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Growth and Spawning Dynamics of Southern Flounder in the North-Central Gulf of Mexico

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Abstract
Southern Flounder Paralichthys lethostigma is the most commonly harvested flatfish in the north-central Gulf of Mexico (GOM), yet knowledge of this species’ growth and reproduction is limited for the Mississippi region. Given the offshore spawning migrations and likely mixing between state-managed units of the GOM Southern Flounder stock, small-scale environmental influences may constitute a major driver of life history dynamics during early life residency in nearshore estuaries. Therefore, estimates of local demographic characteristics are needed for effective fishery management. Here, we describe critical life history traits of Southern Flounder, including estimation of growth rates and maturity. The three-parameter von Bertalanffy growth function best described female-specific growth: mean asymptotic length $L_\infty$ was 514 mm TL, mean growth coefficient $k$ was 0.67 year$^{-1}$, and mean theoretical age at zero length $t_0$ was −0.50 years. The estimated female-specific mean length at 50% maturity ($L_{50}$) was 303 mm TL, and the female-specific mean age at maturity was 0.96 years. Although we observed significant differences between $L_{50}$ estimates in the GOM, length-at-age parameter estimates were similar to those reported for other areas of the GOM. Both individual growth and length-at-maturity estimates were significantly different from those reported for the Atlantic, suggesting basin-level differences in population characteristics, with faster growth and earlier maturation in the GOM.

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Histological indicators and gonadosomatic index data indicated that the spawning season in the north-central GOM occurs from November to January and that Southern Flounder are batch spawners with asynchronous oocyte development. Our study provides a description of growth and spawning dynamics that will contribute to future stock assessment efforts focused on the Southern Flounder fishery in Mississippi and the GOM.

The Southern Flounder _Paralichthys lethostigma_ is a recreationally and commercially valuable species distributed as far north as North Carolina on the U.S. Atlantic coast and throughout the Gulf of Mexico (GOM) from central Florida to northern Mexico (Hensley and Ahlstrom 1984; Enge and Mulholland 1985; Reagan and Wingo 1985). The Atlantic and GOM populations are separated geographically by the southern Florida peninsula, and genetic differences between the two populations have been reported (Blandon et al. 2001; Anderson and Karel 2012; Wang et al. 2015). The Southern Flounder is an estuarine-dependent species and primarily inhabits nearshore waters, where juvenile growth occurs prior to an offshore spawning migration of sexually mature adults (Etzold and Christmas 1979; Allen and Baltz 1997; Craig et al. 2015). Despite genetic homogeneity of the Southern Flounder fishery in the GOM (Anderson and Karel 2012) and likely mixing between fish from the two regions during spawning, the Southern Flounder is managed at the state level as a multispecies complex with Gulf Flounder _Paralichthys albigutta_ and smaller flatfish species, and unique harvest regulations are employed among GOM states (GSMFC 2015). Due to its relatively large body size and abundance, the Southern Flounder is the most commonly harvested flatfish species in the north-central GOM and supports a major recreational fishery in Mississippi (Hensley and Ahlstrom 1984). Harvest in Mississippi is currently regulated by a 305-mm minimum TL limit and a 15-fish daily bag limit. Because the Southern Flounder fishery is managed by individual state agencies, local estimates of demographic characteristics are needed to better inform state management and assessment. However, information on growth and reproduction of Southern Flounder in the north-central GOM, particularly coastal Mississippi, is limited.

Growth is a fundamental life history characteristic that influences population dynamics; therefore, an understanding of growth is necessary for fisheries management (Adams 1980; Denney et al. 2002). Growth parameter estimates from the Southern Flounder length-at-age relationship are spatially variable within the GOM (Midway et al. 2015), but no growth parameter estimates are available for the Mississippi region. The Southern Flounder length-at-age relationship has been described previously with the von Bertalanffy model (Nall 1979; Frick 1988; Wenner et al. 1990; Stunz et al. 2000; Fischer and Thompson 2004). However, this model is not always the most appropriate for describing ontogenetic growth of a species (Cailliet et al. 2006). The approach of fitting multiple models and comparing candidate models can help to reduce potential bias from model selection uncertainty and model misspecification, thereby improving parameter estimates (Burnham and Anderson 2002; Katsanevakis 2006). Multi-model approaches for describing the length-at-age relationship are increasingly being used for marine fishes (Mercier et al. 2011; Harry et al. 2013; Higgins et al. 2015; Dippold et al. 2016), but only one previous study has compared multiple models for describing sex-specific growth in Southern Flounder (Fischer and Thompson 2004). After fitting a three-parameter model for all individuals and a six-parameter model independently for males and females, Fischer and Thompson (2004) determined that growth was significantly different between sexes.

