model approach to model sex-specific and sex-aggregated length-at-age relationships. Age-structured stock assessment models have been shown to be sensitive to reproductive characteristics (Leaf et al. 2008; Fitzhugh et al. 2012). One metric that directly addresses the status of a stock and incorporates an estimate of total mortality is the "escapement rate." The escapement rate metric was developed to evaluate the impact of fishing on SSB and is the number of fish that survive to a given age under conditions of observed fishing mortality relative to the number surviving when no fishing mortality occurs. Escapement rate is a key fishery reference point for Red Drum because the stock is primarily targeted by recreational fishers in the inshore waters. However, it is directly influenced by the estimated age at maturity, necessitating proper estimation of reproductive characteristics. In this work, we also estimated the spawning season and spawning frequency, described the age and length at maturity, and provided evidence of delayed recruitment to the spawning stock (i.e., fish reach maturity at age 3 but become spawning capable at around age 6). Given the spatial variation in growth and the current state-level management of Red Drum, our study provides essential knowledge for the proper assessment and management of this species, particularly in Mississippi.

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SUPPORTING INFORMATION

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