In addition to individual growth parameter estimates, current stock assessment approaches require information on the reproductive biology of stocks because reproduction greatly influences fish population dynamics and stock resilience (Beverton and Holt 1957; Lowerre-Barbieri et al. 2011a). Length- and age-specific maturity information includes critical demographic rates that are used to estimate spawning stock biomass in many stock assessment models (O’Brien et al. 1993; Trippel 1995; Murawski et al. 2001). Few estimates of length at maturity and age at maturity have been reported for Southern Flounder in the GOM. Previous research in Louisiana indicated that 50% of female Southern Flounder were mature at 229 mm TL (Fischer 1995). In Mississippi, length at first sexual maturity was estimated as 230 mm TL, and 100% maturity was reported to occur by 340 mm TL (Etzold and Christmas 1979). Southern Flounder exhibit sexual dimorphism in length at maturity, with length at first maturity and length at 100% maturity being greater for females than for males (Wenner et al. 1990). However, previously reported estimates of Southern Flounder maturity in Mississippi waters were not sex specific and did not include the length at 50% maturity (L50; Etzold and Christmas 1979).

Other characteristics of Southern Flounder spawning, including seasonality and reproductive strategy, have not been recently described for the GOM or Mississippi. The Southern Flounder spawning season in Louisiana has been described by using analysis of the gonadosomatic index (GSI) and histological indicators (Shepard 1986; Fischer 1995). For Southern Flounder collected in Louisiana, GSI values were elevated during August–November and declined in December, indicating that gonadal development increased prior to spawning in December (Shepard 1986). Fischer (1995) used both GSI and ovarian histology to determine that the Southern Flounder spawning season in Louisiana lasts about 60 d and occurs from December through January. The presence of different oocyte stages throughout the spawning season was indicative of batch spawning in Southern Flounder collected from Louisiana waters (Fischer 1995). To our knowledge, this is the
only documented example of batch spawning in wild-caught Southern Flounder. Further research on the spawning dynamics of Southern Flounder is needed because spawning affects lifetime fecundity, reproductive potential, stock resiliency, and ultimately population dynamics (McEvoy and McEvoy 1992; Lowerre-Barbieri et al. 1998).

Here, we describe the age and growth dynamics and the reproductive biology of Southern Flounder in Mississippi waters of the GOM. We (1) estimate female-specific growth parameters for the length-at-age relationship of Southern Flounder by using four candidate models, (2) estimate the length and age at maturity by using logistic models, (3) define the spawning season duration, and (4) characterize the Southern Flounder reproductive strategy. This information increases the understanding of Southern Flounder biology in the GOM and addresses critical knowledge gaps for Southern Flounder fishery management in Mississippi.

METHODS

Southern Flounder were collected from September 2014 to February 2016 in the north-central GOM by using fishery-dependent (gigging, hook-and-line fishing, and dockside sampling) and fishery-independent (trawl and gill-net surveys) methods. Sampling occurred at multiple locations throughout the Mississippi Sound (Figure 1) and in other GOM states at offshore locations. Each fish was measured for TL (mm), SL (mm), and wet body weight (g). Otoliths were extracted and sectioned for age determination (VanderKooy 2009). Whole gonads were removed, weighed to the nearest 0.01 g, and evaluated macroscopically for reproductive phase (Brown-Peterson et al. 2011). The sex of each fish was determined by macroscopic examination, and gonadal tissue was preserved in 10% neutral buffered formalin for histological analysis.

Age validation.—The left sagittal otolith was processed for age estimation (VanderKooy 2009) from a subsample of fish that were selected to represent all 50-mm TL bins collected in this study; individuals were randomly selected within size bins to reflect the sampled distribution of TL. Two independent readers produced an age estimate (years) by counting annuli, and the age estimate was excluded from analysis if exact agreement between readers was not reached. The otolith radius (µm), annulus width (µm), and translucent area under reflected light on the outer edge margin (µm; defined as the area past the most recent fully formed annulus, as measured along the sulcus) were measured from images by using i-Solution Lite software. Otoliths were assigned a categorical margin code (1 = 0% translucent area; 2 = >0–33%; 3 = >33–66%; 4 = >66–99%) based on the proportion of outer margin width relative to the width of the last fully formed annulus, where a margin code of 1 indicates opaque ring formation (VanderKooy 2009). Marginal increment analysis (MIA) was used to validate the frequency of annulus deposition with aggregated data from age-1 otolith samples collected by the Mississippi Department of Marine Resources (2007, 2009–2013) and samples collected for this study (2014 and 2015). The proportion of annuli formed was examined as a function of capture month to estimate the timing of annulus deposition. An age estimate was then assigned as

\[
\text{Age} = \left[ \frac{\text{(annulus count} \cdot 365) + (\text{month} - 1) \cdot 30}{365} \right]
\]

using the annulus count and the month of capture, assuming January 1 as the birth date and April 1 as the annulus deposition date (Nieland et al. 2002). The age estimate was adjusted based on the margin code: individuals that were captured before or during April with a margin code of 3 or 4 were advanced in age by 1 year, and individuals that were captured after April with a margin code of 1 or 2 were reduced in age by 1 year.

Female growth.—The length-at-age relationship for female Southern Flounder was described using four nonlinear models, including the three-parameter von Bertalanffy growth function (VBGF), the two-parameter VBGF, the Gompertz growth model, and the logistic model. Measured TL and age estimate data used for model fitting were from aged females collected within Mississippi state waters. A three-parameter VBGF (Von Bertalanffy 1938) was used to estimate length at age,

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

where \( t \) represents age (years); \( L_t \) is the TL (mm) at a given age; \( L_\infty \) is the asymptotic length (mm TL); \( k \) is the growth
coefficient (year\(^{-1}\)); and \(t_0\) is the theoretical age at zero length (years). The two-parameter VBGF is

\[ L_t = L_\infty (1 - e^{-kt}) , \]

where the absence of the \(t_0\) parameter anchors the growth curve to the origin. The Gompertz growth model (Gompertz 1825) is

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

where \(\lambda\) is the theoretical initial relative growth rate at age zero (year\(^{-1}\)); and \(k\) is the rate of exponential decrease in the relative growth rate with age (year\(^{-1}\)). The logistic length-at-age model (Ricker 1975) is

\[ L_t = \frac{L_\infty}{1 + e^{-k(t - t_0)}} , \]

where \(k\) is a relative growth rate parameter (year\(^{-1}\)); and \(t_0\) corresponds to the age where the growth rate is at a maximum. The four candidate length-at-age models were evaluated for goodness of fit and parsimony to determine the best-supported model, as indicated by the lowest value of Akaike’s information criterion (AIC). The AIC difference (\(\Delta\text{AIC}\)) and Akaike weight (\(\omega_i\)) were calculated for model comparison and to evaluate relative model support. The 95% confidence intervals (CIs) were calculated for each mean parameter estimate and were used to compare results to previously published estimates.

**Weight at length.**—The weight-at-length relationship for females collected in Mississippi waters of the GOM was modeled using a power function,

\[ W = al^b , \]

where \(W\) is wet weight (g); \(L\) represents TL (mm); \(a\) is a coefficient term; and \(b\) is an exponent describing the change in length relative to weight. The 95% CIs were calculated for each mean parameter estimate. The relative condition of mature females was evaluated by using the relative condition index \(K_{rel}\) (Le Cren 1951), which is calculated based on the relationship between observed wet weight \((W)\) and expected mean weight \((W_{exp})\) predicted by the female weight-at-length relationship:

\[ K_{rel} = \frac{W}{W_{exp}} . \]

A \(K_{rel}\) value of 1.0 indicates perfect agreement between the observed weight and the expected mean weight.

**Histological maturity estimation.**—A subsample of ovarian tissue samples that were representative of all 50-mm TL bins and sample collection months was dehydrated, embedded in paraffin, sectioned at 4 µm, and stained with hematoxylin and eosin by using standard histological techniques (Luna 1968). Females were assigned to a reproductive phase in accordance with the classification terminology described by Brown-Peterson et al. (2011) and were coded as immature (0) or mature (1). Maturity was determined by the presence of cortical alveolar oocytes in reproductively active females or by the presence of atresia in reproductively inactive females. Mean length at 50% maturity for female Southern Flounder collected in Mississippi was estimated using a two-parameter logistic model,

\[ M_{TL} = \frac{1}{1 + e^{-r(TL - L_{50})}} , \]

where \(r\) is the instantaneous rate of change (mm\(^{-1}\)); and \(L_{50}\) is the TL at 50% maturity (mm). Age at maturity was also estimated with a two-parameter logistic model,

\[ M_{Age} = \frac{1}{1 + e^{-r(Age - Age_{50})}} , \]

where \(r\) is the instantaneous rate of change (year\(^{-1}\)); and \(Age_{50}\) is the age at 50% maturity (years). The 95% CIs of the mean parameter estimates were also calculated. The percentage of samples in agreement between macroscopic identification and histological phase identification was calculated to assess the accuracy of phase assignment.

**Reproductive analyses.**—To characterize female reproductive development, the percent coverage of each oocyte stage present in individual tissue sections was determined using an ImageJ point grid analysis (modified from Tomkiewicz et al. 2011), with oocyte stage terminology following Brown-Peterson et al. (2011) and Lowerre-Barbieri et al. (2011a). Histological samples were examined from the anterior, middle, and posterior sections of both the left and right gonads in three spawning-capable females \((n = 6\text{ samples/female})\) to determine whether oocyte development was homogeneous throughout the gonads. Pearson’s chi-square test was used to identify significant differences in the distribution of oocyte stages between the left and right ovaries and among the anterior, middle, and posterior regions of the ovary \((\alpha = 0.05)\). When significant differences in the distribution of oocyte stages were detected, a pairwise comparison was made by using multiple chi-square tests with a Bonferroni-adjusted critical value \((\alpha = 0.017 [0.05/3\text{ pairwise tests}])\). Because the sample size of spawning-capable females collected in Mississippi waters was low, data for Mississippi females were supplemented with data from females collected in Louisiana and Texas for histological reproductive analyses.

The spawning season duration was estimated based on a combination of GSI data and histological examination of gonadal development. The GSI value was calculated for each individual as
where \( GW \) is the gonad weight (g) and \( GFBW \) is the gonad-free body weight of the fish (g). A linear regression of GSI and \( GFBW \) was conducted to confirm that GSI could serve as an indicator of reproductive development independent of body size (Jons and Miranda 1997). Mean monthly GSI values were calculated for sexually mature females and are reported with SEs. After the parametric assumptions of normality and homogeneity of variance were tested, a one-factor ANOVA and a post hoc Tukey honestly significant difference (HSD) test were used to detect differences in mean monthly GSI for females. The distribution of females in each reproductive phase was also examined by month to estimate spawning seasonality.

RESULTS

In total, 440 Southern Flounder females were collected using various fishery-dependent and fishery-independent sampling methods. Two gear types were primarily used: 201 females were collected by gigging, and 141 were collected via hook-and-line fishing. The remaining females were collected by use of other gear types (trawl, gill-net surveys, and dockside sampling). Fish were collected during all months of the year, although sample sizes during December, January, and March were limited. The majority of females collected for this study were captured within Mississippi waters, but about 10% of the fish were captured via trawling in offshore waters of Louisiana and Texas. The length of sampled females ranged from 190 to 576 mm TL, and body weight ranged from 72 to 2,629 g. If TL measurements were unavailable, SL measurements were converted to TL using the following relationship:

\[
TL = 1.14 \cdot SL + 18.94 \quad (r^2 = 0.97, P < 0.001)
\]

Few male Southern Flounder were encountered throughout this study; therefore, males were excluded from analyses.

Age Validation

Based on a subsample of 313 otoliths that were processed for age estimation, the age-class of Southern Flounder ranged from 0 to 4+ years (maximum = 4.65 years). Age estimates agreed between readers for all age-classes (Table 1). Width measurements for use in MIA were obtained from the otoliths of 403 age-1 fish. There was high individual variability in annulus deposition within age-1 otoliths. Median incremental width expressed as a proportion of the last fully formed annulus decreased between March and July, with the minimum proportion observed in May, indicating that annulus formation occurred during these months (Figure 2). The greatest decrease in median proportion values was detected between March and April; thus, we estimated that annulus formation occurred in April for the
greatest number of individuals, and we used April 1 as the assumed annulus deposition date for age estimation. There was a strong seasonal trend in the proportion of annuli formed, supporting the assumption that annulus formation in Southern Flounder otoliths occurs once per year.

Female Growth

The four models used to describe the length-at-age relationship for female Southern Flounder (\( n = 277 \)) were all similar in their mean length-at-age predictions (Figure 3). Among the candidate models that were evaluated to describe female-specific length at age, the three-parameter VBGF was the best-supported model (Table 2). The Gompertz model and the logistic model had lower model support than the three-parameter VBGF, and the two-parameter VBGF was not well
was greater than 1.0 (95% CI = 0.033–1.90 × 10\(^{-6}\) to 4.17 × 10\(^{-6}\) and \(b = 3.24\) (95% CI = 3.17–3.30). There were insufficient data to fit a male-specific model \((n = 18)\), although dimorphism in TL ranges was observed between male and female Southern Flounder and all fish larger than 352 mm TL were female (Figure 4). There was a weak seasonal trend in \(k_{rel}\) of females, with elevated mean values observed in the fall months preceding the winter spawning season (Figure 5a). Specifically, the mean monthly \(k_{rel}\) was greater than 1.0 during September–November and was less than 1.0 during December–April and June–July.

**Histological Maturity Estimation**

With the exception of active spawning, all reproductive phases and subphases were identified histologically for female Southern Flounder. Agreement between macroscopic classification and histological phase classification was 39%. The developing phase was most accurately identified by macroscopic examination (94% agreement), while the immature and regenerating phases were poorly classified by macroscopic examination (23% and 26% agreement, respectively). The smallest mature female Southern Flounder collected was 245 mm TL, and all females were mature by 368 mm TL. Based on the two-parameter logistic function (Figure 6), the mean estimate of the \(r\) parameter was 0.0412 mm\(^{-1}\) (95% CI = 0.033–0.053 mm\(^{-1}\)), and the mean \(L_{50}\) estimate was 303.80 mm (95% CI = 295.53–310.82 mm) for females \((n = 277)\). The mean \(Age_{50}\) was 0.96 years (95% CI = 0.77–1.12 years), and the mean \(r\)-estimate was 3.44 year\(^{-1}\) (95% CI = 2.10–6.11 year\(^{-1}\)).

**Weight at Length**

All available female-specific weight and TL data collected in this study were used to describe the weight-at-length relationship and \(L_{rel}\) for female Southern Flounder \((n = 395)\). The female weight-at-length relationship was described by the power function, with parameters \(a = 2.82 \times 10^{-6}\) (95% CI = 1.90 × 10\(^{-6}\) to 4.17 × 10\(^{-6}\) and \(b = 3.24\) (95% CI = 3.17–3.30). There were insufficient data to fit a male-specific model \((n = 18)\), although dimorphism in TL ranges was observed between male and female Southern Flounder and all fish larger than 352 mm TL were female (Figure 4). There was a weak seasonal trend in \(k_{rel}\) of females, with elevated mean values observed in the fall months preceding the winter spawning season (Figure 5a). Specifically, the mean monthly \(k_{rel}\) was greater than 1.0 during September–November and was less than 1.0 during December–April and June–July.

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Reproductive Analyses

Because various stages of oocyte development were observed simultaneously within spawning-capable ovaries from 15 individual females collected in this study, Southern Flounder were classified as batch spawners with asynchronous oocyte development (Figure 7; Supplementary Table S.1 available separately online). There were no significant differences in oocyte stage distribution between the left and right ovaries of spawning-capable females ($\chi^2 = 7.19, df = 6, P > 0.05$). However, there were significant differences in oocyte stage distribution among the anterior, middle, and posterior regions of the ovary ($\chi^2 = 26.78, df = 12, P = 0.0083$). Specifically, after Bonferroni adjustment ($\alpha = 0.017$), there were no significant differences in oocyte distribution between the middle and posterior regions ($\chi^2 = 2.72, df = 6, P = 0.84$) and the anterior and posterior regions ($\chi^2 = 15.31, df = 6, P = 0.018$), but there were significant differences between distributions in the middle and
antior regions \((\chi^2 = 19.49, \text{df} = 6, P = 0.0034)\), indicating that oocyte distribution was homogeneous within the mid-posterior region of the ovary. Our sampling of tissue from the lower-middle region of the lobe was considered representative of ovarian development since the same region was consistently sampled throughout the study.

Spawning seasonality of Southern Flounder was described initially using GSI data and was further defined based on histological classification of reproductive phase. In sexually mature females, the linear relationship between GSI and GFBW was significant but explained little of the variance in GSI \((\chi^2 = 0.06, P = 0.04)\). Thus, GSI can be used to indicate reproductive development. Female mean GSI values remained constant during January–September and were elevated in October–December (Figure 5b). The mean monthly GSI value was significantly higher in November than in all other months (Tukey HSD test: \(P < 0.05\)), although several individuals had elevated mean GSI values in December. When only age-1 individuals were examined, a small increase in mean monthly GSI occurred in October and was lower in magnitude than that for all ages combined. Through histological analyses of spawning seasonality, immature and regenerating females were observed throughout the year (Table 3). The greatest percentages of early developing and developing females were observed in October; spawning-capable females were most frequently observed in November, indicating the beginning of the reproductive season. Regressing females were observed in January and February, suggesting an end of spawning activity. The results of these analyses indicate that spawning by Southern Flounder likely occurs from November to January and ceases in February.

**DISCUSSION**

Southern Flounder constitute the majority of harvest for the state-managed flounder fishery in the GOM (>10% of flatfish collected in our sampling were identified as Gulf Flounder), yet life history information is currently lacking for Southern Flounder in the Mississippi region. Over the last two decades, research on Southern Flounder life history has focused on the management units in Louisiana (Fischer and Thompson 2001, 2004) and Texas (Stunz et al. 2000; Glass et al. 2008; Nims and Walther 2014). In the most recent regional management profile by the Gulf States Marine Fisheries Commission, data from Louisiana and Texas were used to represent the entire Southern Flounder fishery in the GOM (GSMFC 2015). The scarcity of state-specific data in the north-central GOM region has historically prevented a GOM-wide stock assessment from being conducted for the flounder fishery. By describing growth and reproduction of Southern Flounder in the north-central GOM, the present study contributes knowledge to inform future stock assessments and improve state-level management in Mississippi.

Although the use of multiple models to describe the length-at-age relationship is a recent development (Burnham and Anderson 2002; Katsanevakis 2006), our study is the first to use a multi-model approach to provide robust estimates of Southern Flounder length-at-age parameters. Our results indicated that the three-parameter VBGF was well supported to describe the observed data, thus confirming the widespread use of this model in previous research (Frick 1998; Wenner et al. 1990; Stunz et al. 2000; Fischer and Thompson 2004). Although the three-parameter VBGF had the lowest AIC value, the top-three models all had \(\Delta AIC\) values less than 4, indicating substantial model support (Burnham and Anderson 2004). In contrast, the two-parameter VBGF received lower model support than the other candidate models evaluated, likely due to the limited number of fish smaller than 200 mm TL in the present study. The lack of smaller individuals is one potential source of bias in our length-at-age

**TABLE 3.** Percentages of females observed in each reproductive phase by month for Southern Flounder \((n = \text{sample size})\) collected from the north-central Gulf of Mexico between September 2014 and February 2016.

<table>
<thead>
<tr>
<th>Month</th>
<th></th>
<th>Immature</th>
<th>Early developing</th>
<th>Developing</th>
<th>Spawning capable</th>
<th>Regressing</th>
<th>Regenerating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>14</td>
<td>86</td>
</tr>
<tr>
<td>Feb</td>
<td>38</td>
<td>58</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>13</td>
<td>29</td>
</tr>
<tr>
<td>Mar</td>
<td>17</td>
<td>24</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>76</td>
</tr>
<tr>
<td>Apr</td>
<td>21</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>90</td>
</tr>
<tr>
<td>May</td>
<td>33</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>94</td>
</tr>
<tr>
<td>Jun</td>
<td>47</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>94</td>
</tr>
<tr>
<td>Jul</td>
<td>21</td>
<td>19</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>81</td>
</tr>
<tr>
<td>Aug</td>
<td>20</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Sep</td>
<td>29</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>86</td>
</tr>
<tr>
<td>Oct</td>
<td>43</td>
<td>2</td>
<td>58</td>
<td>21</td>
<td>39</td>
<td>0</td>
<td>19</td>
</tr>
<tr>
<td>Nov</td>
<td>36</td>
<td>22</td>
<td>17</td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Dec</td>
<td>20</td>
<td>35</td>
<td>15</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td>Total</td>
<td>332</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Study</td>
<td>Location</td>
<td>n</td>
<td>$L_\infty$</td>
<td>$k$</td>
<td>$t_0$</td>
<td>Age$_{50}$</td>
<td>$L_{first}$</td>
</tr>
<tr>
<td>-----------------------------</td>
<td>-----------------</td>
<td>-----</td>
<td>-----------</td>
<td>-------</td>
<td>--------</td>
<td>------------</td>
<td>------------</td>
</tr>
<tr>
<td>Present study</td>
<td>Mississippi</td>
<td>5145</td>
<td>0.67</td>
<td>-0.50</td>
<td>0.97</td>
<td>245</td>
<td>304</td>
</tr>
<tr>
<td>Etzold and Christmas 1979</td>
<td>Texas</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nall 1979</td>
<td>Mississippi</td>
<td>3</td>
<td>230</td>
<td>340</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frick 1988</td>
<td>Florida</td>
<td>153</td>
<td>1.461</td>
<td>0.03</td>
<td>1.86</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wenner et al. 1990</td>
<td>Florida, Alabama</td>
<td>139</td>
<td>540</td>
<td>0.47</td>
<td>0.10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fischer 1995</td>
<td>South Carolina</td>
<td>708</td>
<td>759</td>
<td>0.23</td>
<td>-0.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monaghan and Armstrong 2000</td>
<td>North Carolina</td>
<td>1,915</td>
<td>1</td>
<td>320</td>
<td>345</td>
<td>430</td>
<td></td>
</tr>
<tr>
<td>Stunz et al. 2000</td>
<td>Texas</td>
<td>718</td>
<td>483</td>
<td>0.75</td>
<td>-0.31</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fischer and Thompson 2004</td>
<td>Louisiana</td>
<td>1,128</td>
<td>556</td>
<td>0.51</td>
<td>-0.62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midway and Scharf 2012</td>
<td>North Carolina</td>
<td>451</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
parameter estimates (Pardo et al. 2013), and the parameter estimates from this study may not be appropriate for describing early growth of larvae and juveniles. Our sampling used multiple gear types to collect different-sized individuals, which reduced bias associated with selectivity from a single gear type (Wilson et al. 2015) and replicated the recreational fishing pressure in Mississippi, where gill and hook-and-line fishing are commonly used by anglers. Although the gears used in this study display selectivity differences that we were unable to characterize, the variance of length-at-age parameters decreases when gear types are combined (Wilson et al. 2015). Wilson et al. (2015) reported that a combination of fishery-independent trawl sampling and fishery-dependent angler surveys increased precision in VBGF mean parameter estimates compared with the use of a single gear type. However, more rigorous sampling across all age-classes and size-classes would be beneficial to describe Southern Flounder growth through ontogeny. Our sampling design revealed a narrow age range and female-biased sex ratios, likely due to limited offshore sampling opportunities. Fischer and Thompson (2004) reported different age structuring by depth, with a higher proportion of older females found offshore, suggesting that older females may inhabit deeper waters than we were able to sample. In addition to similar depth structuring for males (Fischer and Thompson 2004), the female-biased sampling suggests that selectivity associated with the gear used in this study precluded the capture of smaller males. Therefore, we recommend increased sampling along a depth gradient with multiple standardized gears for describing Southern Flounder growth in future research.

We observed that Southern Flounder in the GOM exhibit faster growth rates (i.e., higher \( k \)-values) than Southern Flounder in the Atlantic, although our growth parameter estimates did not differ significantly from others reported within the GOM (Table 4). There were significant differences between our mean parameter estimates and estimates of \( L_\infty \) and \( k \) reported for South Carolina (Wenner et al. 1990), with a significantly lower \( L_\infty \) and higher \( k \) reported in the present study. Different management strategies may influence the differences in growth parameter estimates between the Atlantic and the GOM, as the flounder fishery in South Carolina is currently managed by a higher length limit than is enforced in Mississippi (South Carolina Department of Natural Resources 2016). Although growth parameter estimates are variable among GOM states, we observed that none of the female-specific mean parameter estimates from the three-parameter VBGF fell outside the 95% CIs we reported (Table 4). Temperature-dependent growth is a driver of intraspecific variation in demographic rates (Yamahira and Conover 2002; Folkvord 2005), and the observed differences between basins are likely influenced by warmer climate conditions in the GOM than the Atlantic. Midway et al. (2015) also suggested that spatial differences in Southern Flounder growth within the GOM are due to adaptations to small-scale local environmental conditions. In addition, the small differences in parameter estimates within the GOM may be related to unique sampling designs among studies (e.g., variable age ranges and gear types) or to variable management regulations and fishing pressure among states (Froeschke et al. 2011). However, the general similarity of growth parameter estimates within the GOM may be explained by the reported genetic homogeneity in the GOM Southern Flounder population (Anderson and Karel 2012).

Along with exhibiting greater growth rates, Southern Flounder in Mississippi waters of the GOM reached maturity more rapidly than Southern Flounder in the Atlantic and at a larger size than previously reported for the GOM. Our mean \( L_{50} \) estimate was significantly lower than the \( L_{50} \) estimates reported for Southern Flounder in North Carolina (Monaghan and Armstrong 2000; Midway and Scharf 2012) and significantly higher than those reported for Louisiana (Fischer 1995). These results further demonstrate that the GOM and Atlantic populations have unique demographic characteristics and that maturation rates vary among state-managed units within the GOM (Table 4). The estimate of \( L_{50} \) reported in this study is approximately equal to the current minimum length limit of 305 mm in Mississippi (GSMFC 2015), which suggests that a proportion of individuals are harvested from the population before spawning. In contrast, the most recent \( L_{50} \) estimate for Louisiana was nearly 75 mm smaller than our \( L_{50} \) estimate and fell outside the 95% CI of our estimate (Fischer 1995). Given that the Fischer (1995) study occurred over two decades ago, temporal shifts in Southern Flounder maturity are possible and may indicate changes in population size (Trippel 1995). We also estimated \( Age_{50} \) at about 1 year (Table 4), which is in agreement with results reported for Atlantic Southern Flounder but significantly lower than previous reports from the GOM (Stokes 1977; Etzold and Christmas 1979). Monaghan and Armstrong (2000) observed that 73.5% of age-1 fish were sexually mature but that age-1 females did not exhibit increasing GSI before the spawning season. Thus, age-2 females may be more likely to migrate offshore for spawning, as was suggested by Stokes (1977). Although the magnitude of change in GSI was lower for age-1 individuals considered separately, we observed an increasing GSI in October for age-1 females, indicating that some reached sexual maturity and supporting our estimation of \( Age_{50} \).

Accurate descriptions of Southern Flounder maturity are critical for assessing population status, especially because maturity estimates for this species are variable. With the exception of Fischer (1995), previous studies in the GOM have not used histological classification to estimate Southern Flounder maturity (Stokes 1977; Etzold and Christmas 1979), which may have led to overestimation of maturity status in those studies. The low percent agreement between macroscopic and histological classifications in our study indicates the value of histology for accurately
classifying maturity (West 1990; Lowerre-Barbieri et al. 2011a). The misidentification of reproductive phases can have implications for estimation of biological reference points and consequently for management (King and McFarlane 2003). For example, $L_{50}$ estimates for Southern Flounder in North Carolina increased by 33 mm TL—leading to a 10% decrease in predicted spawning potential ratio—when using histological phase assignment methods relative to macroscopic phase assignment (Midway and Scharf 2012). Although macroscopic classification of reproductive phase is commonly employed as a rapid assessment method, Midway and Scharf (2012) demonstrated that the resulting error in maturity estimates can contribute to shifts in biological reference points from spawning stock biomass-per-recruit models.

Multiple results from the present study indicate that Southern Flounder spawn from November to January in the north-central GOM. First, mean GSI values were elevated during October–December. These results are in agreement with those of previous studies, which have reported peak GSI values in November and December (Shepard 1986; Fischer 1995). Gonadal development is expected to increase prior to the spawning season and to decrease as spawning activity diminishes (West 1990), although GSI may remain elevated in asynchronous batch-spawning fish species due to the continuous production of oocytes throughout the spawning season. We also found that Southern Flounder $K_{rel}$ was elevated during September–November, presumably because of increasing energetic investment in reproductive development during the months preceding the spawning season (Reagan and Wingo 1985; Shepard 1986; Fischer 1995). However, the magnitude of observed variations in both $K_{rel}$ and GSI was low. Similarly, condition remained relatively constant in another flatfish species, the Dab Pleuronectes limanda, throughout the spawning season in the North Sea (Htun-Han 1978). For Southern Flounder and other flatfish species in which the body cavity size is small compared to overall body size, intra-annual development patterns may be difficult to observe when examining condition. Finally, histological indicators were used to identify spawning-capable individuals in November, indicating spawning preparedness; regressing individuals were observed in February, indicating the end of the spawning season. Our results not only support conclusions from previous studies that the Southern Flounder spawning season extends from December to January in the GOM (Shepard 1986; Fischer 1995) but also indicate that spawning activity begins as early as November and may continue into February. However, the absence of actively spawning individuals in the winter samples is a major limitation to understanding the reproductive potential of this species.

Batch spawning and asynchronous oocyte development in Southern Flounder were evidenced by the presence of oocytes in various developmental stages within the ovaries of spawning-capable females collected in this study (Wallace and Selman 1981; Lowerre-Barbieri et al. 2011b). Our histological observations from spawning-capable females provide strong support for batch spawning in Southern Flounder, although our conclusions would be strengthened based on evidence from actively spawning females. The present results accord with the conclusions of studies focused on both laboratory-spawned (Arnold et al. 1977) and naturally spawning (Fischer 1995) Southern Flounder. Batch spawning is common in other flatfish species, including Dab in the North Sea (Htun-Han 1978), Dover Sole Microstomus pacificus (Hunter et al. 1992), Greenback Flounder Rhombosolea tapirina in Tasmania (Barnett and Pankhurst 1999), and Summer Flounder Paralichthys dentatus in the Middle Atlantic Bight (Morse 1981). The Southern Flounder is a warmwater species, so multiple spawning events throughout an extended spawning season may represent one adaptation to increase lifetime fecundity (Morse 1981; Murua and Saborido-Rey 2003). The documentation of batch spawning in Southern Flounder is useful to inform estimates of reproductive potential in spawning stock biomass models (McEvoy and McEvoy 1992).

Southern Flounder exhibit a seasonal migration for spawning, and the spatial dynamics of this estuarine-dependent species have implications for management (Secor and Rooker 2005). Given the uncertainty surrounding offshore migration in terms of the spawning habitats used, the degree of mixing among Southern Flounder from different states is undefined. Recently, there has been interest in understanding the stock structure of Southern Flounder. Past research has focused on using genetics (Blandon et al. 2001; Anderson and Karel 2012), otolith morphometrics (Midway et al. 2014), tagging methods (Furey et al. 2013; Craig et al. 2015), and models of growth variability (Midway et al. 2015) to better describe Southern Flounder stock structure. Based on these studies, the Southern Flounder population appears to exhibit homogeneity, with little structuring among or within GOM states. These results from previous research indicate that mixing occurs offshore during spawning and that local environmental factors during early life estuarine residency are drivers of variability in demographic traits, such as growth and maturation. Temporal variation in Southern Flounder demographics is also notable, since our updated $L_{50}$ parameter estimate revealed changes through time in the GOM. Thus, both local and current estimates of life history parameters that reflect the status of the fishery are needed to inform stock assessments and the resulting management decisions. By describing the age and growth dynamics and the reproductive biology of a popular recreationally and commercially harvested species, our study provides a comprehensive examination of Southern Flounder life history with information specific to the Mississippi region.

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GROWTH AND SPAWNING OF SOUTHERN FLounder


